HARVARD UNIVERSITY

BUSSEY INSTITUTION OF APPLIED BIOLOGY

CONTRIBUTIONS

FROM THE

Laboratory of Genetics

Vol. II.

BOSTON
1913–1919

188915

CONTENTS

Studies on Self-sterility. IV. Selective Fertilization. E. M. East.
Studies on Self-sterility. V. A Family of Self-sterile Plants Wholly Cross-sterile Inter se. E. M. East.
The Rôle of Reproduction in Evolution. E. M. East.
Intercrosses Between Self-sterile Plants. E. M. East.
The Effects of Inbreeding and Crossbreeding Upon Development. D. F. Jones.
Heredity of Quantitative Characters in Wheat. George F. Freeman.

XENIA AND THE ENDOSPERM OF ANGIOSPERMS

E. M. EAST

Reprinted for private circulation from
The Botanical Gazette, Vol. LVI, No. 3, September 1913

XENIA AND THE ENDOSPERM OF ANGIOSPERMS

E. M. EAST

As is well known, the term "xenia" was proposed by FOCKE to describe any effect of pollen of another race upon the tissue of a seed plant apart from that initiating the formation of an embryo. As it has been exceedingly questionable whether any such effect beyond a chemical irritation ever occurs, the word has come to be applied to the appearance of the F_1 hybrid endosperm produced by the fusion of the second male nucleus with the so-called endosperm nucleus of the embryo sac, when its characters are different from those exhibited by the mother plant after self-fertilization.

Since the fact of this fusion was proved cytologically by GUIGNARD (10) and NAWASCHIN (11), data on this type of xenia have interested botanists because of the differences of opinion existing concerning the phylogenetic significance of the angiosperm endosperm.

The most detailed observations on xenia have been those on maize, since numerous maize varieties exist with differences in endosperm characters. The behavior of the following factors in heredity is known from the researches of DEVRIES (5), CORRENS (2), WEBBER (12), EAST and HAYES (7), and EMERSON (9). In addition, EAST (6) has found good indications of at least three additional factors that modify the expression of the red and the purple aleurone colors.

Factor	Action
S	Causing full development of starch grains
Y_1	Causing yellow color throughout endosperm
Y_2	Similar to Y_1 but not allelomorphic to it
C	Basic color factor necessary for color in aleurone cells
R	Present with C gives red color in aleurone cells
P	Present with R and C gives purple color in aleurone cells
I	Inhibits aleurone color when present with RC or PRC

Observations on crosses wherein these characters have been concerned have made it possible to formulate the following law regarding xenia:

> When two races differ in a single visible endosperm character in which dominance is complete, xenia occurs only when the dominant parent is the male; when they differ in a single visible endosperm character in which dominance is incomplete or in two characters both of which are necessary for the development of the visible difference, xenia occurs when either is the male.

It is evident that such a statement can be true only if the two male nuclei always carry the same hereditary factors and if a male nucleus always enters into the formation of the endosperm. The first requirement has been satisfied in every experiment thus far recorded; the second requirement will now be considered.

In particular cases where xenia has followed the crossing of races differing in endosperm color, aleurone color, or ability to mature starch grains, the seeds are not uniform in appearance. One may be half starchy and half wrinkled; another may be half yellow and half colorless; still another may have half of the aleurone cells red or purple and the other half colorless. Examples of this kind are rarely found, although it is a common thing to find seeds with a mottled appearance affecting only the aleurone colors.

CORRENS and WEBBER suggested independently that in these cases the male nucleus may fail to unite with the fusion nucleus and each divide independently, forming either the half-and-half seeds or those which are mottled. WEBBER also suggested, as an alternate hypothesis, the fusion of the male nucleus with one of the polar nuclei, the other polar nucleus remaining independent and dividing.

EAST and HAYES have shown that CORRENS and WEBBER were dealing here with two phenomena. The seeds that are mottled become so only from the development or non-development of color in the aleurone cells. They merely exhibit irregularity of Mendelian dominance, since in some crosses practically all seeds heterozygous for one of the factors producing aleurone color are mottled, although homozygotes are fully colored. Furthermore, the mottling does not extend to the color or other character of the deeper endosperm tissue in case the parental varieties had such differences, which necessarily would be the condition if the endosperm had been formed according to either of WEBBER'S independent development hypotheses. This criticism has also been made independently by EMERSON (8).

The other cases, where the endosperm is divided more or less equally into two types, remain to be explained. The hypothesis of independent development of the male nucleus seems improbable if one may judge from relevant cytological data on both animals and plants. The second hypothesis is very plausible. As a third possibility, EAST and HAYES have suggested ordinary "endosperm fertilization" with subsequent vegetative segregation similar to that occurring in bud sports. This could be proved, according to them, if among the F_1 seeds of a cross between parents differing in two allelomorphic pairs, individuals should be found in which the parental characters were combined differently. No such cases have been recorded.

The difficulty of deciding between the first and the second hypothesis of WEBBER lies in the fact that individuals of this kind are very rare, and when they have been found the investigator has not been able to say which particular endosperm character was carried by the male cell and which by the female cell. This was because they have occurred in selfed hybrids where both pollen and egg cells were segregating various Mendelian factors. In the experiments now to be described, this difficulty has been overcome.

The red color in the aleurone cells of maize is due to the interaction of two factors that may be represented by the letters *C* and *R;* this color may be changed to purple by the presence of a third factor *P*. Red is *RC* and purple is *PRC*, therefore, although it must be understood both that other factors which have never been lost in any variety may enter into the combination, and that other factors which have been lost in certain varieties may affect the development of color.

Six homozygous white varieties may exist with the following zygotic formulae: *PPRRcc*, *PPrrcc*, *PPrrCC*, *ppRRcc*, *pprrCC*, and *pprrcc*. Any cross between these varieties of such a nature that *R* and *C* or *P*, *R*, and *C* are brought together results in the red or the purple color respectively.

Among the selfed maize ears that had been produced in the course of the writer's experiments were a number giving red wrinkled and white wrinkled seeds in the ratio of 3:1. These white seeds must have either the formula *ppRRcc* or *pprrCC*.

White seeds from three such ears were planted in isolated plots and used as male parents on the flowers of plants arising from *white* seeds found on selfed ears of 13 other families. A number of these families had the proper formulae to produce color, and about 60,000 red or purple seeds were produced. There were all-purple ears and all-red ears in several families. Other combinations gave purple and white seeds or red and white seeds in the ratio of 1:1. How this came about is clear if one assumes either of the formulae given above for the male parent. Suppose the male parent had the formula *ppRRcc:* a family with the formula *pprrCC* gives all-red ears, while one with the formula *pprrCc* gives ears with red and white seeds in the 1:1 ratio; a family with the formula *PPrrCC* gives all-purple ears, while one with the formula *PprrCC* or *PPrrCc* gives ears with purple and white seeds in the 1:1 ratio.

Considering first only the all-purple and the all-red ears, one must conclude that the fusion of the "endosperm nucleus" and the second male nucleus always occurs. If it did not occur, white seeds would result, because a factor from each parent is essential for the production of color.

Among these 60,000 seeds, 6 were found that showed the half-and-half condition; that is, color had developed on one side and not on the other. They were typical illustrations of the phenomenon which WEBBER'S two hypotheses were devised to explain. They occurred in only 0.01 per cent of the fertilizations, but in spite of their rarity they show that WEBBER'S first hypothesis, assuming independent development of the male nucleus, is untenable, since independent development of the paternal and the maternal nuclei could produce no color. No decision can be made between WEBBER'S second hypothesis—fusion of the male nucleus with one polar nucleus and independent development of the other—and the hypothesis of vegetative segregation after partial development. The bilateral symmetry of the halves of the seeds with and without color favors WEBBER'S idea; at the same time, it must be pointed out that the frequency of the occurrence is not too great to compare favorably with the frequency with which "bud sports" originate. Though it would afford some satisfaction, a precise explanation of these rare aberrations is not a necessary requisite to several conclusions indicated by the experiments. It is evident that in the varieties of maize used, a paternal and a maternal nucleus carrying the same hereditary factors as are borne by the true gametes—in the case of the 7 factors investigated—always fuse in the formation of the endosperm. For this reason geneticists investigating maize have been correct in treating the endosperm as if it were an embryo. The endosperm characters have behaved exactly like plant characters. Two white varieties of sweet peas may carry factors both of which are necessary for the production of color. When they are crossed, color develops. Color develops in maize in a quite similar manner when the two complementary factors are carried by the "endosperm nucleus" and the second male nucleus. Nevertheless, one should keep in mind that the problem is complicated. COLLINS (1) found a white ear of maize in a yellow variety that behaved as if its seeds were crossed with the yellow. He interpreted the phenomenon as a mutation showing reversal of dominance, although the data on succeeding generations corroborated those obtained by previous investigators in which yellow was partially or completely dominant. It is not unlikely, however, that COLLINS merely happened upon a plant from white seed in which the male nucleus did not enter into the formation of the endosperm, although other interpretations are possible. This may seem like an odd statement after having shown that the two nuclei always fuse, but it is made advisedly. In most varieties of maize the two nuclei do appear always to fuse, but HAYES is now working out the details in a cross in which a Mexican starchy corn is one of the parents where the nuclei appear never to fuse. In other words, it seems that there may be varieties of maize in which endosperm formation is the opposite of that just described, and within each category *no change to the other has been found.* But may not such a change occur?

Whether or not the last suggestion ever proves to be true, it seems to me that from the data now collected one is entitled to discuss angiosperm endosperm formation from the viewpoint of experimental genetics.

The endosperm of the gymnosperms is essentially vegetative tissue of the female gametophyte. It results from continuous cell formation originating with the germination of the megaspore, although fertilization occurs during the process. From the time of HOFMEISTER the morphological character of the endosperm of angiosperms was considered to be the same as that of the gymnosperms until the double fertilization was discovered. This fact gave rise to the idea that the angiosperm endosperm might be a sporophytic rather than a gametophytic structure, its nature being that of a monstrous embryo, or possibly that it is a composite tissue neither gametophytic nor sporophytic.

Most botanists, however, have held with STRASBURGER to the original idea that the endosperm is gametophytic. STRASBURGER concluded that the second fusion is not a true act of fertilization uniting the parental qualities and forming an embryo, but a vegetative fusion acting merely as a stimulus to growth. Miss SARGENT, however, believes that it is a degenerate embryo, the monstrous character being caused by the interference of the antipodal nucleus having a vegetative character and an indefinite and usually redundant number of chromosomes in the act.

The difficulty in the situation appears to be the obscurity of the phylogenetic history of the fusion of the two nuclei in the embryo sac and the subsequent fusion with the second male nucleus. The problem is further complicated by the irregularity of endosperm formation in various species. Although triple fusion appears to occur in the majority of angiosperms, the following important general variations have been noted. In addition to these general variations many minor deviations have been found (COULTER and CHAMBERLAIN 4). (1) Vegetative endosperm formation may take place in a similar manner to that occurring in gymnosperms. This may occur without fertilization, or before or after fertilization. Usually the endosperm tissue is formed from the descendants of the antipodal cells, but the chalazal nucleus may degenerate and the endosperm be formed from the micropylar polar nucleus. (2) The polar nuclei may not fuse, but divide independently. (3) Fusion may include many cells.

Furthermore, endosperm formation may be initiated by free nuclear division, or the sac may be divided into two parts by a cell wall after the first division. Even when the latter phenomenon occurs, endosperm tissue may be formed in both chambers, although usually division proceeds only in the micropylar chamber.

These general cytological data being given, how do the facts from pedigree cultures bear upon the problem?

Just how much weight should be given to data from only one species when discussing the morphological significance of the endosperm is questionable. But in maize it is evident that STRASBURGER'S distinction between vegetative and generative fertilization will not hold. Cytological work on other species does not bear out Miss SARGENT'S conception, since endosperms form quite regularly without the interference of the antipodal vegetative (?) nucleus. If the perfectly regular manner in which the above-mentioned endosperm characters of maize are transmitted is considered apart from other facts, there appears to be no escape from the conclusion that the endosperm is sporophytic in character. But there is another way of looking at the matter that makes the view of COULTER seem more probable.

COULTER (3) has concluded that conditions in the embryo sac favor fusions of any number or kind of free nuclei—an indefinite process without a necessary phylogeny that results in a growth which is practically gametophytic. It is not dependent upon a male nucleus, a polar nucleus, or even a reduction division.

The experimental evidence accords perfectly with this view. The superficial endosperm characters are indeed transmitted regularly when a male nucleus takes part in the fusion, but there is no reason for believing that the remaining maternal nuclei carry *all* the characters borne by the egg because *these* characters are the same in the nuclei concerned. The egg must usually have an organization somewhat different from that of the other maternal nuclei; although it is recognized that other nuclei sometimes function as eggs. It is likely that a differentiation has ensued which makes a particular nucleus an egg, and that it is not wholly a matter of position. The general belief in the vegetative character of the antipodal cells of the embryo sac is an admission that they have not received *all* the properties retained by other four cells. It is not very heretical, therefore, to assume that the cell that becomes the egg is different from its associates. Botanists hesitate to assume the differentiation during ontogeny admitted by zoologists. They desire to believe that most plant cells can reproduce the whole plant. But this is a belief and not a fact, and until it becomes a fact it is well to recognize this plausible alternative in considering matters such as periclinal and sectorial chimeras as well as endosperms.

HARVARD UNIVERSITY

LITERATURE CITED

1. COLLINS, G. N., Heredity of a maize variation. U.S. Dept. Agr. Bur. Plant Ind. Bull. 272. pp. 7–23. 1913.
2. CORRENS, C., Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenien. Bibliotheca Botanica **53**:1–161. 1901.
3. COULTER, J. M., The endosperm of angiosperms. BOT. GAZ. **51**:380–385. 1911.
4. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. pp. x+348. New York. 1909.
5. DEVRIES, H., Sur la fécondation hybride de l'albumen. Compt. Rend. Acad. Sci. **129**:973–975. 1899.
6. EAST, E. M., The Mendelian notation as a description of physiological facts. Amer. Nat. **46**:633–655. 1912.
7. EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agr. Exp. Sta. Bull. 167. pp. 1–141. 1911.
8. EMERSON, R. A., Inheritance of color in the seeds of the common bean, *Phaseolus vulgaris*. Ann. Rep. Neb. Agr. Exp. Sta. **22**:67–101. 1909.
9. ———, Aleurone colors in F_2 in a cross between non-colored varieties of maize. Amer. Nat. **46**:612–615. 1912.
10. GUIGNARD, L., Sur les anthérozoides et la double copulation sexuelle chez les végétaux angiospermes. Rev. Gén. Botanique **11**:129–135. 1899.
11. NAWASCHIN, S., Resultäte einer Revision des Befruchtungsvorgangs bei *Lilium Martagon* und *Fritillaria tenella*. Bull. Acad. Imp. Sci. St. Pétersbourg **9**: no. 4. 1899.
12. WEBBER, H. J., Xenia, or the immediate effect of pollen in maize. U.S. Dept. Agr., Div. Veg. Phys. and Path. **22**:1–44. 1900.

A GENETIC ANALYSIS OF THE CHANGES PRODUCED BY SELECTION IN EXPERIMENTS WITH TOBACCO

PROFESSOR E. M. EAST AND H. K. HAYES

NEW YORK
1914

[Reprinted without change of paging, from the AMERICAN NATURALIST, 1914.

[Reprinted from THE AMERICAN NATURALIST, Vol. XLVIII., Jan., 1914.]

A GENETIC ANALYSIS OF THE CHANGES PRODUCED BY SELECTION IN EXPERIMENTS WITH TOBACCO[1]

PROFESSOR E. M. EAST AND H. K. HAYES

BUSSEY INSTITUTION OF HARVARD UNIVERSITY

THE PROBLEM

IN 1903 Johannsen announced that continued selection of the extreme values of certain quantitative characters in successive self-fertilized generations of a number of strains of beans had produced no changes in the mean values of the characters. He concluded that these particular strains were homozygous for the gametic factors whose interaction resulted in the characters investigated, that these homozygous characters may be properly described by one or more gametic factors nonvariable in transmissible qualities and properties, and that the variations observed in the characters of any single fraternity were due entirely to the action of environmental conditions during ontogeny and were not inherited. Fundamentally, these conclusions were a recognition of the general value of Mendelian description for all forms of inheritance through sexual reproduction, combined with an

---

[1] These investigations were conducted with funds furnished by the Connecticut Agricultural Experiment Station from their Adams' appropriations, by the Bureau of Plant Industry of the United States Department of Agriculture, and by the Bussey Institution of Harvard University, and the writers desire to take this opportunity of expressing their sincere appreciation of this hearty cooperation which made the work possible.

admission of disbelief in the inheritance of ordinary adaptive changes. The latter conception was Weismannian in that all inherited variations were held to be changes in the germ cells. It was not necessary to suppose it impossible for the environment to produce such changes and therefore to have been of no value during the course of evolution, but merely to suppose that during the comparatively short period of experimental investigations no gametic variations have occurred traceable to such a cause. For his first conclusion to be justified, it was assumed that the changes which every biologist knows do follow the continuous selection of extremes under certain conditions are to be interpreted entirely by the segregation and recombination of hypothetical gametic factors which are constant in their reactions under identical conditions.

Numerous investigators working on "pure lines" with different material corroborated Johannsen's conclusions, and, as it was seen to be possible to interpret in the same manner changes made by selection in experiments where self-fertilized lines were not used, such as those of the Vilmorins and others on sugar beets and those of the Illinois Agricultural Experiment Station on maize, many biologists accepted them and considered them a great advance over former conceptions of the mechanism of heredity. On the other hand, there were those who maintained a skeptical attitude, the chief criticism directed against the conception being that all progress due to selection must have a limit, which in many of these experiments had already been reached, and that even if results were being obtained action might be too slow to be detected.

The Material

These criticisms were reasonable when applied to certain specific cases, and in 1908 the experiments reported in this paper were designed with the hope of testing their validity, using the species ordinarily grown for commercial tobacco, *Nicotiana tabacum,* as the material. This plant satisfies the conditions which are requisite for material used in pure line studies. It has characters that can be estimated readily and accurately and which are affected only slightly by external conditions. It is easily grown, is naturally self-fertilized, reproduces prolifically, and is known in many markedly different varieties. In fact, it is an ideal subject for work of this kind.

The investigations were not patterned after the standard type set by Johannsen wherein the constancy of successive generations of pure lines grown from selected extremes were tested, since even if it were possible to gather a quantity of data at all comparable to that collected by Johannsen (:09) and Jennings (:08) in their brilliant investigations, the criticisms mentioned above might still be made. The plan chosen was that of crossing two varieties of tobacco which differed in a character complex easily and precisely determined, and of selecting extremes from a number of families of the F_2 generation. If Johannsen's views be incorrect, such continued selection should affect each family in the same degree. If his conclusions be justified, selection should reach an end-point in different generations in different families, and there should be no relation between the number of generations required to reach this end-point and the progress that is possible.

There should be no need of a historical summary of the previous investigations that have been interpreted as corroborating or refuting Johannsen's conclusions. Such summaries have been made in other papers. It should be mentioned, however, that the classical researches of Pearl (:11) on the inheritance of fecundity in the domestic fowl have been so planned and executed that certain of the criticisms directed against Johannsen mentioned above are not justified, yet Pearl finds himself thoroughly in accord with the Danish physiologist's position.

Several hundred varieties of *Nicotiana tabacum* exist which differ from each other by definite botanical characters, yet only two general characters suitable for our purpose were found. We desired to confine our observations to quantitative characters that were influenced but little by environment, and number of leaves and size of corolla were the only ones that satisfied this requirement. Such character differences as height of plant and size of leaf, while undoubtedly transmissible, are influenced so strongly in their development by nutrition that work with them is exceedingly difficult. For example, if a certain variety of *Nicotiana tabacum* is grown under the best of field conditions, the longest leaves are about 28 inches and the total height about 6 feet, but a portion of the same seed fraternity may be grown to maturity in 4-inch pots without reaching a height of over 16 inches or having leaves longer than 4 inches. On the other hand, several experiments conducted in the same manner have shown no difference between the frequency curves of variation in number of leaves or of size of corolla, whether starved in small pots or grown under optimum conditions. The character complex number of leaves was chosen for this investigation rather than the size of corolla because varieties that differ greatly in number of leaves are common.

TABLE I

Frequency Distribution of Number of Leaves per Plant when Starved in Small Pots

(Compare with frequency distribution under normal field conditions at Forest Hills, Massachusetts, in Tables VII and XI)

Plant No.	No. of Leaves per Plant															
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
(6–1)	...	2	3	10	15	8	7	1	...	...	...	...	...	...	...	...
(6–1)–1	...	1	6	8	15	16	12	5	...	...	...	...	...	...	...	...
(6–2)	...	...	...	1	0	8	7	14	15	14	8	3	3	...	...	...
(6–2)–2	...	...	...	...	1	0	1	0	2	3	12	17	16	8	0	1
(56–1)	...	1	4	8	12	6	7	2	...	...	...	...	...	...	...	...
(56–2)	...	...	...	4	6	10	13	8	3	1	...	...	...	...	...	...

Previous Work of the "Havana" × "Sumatra" Cross

Several crosses have been made between varieties of tobacco that had a mean difference of seven or eight leaves, but the majority of the data reported here were collected from the descendants of a cross made by A. D. Shamel between the types known in Connecticut as "Havana" and "Sumatra." The "Havana" parent was from a variety that had been grown for a number of years at Granby, Connecticut. It averages about 20 leaves per plant although ranging from 16 to 25 leaves. The average height is about 1.4 m. and the average leaf area about 7 sq. dm. The ''Sumatra'' parent was a type specimen of a variety that had been introduced into Connecticut to be grown under cloth shade. It averages between 26 and 27 leaves per plant with a range of from 21 to 32 leaves. The average height is nearly 2.0 m., but the average leaf area is only about 3 sq. dm.

According to Shamel, the first hybrid generation of this cross developed somewhat more vigorously than the parent types and was uniform in its habit of growth. The second generation, he thought, was hardly more variable than the first. Several F_3 families, the progeny of inbred F_2 individuals, were grown in 1906 and proved to be a variable lot. One of these plants produced 26 small, round-pointed leaves with short internodes between them. This plant was thought by Mr. E. Halladay, upon whose farm the experiment was conducted, and Mr. J. B. Stewart, of the U. S. Department of Agriculture, to be worth saving from its promise of producing a desirable commercial type.

In 1907 the Department of Agriculture made an agreement with Mr. Halladay to grow two acres of tobacco for experimental purposes, and on his own initiative Mr. Halladay grew a number of plants from inbred seed of the one that bore 26 leaves. This selection, numbered 2 h-29 in accordance with the department nomenclature, was comparatively uniform in appearance and several plants were selfed. In Mr. Halladay's absence, however, all of the plants were ''topped,'' except one that happened to be rather late. This plant was selfed. It had 26 medium-sized, round leaves and grew to about the same height as the Connecticut Havana.

In view of Mr. Halladay's high opinion of the type, the seed of this plant and the remaining seed of its parent were planted in 1908. The plants of this generation presented a uniform appearance and promised a high grade of wrapper tobacco, but the crop when cured lacked uniformity. Some leaves of exceptionally high quality were produced, but the crop in general lacked that characteristic known as "grain" and had too large a proportion of heavy leaves—the so-called "tops."

From this 1908 generation 100 seed plants were selfed, their leaves harvested, cured and fermented separately, and data on quality recorded. The type was also grown commercially on a large scale. The commercial results, however, have been reported in another paper. We are to consider only the results of the selection experiment that began in 1908, through the cooperation between the U. S. Department of Agriculture and the Connecticut Agricultural Experiment Station, a joining of forces that in 1909 included the Bussey Institution of Harvard University. Shamel (:07) considered the strain produced by this cross to be the result of a mutation. From a study of the data from the previous work on the cross it seemed to the writers that a different interpretation of the results might be made. While it was not impossible that the many-leaved type that had been isolated was the result of a mutation, it appeared much more probable that it had arisen through a recombination of Mendelian factors. The type had the habit of growth and size of leaf of the pure "Havana" variety and the number of leaves of the "Sumatra" variety, a combination that might reasonably be expected to be the result of the Mendelian law.

Results on the Reciprocal Cross, "Sumatra" × "Havana"

To test the hypothesis that the new tobacco was the result of such recombination and could be reproduced whenever desired, the reciprocal of the original cross was made in 1910. The female parent, "Sumatra," was the direct descendant of a sister of the plant used as the male parent of the original cross by Shamel in 1903 through seven generations of selfed plants. The male parent, "Havana," was from the commercial field of the Windsor Tobacco Growers' Corporation at Bloomfield, Connecticut. It was a descendant in a collateral line of the plant used by Shamel in 1903 as the female parent in his cross.

Table II, giving the frequency distribution for the number of leaves of the two parents and the first and the second hybrid generations, is a complete justification of our prediction as to how the hybrid type produced by Shamel originated. The "Sumatra" and the F_1 generation were grown at New Haven, Connecticut, in 1911, the "Havana" was grown at Bloomfield, Connecticut, in 1911 from commercial seed of the same variety as the plant used for the male parent, while the F_2 generation was grown at New Haven, Connecticut, in 1912. The F_1 generation, producing an average of 23.3 ± .14 leaves per plant, is intermediate in leaf number, since the "Havana" variety shows an average leaf number per plant of 19.8 ± .08 and the "Sumatra" variety 26.5 ± .11. The variation as determined by the coefficient of variability is somewhat less for the F_1 than for either parent. The value for the "Sumatra" variety is 6.64 per cent. ± .28 per cent., for the "Havana" variety 6.98 per cent. ± .27 per cent. and for the F_1 generation 6.24 per cent. ± .41 per cent. Taking into consideration the probable error in each case, one may say that the variability of the three populations is almost the same.

The variability of the F_2 generation, however, is greatly increased. This is shown by the high coefficient of variability, 10.29 ± .23 per cent., although a glance at the frequency distribution with its range of from 18 to 31 leaves brings home the point without recourse to biometrical calculation.

The appearance of the plants in the field corroborated the data of Table II in other characters. The F_1 generation was intermediate in the various leaf characters, such as shape, size and texture, that distinguish "Sumatra" from "Havana" tobacco, and in these characters it seemed as uniform as either of the parental varieties. On the other hand, the F_2 generation was extremely variable. Some plants could not be distinguished from the pure "Sumatra,'' others resembled ''Havana,'' although of course the majority were intermediate in various degrees. Several plants combined the leaf size and habit of growth of the ''Havana'' parent with the leaf number of the ''Sumatra'' parent. *In other words, plants were produced in the F_2 generation by the recombination of Mendelian factors that exactly repeated the type which Shamel had obtained in the F_3 generation of the reciprocal cross made in 1903 and which he thought was due to a mutation.* This fulfilled adequately the prediction made by us in 1908.

Results of Selecting for High Number and Low Number of Leaves in the ''Havana'' × ''Sumatra'' Cross

In describing the reproduction of Shamel's hybrid with numerous large leaves by a reciprocal cross, there has been a chronological inversion. This was done simply to show that the original hybrid known commercially as ''The Halladay'' was actually a recombination of Mendelian factors in which the ''Havana'' and the ''Sumatra'' varieties differed. We will now describe the effects of selection on the original ''Halladay hybrid.''

It will be recalled that the selection experiment which is the principal subject of this paper began with the selfing of 100 seed plants of Shamel's Halladay hybrid in 1908. These plants were the F_4 and F_5 generations of the cross ''Havana'' × ''Sumatra.'' Plants numbered from 1 to 49 were the F_4 generation; those numbered from 50 to 100 were the F_5 generation. They were apparently breeding true for the short habit of growth and large-sized leaf of the ''Havana'' parent and the goodly number of leaves of the ''Sumatra'' parent. The casual observer either would have said with Shamel that here was a mutation breeding as true as any tobacco variety, or that a fixed hybrid, a hybrid homozygous in all of its gametic factors, had been produced. Accurate data taken on the progeny of those of the F_4 and F_5 seed plants which it was possible for us to grow in our limited space, however, show that such judgments would have been superficial. The general type of the plant did appear to be fixed, but the frequency distribution for number of leaves of the F_5 and F_6 populations were not the same. Strictly speaking, they were not fixed. What would be the result of selecting (and selfing) extremes from these different families for a number of years? A tentative answer to this question is to be obtained by examining the remainder of our tables.

The tables are arranged roughly in the order of the effect that selection has had in changing the mean of the various families that were the starting points of this part of the experiment. The selections were grown near Bloomfield, Connecticut, on the light sandy loam of that region, soil typical of that which produces the famous Connecticut River Valley wrapper tobacco. Duplicate experiments with several of the original families were made at New Haven, Connecticut, however, on an impoverished soil not fitted to grow a good quality of tobacco even after supplying large quantities of tobacco fertilizer, and in the condition used not fitted to grow good crops of any kind. Two families were also grown in triplicate, the third selections being planted at Forest Hills, Massachusetts, on a very fine type of rich garden land which brought out maximum luxuriance of growth, but which did not produce good tobacco quality. These experiments were not true repetitions of the experiments at Bloomfield, Connecticut, since aliquot portions of the seed from the selfed plant grown there were not sent to the other places to be grown. But they were duplicates in that each family came from the same F_4 or F_5 mother plant, although, beginning with the F_5 or F_6 population, different selfed seed plants furnished the starting point of selections carried on independently. In this way there were afforded a greater number of chances to see what selection could do.

Table III shows the results obtained from family No. 77. This family arose from an F_5 plant having 23 leaves, one below the modal leaf number if we may judge from

TABLE II

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES PER PLANT IN CROSS BETWEEN HAVANA (FEMALE) AND SUMATRA (MALE) TOBACCOS

Variety	Number of Leaves per Plant															Total	A.	S. D.	C. V.
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31				
Havana	3	22	44	42	22	10	6	1	...	...	...	...	...	...	...	150	19.8 ±.08	1.38 ±.05	6.98 ±.27
Sumatra	...	...	...	...	...	...	3	13	27	25	21	16	15	4	1	125	26.5 ±.11	1.76 ±.08	6.64 ±.28
Sumatra × Havana, F_1	...	...	...	2	4	9	14	15	5	2	1	...	...	...	...	52	23.3 ±.14	1.45 ±.10	6.24 ±.41
Sumatra × Havana, F_2	...	1	9	21	33	48	66	71	71	59	49	25	18	7	2	480	24.4 ±.08	2.51 ±.06	10.29 ±.23

TABLE III

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 77, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																				Total	A.	S. D.	C. V.
				14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33				
(77-1)-1-2	F_9	1912	20	1	3	16	46	67	58	31	6	4	2	1	1	...	...	...	...	...	...	...	...	236	18.4 ±.07	1.54 ±.05	8.37 ±.26
(77-1)-*1*	F_8	1911	20	...	...	...	...	2	20	68	97	65	32	14	6	2	...	...	...	...	...	...	...	306	21.3 ±.05	1.41 ±.04	6.60 ±.18
(77-1)	F_7	1910	20	...	...	...	1	5	20	49	53	47	37	20	21	9	2	2	...	...	...	...	...	266	21.9 ±.08	2.03 ±.06	9.27 ±.27
77	F_6	1909	23	...	...	...	...	...	...	10	12	24	23	10	5	0	1	...	...	...	...	...	...	85	22.4 ±.11	1.35 ±.07	6.38 ±.33
(77-2)	F_7	1910	27	...	...	...	...	...	...	4	11	15	34	35	39	30	27	15	6	5	2	1	...	224	24.9 ±.11	2.32 ±.07	9.32 ±.30
(77-2)-1	F_8	1911	30	...	...	...	...	...	...	...	...	2	10	24	38	68	59	41	21	12	4	1	1	281	26.6 ±.07	1.84 ±.05	6.92 ±.20
(77-2)-1	F_8	1912	30	...	...	...	...	...	...	...	1	5	25	44	50	62	43	29	12	3	4	1	1	280	25.8 ±.08	1.93 ±.06	7.48 ±.21

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																					Total	A.	S. D.	C. V.
				17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37				
(77–1)–1–1	F_9	1912	21	1	7	10	29	44	34	9	1	...	...	...	...	...	...	...	...	...	...	...	...	..	135	20.9 ± .08	1.29 ± .05	6.17 ± .25
(77–1)–1	F_8	1911	20	..	..	4	17	41	45	25	6	3	...	...	...	...	...	...	...	...	...	...	...	..	141	21.7 ± .07	1.22 ± .05	5.61 ± .23
(77–1)	F_7	1910	20	..	..	5	18	35	44	51	27	18	7	4	4	0	0	1	...	...	...	...	...	..	214	22.7 ± .09	1.90 ± .06	8.37 ± .27
77[3]	F_6	1909	23	..	..	...	10	12	24	23	10	5	0	1	...	...	...	...	...	...	...	...	...	..	85	22.4 ± .11	1.35 ± .07	6.38 ± .33
(77–2)	F_7	1910	27	..	..	...	1	1	10	31	33	37	32	23	13	10	2	3	2	2	1	...	...	..	201	25.4 ± .11	2.35 ± .08	9.25 ± .31
(77–2)–1	F_8	1911	28	..	..	...	...	...	3	7	12	20	27	31	23	13	6	2	...	...	...	...	...	..	144	26.5 ± .11	1.92 ± .08	7.23 ± .29
(77–2)–1–1[4]	F_9	1912	30	..	..	...	...	...	...	...	...	1	1	11	33	30	17	11	10	3	2	7	0	2	128	29.7 ± .14	2.29 ± .10	7.71 ± .04

TABLE IV

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 76, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total	A.	S D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(76–1)–1	F_8	1911	23	1	4	34	72	105	66	18	9	1	...	...	...	...	310	23.9 ± .05	1.26 ± .03	5.28 ± .14
(76–1)	F_7	1910	22	1	0	0	3	4	8	9	6	...	...	...	...	...	31	25.2 ± .19	1.53 ± .13	6.07 ± .52
76	F_6	1909	23	1	4	9	18	23	15	14	4	1	...	...	...	...	89	24.1 ± .11	1.60 ± .08	6.64 ± .34
(76–2)	F_7	1910	27	...	4	16	40	54	50	27	10	6	1	1	...	...	209	24.4 ± .07	1.53 ± .05	6.27 ± .21
(76–2)–1	F_8	1911	28	...	...	2	9	31	54	48	35	24	20	5	1	1	230	26.1 ± .08	1.80 ± .06	6.88 ± .22
(76–2)–1–1	F_9	1912	29	...	...	1	4	16	38	59	59	54	27	14	2	1	275	26.9 ± .07	1.69 ± .05	6.28 ± .18

---

[3] Grown at Bloomfield, Connecticut.

[4] A number of plants showed leaf doubling.

the F_2 generation of the reciprocal cross where the mode was at 24 to 25 leaves. The F_6 fraternity that it produced was somewhat smaller than one would wish if he were to be confident of the calculations made. The mode is 22 leaves and the mean nearly the same, 22.4 ± .11 leaves. From among these plants, a minus variant having 20 leaves and a plus variant having 27 leaves were selected to produce the F_7 generation. The modes in this generation are 21 and 25 leaves, respectively, a difference of 4 leaves; and the means are 21.9 ± .08 and 24.9 ± .11 leaves, respectively, a difference of 3 leaves. Progress in both directions continued when a 20-leaved plant was selected to carry on the minus strain, and a 30-leaved plant was selected to carry on the plus strain. The modal classes of the F_8 generation are 21 leaves in the minus selection and 26 leaves in the plus selection, while the means are 21.3 ± .05 leaves and 26.6 ± .07 leaves, respectively. In the F_9 generation the plus selection was lost, but the minus selection grown from a 20-leaved plant had the mode dropped to 18 leaves and the mean to 18.4 ± .08 leaves. In order not to lose the plus selection entirely, however, more of the F_8 generation seed was grown in 1912. The mode is the same as in 1911, but the mean dropped slightly to 25.8 ± .08 leaves.

Here one notices what is very common throughout the experiment; the extremes selected for mother plants were not members of the most extreme classes. This means simply that vigorous healthy specimens were always selected as the mother plants, and often the most extreme variants did not come up to the standard. It is hardly just to criticize this procedure, however, for with the best care that it was possible to give, the experiments with several families were terminated on account of non-germination of seed or for some similar reason, it being impossible, on account of the pressure of other work, to self many plants in each selection. Even where seed from several mother plants was collected, it did not insure the continuation of that selection. The necessary space and care involved in growing so many seedlings in

TABLE V

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 19, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(19–1)–1	F_7	1911	24	1	3	13	30	42	46	25	16	7	4	1	1	1	...	...	...	190	25.8 ± .09	1.87 ± .07	7.26 ± .25
(19–1)	F_6	1910	24	...	...	3	19	26	41	53	43	26	12	2	2	...	...	...	...	227	26.9 ± .08	1.76 ± .06	6.54 ± .21
19	F_5	1909	26	1	4	6	12	23	29	34	24	12	2	...	...	...	...	...	...	147	26.3 ± .10	1.79 ± .07	6.81 ± .27
(19–2)	F_6	1910	29	...	...	...	3	5	18	24	28	46	28	12	7	5	1	1	1	179	28.7 ± .10	2.05 ± .07	7.14 ± .26
(19–2)–2	F_7	1911	30	...	...	...	1	2	10	24	39	41	51	23	14	5	2	...	...	212	29.2 ± .08	1.78 ± .06	6.11 ± .20

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				17	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35				
(19–1)–1–1	F_8	1912	24	...	...	...	...	3	5	29	51	30	17	4	3	...	...	...	...	142	27.3 ± .08	1.32 ± .05	4.84 ± .19
(19–1)–1	F_7	1911	22	1	1	7	9	16	17	18	10	8	1	2	...	...	...	...	...	90	25.1 ± .15	2.08 ± .11	8.29 ± .42
(19–1)	F_6	1910	24	...	1	2	15	43	57	45	29	7	...	...	...	...	...	...	...	199	25.2 ± .06	1.33 ± .05	5.28 ± .18
19[5]	F_5	1909	26	...	1	4	6	12	23	29	34	24	12	2	...	...	...	...	...	147	26.3 ± .10	1.79 ± .07	6.81 ± .27
(19–2)	F_6	1910	29	...	...	...	...	7	25	34	47	46	22	7	2	...	...	...	...	190	27.1 ± .07	1.50 ± .05	5.54 ± .19
(19–2)–1	F_7	1911	29	...	...	...	...	...	2	14	21	27	17	16	7	3	0	1	...	108	28.3 ± .11	1.70 ± .08	6.01 ± .28
(19–2)–1–2	F_8	1912	32	...	...	...	...	1	1	4	9	19	30	36	31	12	7	6	4	160	30.0 ± .11	2.02 ± .08	6.73 ± .25

[5] Grown at Bloomfield.

isolated seed pans filled with sterilized soil made it impossible to start more than two sets of plants for each plus and each minus selection. Generally both sets grew perfectly, but occasionally both failed, and in that case it was usually too late in the season to start a third set even if it were available.

The second part of Table III shows the results obtained on the poor soil of New Haven, Connecticut, with the same family. There was continuous progress in both directions. The minus selections during the three generations show a constant reduction of mode, the figures being 23, 22 and 21; the plus selections show an even greater increase in mode, the figures being 25, 27 and 28. The same decrease and increase occur in the means until in the F_9 generation there is a difference of nearly 9 leaves, the calculated means being 20.9±.08 leaves and 29.7±.14 leaves, respectively.

Figs. 1 and 2 show typical plants of the plus and minus strains of this family as developed by 3 years of selection. Fig. 3 illustrates an interesting change of phyllotaxy in some plants of (77–2)–1–1 as grown at New Haven in 1912.

Passing to the data on Family No. 76 (Table IV) there is the same evidence of the effectiveness of selection, excluding the minus strain in 1910, of which only 31 plants were healthy. This effect is markedly less than with the other family. The mode of the minus selection remained at 24 leaves and the mean was reduced only from 24.1 ± .11 leaves to 23.9 ± .05 leaves,—hardly a significant figure. The mode of the plus selection crept up to 26–27 and the mean to 26.9 ± .07 leaves, there being here one more generation than in the case of the minus strain.

Table V gives the data on plus and minus selections of Family No. 19 at Bloomfield for two generations. The original family stock of the F_5 generation has the mode at 27 leaves and the mean at about 26 leaves. A 24-leaved plant of this generation became the parent of the minus strain, giving in the F_6 generation a population with the same mode and a slightly higher mean (26.9 ± .08 leaves). Continuation of the strain through a 24-leaved plant gave an F_7 population with the mode one class lower and the mean at 25.8 ± .09 leaves. Whether this slight reduction really means anything we are unable to say. At least, if it yields at all to selection, the progress is very slow. On the other hand, a considerable gain has been made in the plus selections. The mode rose immediately to 29 leaves when the progeny of a 29-leaved plant were grown, and went up to 30 leaves the next generation, the modal condition being the same as the number of leaves of the parent plant. The means are 26.3 ± .10 leaves, 28.7 ± .10 leaves and 29.2 ± .08 leaves, the amount of progress being — as may be seen — 2.4 leaves and 0.5 leaf in the two successive generations. This result apparently indicates a slowing down of the effect of selection.

FIG. 1. PLANT OF HALLADAY HAVANA TOBACCO (77-2)-1-1, WHICH AVERAGES 29.7 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR HIGH LEAF NUMBER IN FAMILY 77, WHICH AVERAGED 22.4 LEAVES PER PLANT IN 1909. NEW HAVEN, 1912.

The continuation of the table gives the results obtained at New Haven on this same family. Here there are data from three generations, and these data modify the conclusions based on the results obtained at Bloomfield. Both plus and minus strains nearly parallel the Bloomfield results for two generations, the F_7 generation means being 28.3 ± .11 leaves and 25.1 ± .15 leaves, respectively, but in the F_8 generations they differ. Selecting minus extremes for the first two generations reduced the mean of that line from 26.3 ± .10 leaves to 25.1 ± .15 leaves, but the third selected generation (F_8) had a higher mean than the original family (27.3 ± .08 leaves). The parent plant of this F_3 generation produced

FIG. 2. PLANT OF HALLADAY HAVANA TOBACCO (77-1)-1-1, WHICH AVERAGES 20.9 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR LOW LEAF NUMBER IN FAMILY 77. NEW HAVEN, 1912.

24 leaves, and as the strain indicated that it was heterozygous for a number of factors by showing a coefficient of variability of 8.29 ± .42 per cent., it is possible that the selected parent plant may have belonged gametically to a higher class than was indicated somatically; nevertheless, it can not be denied that three generations of selected minus extremes have produced no results. This conclusion is not valid for the plus strain. Starting with 26.3 ± .10 as the mean number of leaves (F_5), the succeeding generations had means of 27.1 ± .07 leaves, 28.3 ± .11 leaves and 30.0 ± .11 leaves. The differences are 0.8, 1.2 and 1.7 leaves, respectively. Progressive change has certainly fol-

FIG. 3. CHANGE OF PHYLLOTAXY IN SOME PLANTS OF (77-2)-1-1 GROWN IN NEW HAVEN IN 1912.

lowed, and unless one considers that the results of 1912 are somewhat too high (probably a valid assumption), the change has increased instead of decreased. Naturally there must be a decreased momentum in change of mean time, but this decrease is not yet shown by the figures.

Fig. 4. Plant of Halladay Havana Tobacco (19-2)-1-2, which Averages 30 Leaves per Plant. It is the Result of Three Years of Selection for High Leaf Number in Family 19, which in 1909 Averaged 26.3 Leaves per Plant. New Haven, 1912.

Fig. 5. Plant of Halladay Havana Tobacco (19-1)-1-1, which Averages 27.3 Leaves per Plant. Three Years of Selection for Low Leaf Number Have Proved Unsuccessful. New Haven, 1912.

Representative plants of the plus and minus strains of family 19 as obtained by three years of selection at New Haven are shown in Figs. 4 and 5.

Family No. 5 (Table VI) shows a decrease in mode from 28 to 26 leaves, and a similar decrease in mean from 28.1 ± .06 leaves to 26.6 ± .09 leaves as a result of the first minus selection. A second minus selection, however, indicates either that the future progress is to be very slow or that the entire effect of selection was manifested in the first selected generation.

With the three parts of Table VII we take up the results on Family No. 6 at all three stations. The minus strain was carried on only two generations at Bloomfield, but with this exception there are data upon three generations. At Bloomfield the two generations of selected minus extremes resulted in 0.6 leaf decrease in the mean, but at New Haven the results were negative, the means advancing from 25.8 ± .06 leaves to 27.9 ± .12 leaves in three generations, while at Forest Hill the mean remained practically the same. Surely selection was unprofitable here.

The first year of selection from the other end of the curve, however, resulted in marked progress. The mean advanced nearly 5 leaves in each case. The original F_5 mean is 25.8 ± .06 leaves, but the three F_6 means are 30.7 ± .09, 29.6 ± .08 and 30.8 ± .12 leaves. This is a remarkable concurrence of results. The means in the two succeeding generations were about the same in the Bloomfield and New Haven experiments, but there was another definite advance at Forest Hills. Such a result should not be unexpected. If the F_6 generation were almost but not quite a homozygous lot, and if one assumes that selection of extremes from homozygous population has no effect in shifting the mean, it would frequently happen that some individuals selected to continue the line would be homozygous in all factors and some heterozygous in one or more factors.

The cause of the peculiar distribution of the population (high variability) of the F_8 generation grown in Bloom-

TABLE VI

Frequency Distribution of Number of Leaves in Family 5, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34				
(5–1)–1	F_7	1911	24	...	...	3	14	35	71	68	38	5	3	1	1	...	...	239	26.5 ±.06	1.36 ±.04	5.13 ±.16
5–1	F_6	1910	25	2	0	2	24	31	52	45	23	16	8	6	1	1	...	211	26.6 ±.09	1.91 ±.06	7.18 ±.24
5	F_5	1909	28	...	...	1	3	5	26	67	73	72	29	15	2	1	...	294	28.1 ±.06	1.50 ±.04	5.34 ±.15
5–2	F_6	1910	31	...	...	...	...	1	7	26	43	55	46	26	15	4	3	226	29.2 ±.08	1.68 ±.05	5.75 ±.18
(5–2)–1	F_7	1911	32	...	...	...	5	5	13	37	54	53	46	20	8	1	1	243	28.6 ±.08	1.73 ±.05	6.05 ±.17
(5–2)–1–3	F_8	1912	33	...	...	1	2	4	20	32	42	63	63	31	18	5	1	282	29.0 ±.07	1.84 ±.05	6.34 ±.18

TABLE VII

Frequency Distribution of Number of Leaves in Family 6, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																			Total	A.	S. D.	C. V.
				18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(6–1)–2	F_7	1911	23	...	...	...	1	4	30	43	74	47	22	9	4	0	0	1	...	...	...	...	235	25.1 ±.07	1.52 ±.05	6.05 ±.19
(6–1)	F_6	1910	25	...	...	...	2	1	16	44	47	35	28	6	1	0	0	0	1	...	...	...	181	25.2 ±.08	1.53 ±.05	6.07 ±.22
6	F_5	1909	28	...	...	...	...	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	307	25.8 ±.06	1.59 ±.04	6.16 ±.17
(6–2)	F_6	1910	30	...	...	...	...	...	...	...	1	2	3	18	29	44	35	36	23	10	2	2	205	30.7 ±.09	1.90 ±.06	6.18 ±.21
(6–2)–1	F_7	1911	32	...	...	...	...	...	...	...	...	2	17	64	70	61	20	4	0	1	...	...	239	29.1 ±.05	1.21 ±.04	4.17 ±.13
(6–2)–1–4	F_8	1912	32	2	2	3	1	3	2	0	1	2	6	12	23	43	50	48	22	15	6	2	243	30.5 ±.13	3.03 ±.09	9.93 ±.30

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																		Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38				
(6–1)–1–1	F_8	1912	25	...	3	5	12	16	26	31	21	12	17	3	2	...	...	...	...	...	...	148	27.9 ± .12	2.13 ± .08	7.63 ± .30
(6–1)–1	F_7	1911	23	1	5	10	24	36	36	14	9	1	1	1	2	...	...	...	...	...	...	140	25.4 ± .10	1.79 ± .07	7.06 ± .29
(6–1)	F_6	1910	25	...	1	10	41	42	41	32	14	11	2	1	...	...	...	...	...	...	...	195	25.7 ± .08	1.67 ± .06	6.50 ± .22
6[5]	F_3	1909	28	...	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	...	...	307	25.8 ± .06	1.59 ± .04	6.16 ± .17
(6–2)	F_5	1910	30	...	...	...	1	1	1	12	33	50	52	35	11	3	0	0	1	0	1	201	29.6 ± .08	1.63 ± .06	5.51 ± .19
(6–2)–1	F_7	1911	30	...	...	...	1	1	11	24	42	36	21	9	2	3	2	1	1	...	...	154	28.7 ± .10	1.84 ± .07	6.39 ± .24
(6–2)–1–1	F_8	1912	32	...	...	...	...	...	1	3	17	25	41	31	16	10	1	...	...	...	...	145	30.2 ± .09	1.51 ± .06	5.00 ± .20

GROWN IN FOREST HILLS, MASS.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																		Total	A.	S. D.	C. V.
				22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39				
(6–1)–1–1	F_8	1912	24	...	3	14	34	56	28	13	4	...	...	...	...	...	...	...	...	...	...	152	26.0 ± .07	1.24 ± .05	4.77 ± .18
(6–1)–1	F_7	1911	26	...	1	5	19	31	55	31	9	1	1	...	...	...	...	...	...	...	...	153	26.8 ± .07	1.29 ± .05	4.81 ± .19
(6–1)	F_6	1910	25	...	2	14	23	29	15	8	2	...	...	...	...	...	...	...	...	...	...	93	25.8 ± .09	1.30 ± .06	5.04 ± .25
6[7]	F_5	1909	28	4	16	50	55	77	63	29	11	1	1	...	...	...	...	...	...	...	...	307	25.8 ± .06	1.59 ± .04	6.16 ± .17
(6–2)	F_6	1910	30	...	...	...	...	...	2	7	12	21	25	16	10	4	2	...	...	...	...	99	30.8 ± .12	1.70 ± .08	5.52 ± .27
(6–2)–2	F_7	1911	35	...	...	...	...	...	...	...	1	6	16	25	47	27	15	7	2	1	...	147	33.1 ± .09	1.54 ± .06	4.65 ± .18
(6–2)–2–2	F_8	1912	38	...	...	...	...	...	...	...	...	8	19	33	61	34	11	2	...	...	...	168	32.8 ± .07	1.27 ± .05	3.87 ± .14

---

[7] Grown at Bloomfield.

TABLE VIII

Frequency Distribution of Number of Leaves in Family 34, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C. V.
				19	20	21	22	23	24	25	26	27	28	29	30	31	32				
(34–1)–2	F_7	1911	20	...	...	...	3	16	49	53	41	22	9	4	1	...	...	198	25.2 ± .07	1.47 ± .05	5.85 ± .20
(34–1)	F_6	1910	22	1	4	21	37	62	67	34	13	2	...	...	...	...	...	241	23.4 ± .06	1.43 ± .05	6.11 ± .19
34	F_5	1909	24	...	4	12	21	31	17	12	3	...	...	...	...	...	...	100	22.9 ± .09	1.40 ± .07	6.11 ± .29
(34–2)	F_6	1910	26	...	5	8	17	59	55	40	27	8	5	4	...	...	...	228	24.1 ± .08	1.72 ± .05	7.14 ± .23
(34–2)–2	F_7	1911	28	...	...	...	...	1	4	19	42	54	29	19	5	1	2	176	27.0 ± .08	1.48 ± .05	5.49 ± .20

TABLE IX

Frequency Distribution of Number of Leaves in Family 12, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																Total	A.	S. D.	C. V.
				21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36				
(12–1)–1	F_7	1912	29	...	...	...	1	7	15	44	45	59	56	34	24	8	2	1	...	296	29.1 ± .08	1.94 ± .05	6.67 ± .19
(12–1)–1	F_7	1911	29	...	...	...	1	5	22	31	40	48	25	20	11	5	2	...	...	210	28.7 ± .09	1.93 ± .06	6.72 ± .22
(12–1)	F_6	1910	23	...	...	...	...	...	...	...	...	3	2	1	...	...	...	...	...	6	....	....	....
12	F_5	1909	24	6	7	17	23	24	27	8	1	...	...	...	...	...	...	...	...	113	24.5 ± .10	1.60 ± .07	6.53 ± .29
(12–2)	F_6	1910	28	1	5	16	30	37	39	28	25	19	13	1	1	...	...	...	...	215	26.1 ± .10	2.12 ± .07	8.12 ± .26
(12–2)–1	F_7	1911	30	...	...	2	11	21	50	54	41	13	4	1	1	...	...	...	...	188	26.8 ± .07	1.50 ± .05	5.61 ± .20
(12–2)–1	F_7	1912	30	...	...	1	3	6	9	23	39	58	43	34	6	8	0	0	1	231	29.0 ± .08	1.89 ± .06	6.52 ± .21

[6] Grown at Bloomfield.

field is not clear. It is possible that the plants having from 18 to 23 leaves were diseased, but no such condition could be recognized in the field. Again, it is possible that a few Havana plants were mixed in by mistake, although as the leaves of the selection are characteristically different from Havana and as the plants with low leaf numbers resembled the remainder of the row, this supposition is improbable. The most likely explanation is that mutation occurred in a few gametes of the mother plant, a condition that did arise, or that we assume to have arisen, in Family 41 (see Table X). At any rate, *the change did not follow the path of selection.*

In Figs. 6 and 7 are shown typical plants of Family No. 6 obtained by three years of selection in the effort to produce strains of high and low leaf number, respectively.

Family No. 34 (Table VIII) is peculiar—although this is not the only time the phenomenon occurred—in that the F_5 population grown from a 24-leaved F_4 plant seems not to have given the true mean. Plants with a low number of leaves (22 and 20) were selfed to carry on the minus strain, but both gave means higher than was shown by the F_5 generation. Perhaps further selection will produce results, but the case is not a hopeful one. The only evidence for such an assumption is the increased mean of the F_7 plus strain. If it is assumed that 24.0 is nearer the true mean of the F_5 population than the 22.9 actually calculated, then the jump to 27.0 ± .08 leaves in the F_7 generation gives us a basis for expecting results in F_8 in the minus strain.

Nothing can be said as yet about the minus strain of Family No. 12 (Table IX), for it happened that the first selection was a complete failure. Six plants were obtained, but the lowest number of leaves was 29. One of these plants was selfed and gave an F_7 population having a mean of 28.7 ± .09 leaves. Unfortunately the selections from this fraternity did not germinate and in 1912 we had to fall back on the reserve seed from which the 1911 crop came. The crops of 1911 and 1912 are therefore duplicates. The plus strain made an advance from 24.5 ± .10

leaves to either 26.8 ± .07 or 29.0 ± .08 leaves. The first advance is 1.6, the second 0.7. We can give no explana-

Fig. 6. Plant of Halladay Havana Tobacco (6-2)-1-1, which Averages 30.2 Leaves Per Plant. It is the Result of Three Years of Selection for High Leaf Number in Family 6, which Averaged 25.8 Leaves Per Plant in 1909. New Haven, 1912.

tion of the failure of the results of 1911 and 1912 to duplicate. This is the greatest deviation obtained in the course of our experiments. The results of 1912 are probably too high. It is yet too early to say whether or not this

FIG. 7. PLANT OF HALLADAY HAVANA TOBACCO (6-1)-1-1, WHICH AVERAGES 27.9 LEAVES PER PLANT. THREE YEARS OF SELECTION TO DECREASE THE LEAF NUMBER OF THIS TYPE HAVE PROVED UNSUCCESSFUL. NEW HAVEN, 1912.

strain is decreasing in the average annual shift of the mean.

Family No. 41 shown in Table X gave perhaps the most peculiar results of any of the selections. It may be that no great shifting of the mean toward the minus end of the curve should have been expected, because the minus mothers were each rather high in number of leaves. There was one with 25 leaves and one with 24 leaves. This was unfortunate, but was made necessary by the number of late and diseased (mosaic) plants in the selection. Nevertheless, each of these plants was below the mean of the previous generation and if a marked change would have followed the selection of extreme individuals, some change should have followed the selections of the individuals that were the actual mothers. But in spite of this fact the mean persistently rose from 23.9 ± .07 leaves to 26.3 ± .08 leaves, then to 28.1 ± .07 leaves, although the duplicate of this selection grown in 1912 went down slightly to 27.4 ± .07 leaves. In the plus strain successive generations of mothers having 28 and 30 leaves caused a small upward shift of the mean; it became first 25.7 ± .09 leaves then 25.6 ± .14 leaves, although the 1912 duplicate of the last population had a mean of 26.9 ± .08 leaves.

The extraordinary phenomenon to which we wish to call particular attention, however, is not this behavior of the minus and plus strains in the regular selection experiment, but rather the origin of a few-leaved strain from a single individual that appeared in the F_6 generation of the plus strain. Referring to the table, it will be seen that in this generation a 12-leaved plant appeared. This is really a peculiar phenomenon, for we had never before observed a normal 12-leaved plant among the many thousands that have come under our observation. They do not occur. In this population the plant with the next lowest numbers of leaves had 20 leaves, and in classes 20 and 21 there was only a single plant of each. This 12-leaved plant was selfed and gave rise to a population ranging from 8 leaves to 30 leaves, and having a variability of 23.50 per cent. ± .11 per cent. The mean of the distribution was 19.8 ± .28 leaves. A 10-leaved plant of this lot was selfed and gave a progeny with a mean of 17.9 ± .08 leaves and a variability of 11.24 per cent. ± .33 per cent. What interpretation can be given these facts?

We believe a distinct mutation occurred, a mutation different from those of DeVries. At least DeVries believes that the mutations that he has observed always breed true. If the following hypothesis as to the origin of the 12-leaved plant be true, it is unnecessary to suppose with DeVries that mutations always breed true or even that they often breed true. Of course DeVries believes that his *Œnothera* mutations obey laws different from those of whose mechanism we know a little. He believes that species crosses always breed true; that they do not Mendelize. This belief we hold to be unfounded. Species crosses have never been shown to breed true. There have been statements to the effect that crosses between *Rubus* species breed true, but no good evidence has been submitted in their support; while the data of Tammes (:11) on *Linum* species crosses, Davis (:21) on *Œnothera* species crosses, and of East (:13) on *Nicotiana* species crosses, concur in showing that species as well as varieties obey Mendel's Law of segregation and recombination. Furthermore, we think that Heribert-Nilsson's (:12) beautiful experiments on DeVries's own material show that the latter did not collect sufficiently exact data on his own crosses to find out whether they bred true or not.

If one is to believe that a mutation in a hermaphroditic plant breeds true he must suppose that constitutional changes occur both in the male and the female gametes, or that the change occurs after fertilization. But it seems more probable that such a change will take place either in the one or the other gamete and not in both. This we believe to be the explanation of the appearance of the 12-leaved tobacco plant. A mutation occurred in either an egg cell or a pollen cell. It does not matter in which one it is assumed because there is no evidence favoring either case to the exclusion of the other. *This cell with*

TABLE X

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 41, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant																								Total	A.	S. D.	C. V.
				10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33				
(41–1)–2	F_7	1912	25	..	..	..	..	..	..	..	..	..	..	..	..	4	3	8	17	51	74	62	36	24	6	3	..	288	27.4 ± .07	1.76 ± .05	6.42 ± .18
(41–1)–2	F_7	1911	25	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	7	30	47	52	45	25	10	7	..	225	28.1 ± .07	1.64 ± .05	5.85 ± .19
(41–1)	F_6	1910	24	..	..	..	..	..	..	..	..	..	..	..	2	2	16	10	33	54	57	25	21	4	..	..	..	224	26.3 ± .08	1.75 ± .06	6.65 ± .21
41	F_5	1909	26	..	..	..	..	..	..	..	..	..	2	10	15	24	66	65	64	36	11	2	1	..	..	..	..	296	23.9 ± .07	1.71 ± .05	7.25 ± .20
(41–2)	F_6	1910	28	..	..	1[10]	..	..	..	..	..	..	..	1	1	4	24	36	42	44	41	21	13	7	..	..	..	234	25.7 ± .09	1.92 ± .06	7.47 ± .23
(41–2)–1[8]	F_7	1911	30	..	..	..	..	..	..	..	..	1	3	5	3	2	6	13	24	37	25	10	7	2	3	1	..	142	25.6 ± .14	2.49 ± .10	9.71 ± .39
(41–2)–3[9]	F_A	1911	12	5	3	3	3	5	3	0	8	8	8	21	8	14	6	9	8	7	4	0	0	1	..	..	..	126	19.8 ± .28	4.65 ± .20	23.50 ± .11
(41–2)–1	F_7	1912	30	..	..	..	..	..	..	..	..	..	..	2	1	3	10	16	39	54	60	59	35	21	5	4	1	310	26.9 ± .08	2.07 ± .06	7.70 ± .21
(41–2)–3–2	F_B	1912	10	..	1	0	3	5	24	37	60	51	54	17	20	3	1	0	1	0	1	..	..	..	..	..	..	278	17.8 ± .08	2.00 ± .06	11.24 ± .33

TABLE XI

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES IN FAMILY 56, GROWN AT BLOOMFIELD, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant														Total	A.	S. D.	C.. V.
				19	20	21	22	23	24	25	26	27	28	29	30	31	32				
(56–1)–1–3	F_9	1912	24	...	...	...	1	3	3	6	8	3	1	...	...	...	...	25	25.2 ± .19	1.44 ± .14	5.71 ± .55
(56–1)–1	F_8	1911	23	...	...	2	9	31	48	64	35	20	7	2	2	...	...	220	24.9 ± .07	1.57 ± .05	6.31 ± .20
(56–1)	F_7	1910	23	...	1	3	10	33	59	44	34	21	6	2	...	...	...	213	24.7 ± .07	1.59 ± .05	6.44 ± .21
56[11]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	315	24.2 ± .06	1.66 ± .05	6.86 ± .18
(56–2)	F_7	1910	28	...	...	...	...	2	19	23	51	48	28	24	8	2	...	205	26.7 ± .08	1.65 ± .06	6.18 ± .21
(56–2)–1	F_8	1911	27	...	...	1	0	2	10	28	57	60	41	27	6	...	...	232	26.8 ± .07	1.50 ± .05	5.60 ± .18

[8] This was an end row and the plants were very yellow and small, due to insufficient soil fertility.

[9] Also, one each bearing eight and nine leaves.

[10] Not used in computations.

[11] Three Havana plants were found in this row which bore 16, 18 and 21leaves respectively. These were not used in computations.

GROWN AT NEW HAVEN, CONN.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant 19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Total	A.	S. D.	C. V.
(56–1)–1–1	F_9	1912	23	...	...	...	2	34	45	34	21	6	2	...	...	...	...	...	...	...	144	24.4 ±.07	1.23 ±.05	5.04 ±.20
(56–1)–1	F_8	1911	24	...	1	5	18	36	46	28	14	8	2	...	...	...	...	...	...	...	158	24.0 ±.08	1.50 ±.06	6.26 ±.24
(56–1)	F_7	1910	23	...	...	...	5	26	47	47	46	24	16	6	...	...	...	...	...	...	217	25.2 ±.07	1.61 ±.05	6.39 ±.20
56[12]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	...	...	...	315	24.2 ±.06	1.66 ±.05	6.86 ±.18
(56–2)	F_7	1910	28	...	...	...	...	1	3	23	28	42	42	33	10	5	...	...	...	...	187	27.4 ±.08	1.60 ±.06	5.84 ±.20
(56–2)–1	F_8	1911	28	...	...	...	...	5	22	23	34	29	20	10	4	2	1	0	0	1	151	26.4 ±.11	1.93 ±.08	7.32 ±.28
(56–2)–1–2	F_9	1912	30	...	...	...	...	1	7	14	23	24	30	21	12	5	4	1	...	...	142	27.5 ±.11	1.97 ±.08	7.16 ±.29

GROWN AT FOREST HILLS, MASS.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant 19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total	A.	S. D.	C. V.
(56–1)–1–1	F_9	1912	23	...	...	...	2	5	27	44	45	27	18	5	5	...	...	...	...	178	25.9 ±.08	1.59 ±.06	6.14 ±.22
(56–1)–1	F_8	1911	23	...	...	...	1	1	12	31	59	34	10	3	...	...	...	...	...	151	26.0 ±.06	1.17 ±.05	4.50 ±.17
(56–1)	F_7	1910	23	...	...	...	2	7	16	26	36	10	4	...	...	...	...	...	...	101	25.3 ±.09	1.27 ±.06	5.01 ±.24
56[13]	F_6	1909	26	1	4	13	31	49	79	72	43	19	2	2	...	...	...	...	...	315	24.2 ±.06	1.66 ±.05	6.86 ±.18
(56–2)	F_7	1910	28	...	...	...	...	...	1	7	19	40	27	7	3	...	...	...	...	106	27.2 ±.08	1.16 ±.05	4.26 ±.20
(56–2)–2	F_8	1911	32	...	...	...	...	...	...	1	5	19	30	51	24	13	5	1	...	149	28.9 ±.08	1.42 ±.06	4.91 ±.19
(56–2)–2–2	F_9	1912	31	...	...	...	...	...	7	17	37	58	28	6	1	...	...	...	...	154	26.7 ±.06	1.18 ±.05	4.42 ±.17

[12] Grown at Bloomfield.

[13] Grown at Bloomfield.

a changed gametic constitution,—a loss of gametic factors,—was fertilized by an unchanged cell. The unchanged cell may have had any of the gametic possibilities open to the germ cells of the 28-leaved plant of the F_5 family in which the mutation arose, and we know that certain factors in this plant were heterozygous, for progressive change followed the selection of a plus extreme in the next generation. The 12-leaved plant was therefore a hybrid. It resulted from the union of a mutating germ cell of the mother plant that furnished the F_6 generation with an unchanged germ cell. We can even assume that the mutating germ cell, if fertilized by another of the same kind, would have produced a plant with less than 12 leaves. The reasons for believing this are simple. There is experimental evidence (Hayes, 1912) that the F_1 generation of a cross between varieties differing in their number of leaves is intermediate in character. Our 12-leaved plant is the lone representative of such an F_1 generation. The F_2 generation therefore should give plants with less than 12 leaves, and in fact such plants did occur. The distribution marked F_A in the table is the F_2 generation, and this accounts for its extreme variability. The distribution marked F_B is the F_3 generation, and its variability is less than half that of the preceding generation.

Family No. 56 was the second family to be grown at all three of the experimental stations (Table XI). It arose from a 26-leaved plant of the F_5 generation which produced an F_6 progeny with a mean of $24.2 \pm .06$ leaves and a mode at 24 leaves. The three generations of the minus strain grown at Bloomfield remained practically the same. The last generation did indeed show a mean 1.0 leaf higher than the original population, but no dependence can be placed in data from only 25 plants. The data on the minus selections grown at New Haven are for this reason a little more dependable. They show a fluctuating mean, but no progress due to selection, the F_9 generation having a little higher mean than the F_6 generations. The three minus selections grown at Forest Hills also resulted in higher means, those for F_7, F_8 and F_9 being 25.3 ± .09, 26.0 ± .06 and 25.9 ± .08 leaves, respectively.

This peculiar result implies only that the mean of the original F_6 population which was grown at Bloomfield was lower than it would have been if grown on the Forest Hills' soil. This is not a direct effect of environment on the growing plant. It has been shown conclusively in our pot experiments, as stated before, that starvation or optimum feeding has scarcely any effect on the number of leaves, although it has a marked effect on the development of many other characters. On the other hand, environment does appear to have a marked effect on the number of leaves that a plant is to develop, if it acts *during the development of the seed.* It is well known by plant physiologists that the environment produces many of its effects very early in the life history of the individual or in the development of the organ concerned. For example, the so-called light leaves of the beech with two layers of palisade cells are differentiated from the shade leaves with only one row of palisade cells by the amount of light that falls on a branch during the season preceding the development of the leaves: that is, it is determined during the laying down of the bud from which the next season's growth of twig and leaves comes. This period during which a particular change is possible is called the critical period for that change by plant physiologists. Thus a plant may have hundreds of critical periods in its ontogeny, each marking an end-point of development beyond which a certain feature is irrevocably fixed. For example, the critical period for that cell division that determines leaf size in the beech is much later than that which determines the number of layers of palisade cells.

Now the critical period for influencing the number of leaves of the tobacco plant is practically at an end when the embryo plant goes into the resting stage of the seed. Before that time the number of leaves may be influenced by the external and the internal influences that form the total environment of the mother plant; after that time environment has little influence on the number of leaves.

The rise in the mean of the population of the F_8 generation of Family No. 56 is due partially to the effect of environment, therefore, in that the mother plant was grown under better conditions, but is probably not to any great extent due to the conditions under which the plants themselves were produced.

The better environment of the mother plants does not account for all the rise in the means in populations F_8 and F_9, but it accounts for part of it. It will be noticed that all of the populations grown at Forest Hills had higher means than those grown at Bloomfield and New Haven, although the F_6 mother plants were grown at Bloomfield and not at Forest Hills. The greatest shift of the mean, however, comes in the F_8 and F_9 generations, for the mother plants of both of these populations were grown on the more fertile soil. There is a simple explanation of these facts, an explanation that is of great economic importance to practical tobacco growers. A part of the rise in mean at Forest Hills was due to setting the plants in the field there when they were in an earlier stage of development than those at Bloomfield and New Haven. They were not set earlier in the season (at least, one year they were set early, one year they were set at the average time and the third year they were set late), but they were set as small plants. When small plants (about 4 inches high) are set in the open the root system is equal to the task of supporting the aerial parts and the plants start right in to growing normally. There is no period of passivity. The plants produce leaves spaced with normal internodes and these leaves develop sufficiently to have a commercial value. But when the plants reach a height of 8 or 10 inches in the seed pans or seed beds and are then set in the field, the normal metabolism is likely to be upset for a time. The plant takes some time to recover its equilibrium and start a normal growth. During this period basal leaves begin to develop, but the internodes are so close together that they do not obtain their aliquot share of nutriment, hence they grow only to one quarter or one third their normal size and soon wither and drop off. The leaf scars are left, but they are so close together that it is difficult to make a correct count of the number of leaves. But more important than this,

FIG. 8. PLANT OF HALLADAY HAVANA TOBACCO (56-2)-1-1, WHICH AVERAGES 27.5 LEAVES PER PLANT. IT IS THE RESULT OF THREE YEARS OF SELECTION FOR HIGH LEAF NUMBER IN FAMILY 56, WHICH IN 1909 AVERAGED 24.2 LEAVES PER PLANT. NEW HAVEN, 1912.

FIG. 9. PLANT OF HALLADAY HAVANA TOBACCO (56-1)-1-1, WHICH AVERAGES 24.4 LEAVES PER PLANT. THREE YEARS OF SELECTION FOR LOW LEAF NUMBER HAVE PROVED UNSUCCESSFUL, NEW HAVEN, 1912.

TABLE XII

Frequency Distribution of Number of Leaves in Family K, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant: 17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total	A.	S. D.	C. V.
(K–1)–1–2	F_8	1912	24	2	2	15	42	55	43	26	15	6	2	0	1	...	...	209	21.5 ±.08	1.67 ±.06	7.77 ±.26
(K–1)–1	F_7	1911	22	...	...	...	3	14	39	52	46	28	16	2	1	1	...	202	23.5 ±.07	1.53 ±.05	6.52 ±.22
(K–1)	F_6	1910	20(?)	...	...	...	...	7	13	25	34	32	23	9	3	2	...	148	24.4 ±.09	1.69 ±.07	6.93 ±.27
K	F_5	1909	26	...	...	...	2	4	10	12	3	...	...	...	...	...	...	31	22.3 ±.13	1.03 ±.09	4.62 ±.40
(K–2)	F_6	1910	20(?)	...	...	2	16	12	22	34	29	9	1	2	2	1	...	130	22.8 ±.11	1.82 ±.08	7.98 ±.33
(K–2)–1	F_7	1911	26	1	1	0	0	2	15	51	62	49	13	8	1	1	...	204	24.0 ±.07	1.45 ±.05	6.03 ±.20
(K–2)–1–6	F_8	1912	26	...	1	1	15	29	48	54	46	21	6	0	1	0	1	223	22.8 ±.07	1.63 ±.05	7.15 ±.23

TABLE XIII

Frequency Distribution of Number of Leaves in Family 73, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant: 19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total	A.	S. D.	C. V.
(73–1)–2–1	F_9	1912	24	...	...	3	5	19	30	39	54	32	23	15	1	...	...	...	...	221	25.7 ±.08	1.83 ±.06	7.12 ±.23
(73–1)–2	F_8	1911	23	...	...	2	2	8	37	50	67	31	14	5	1	...	...	...	...	217	25.6 ±.07	1.46 ±.05	5.71 ±.19
(73–1)	F_7	1910	25	...	1	2	2	10	25	29	43	46	29	18	8	1	1	1	...	216	26.3 ±.09	2.01 ±.07	7.64 ±.25
73	F_6	1909	28	...	...	...	...	3	18	26	56	88	74	29	4	1	1	...	...	300	26.9 ±.06	1.45 ±.04	5.39 ±.15
(73–2)	F_7	1910	29	1	0	0	0	9	14	34	48	44	29	14	8	...	...	...	...	201	26.3 ±.08	1.73 ±.06	6.58 ±.22
(73–2)–3	F_8	1911	1	...	...	...	...	...	2	11	19	31	48	41	24	11	5	2	1	195	28.2 ±.09	1.80 ±.06	6.37 ±.22
(73–2)–3–3	F_9	1912	332	...	...	...	1	1	4	13	13	21	12	8	3	...	...	...	...	76	26.7 ±.13	1.65 ±.09	6.18 ±.34

the tobacco grower loses an average of from one to two of his most valuable leaves.

The plus strain of Family No. 56, which we were discussing when we digressed to speak of the critical periods of development, did show a considerable shifting of the mean following the selection of high-leaved mother plants. In the Bloomfield selections the mean went from 24.2 ± .06 to 26.7 ± .08 leaves, then to 26.8 ± .07 leaves; in the New Haven experiment the mean shifted to 27.4 ± .08 leaves,—a gain of 3.2 leaves,—and then dropped to 26.4 ± .11 leaves, recovering again in the F_9 generation to 27.5 ± .11 leaves; in the Forest Hills experiment the successive means were 27.2 ± .08, 28.9 ± .08 and 26.7 ± .06 leaves. Summing up the data from this experiment, it may be assumed to be reasonably certain that no progress resulted from the selection of minus extremes, but that there was a slight effect gradually diminishing in quantity when plus extremes were selected.

Representative plants of Family 56 obtained by three years of selection in the effort to produce strains of high and low leaf number, respectively, are shown in Figs. 8 and 9.

Family No. K (Table XII) was grown on a farm near the Bloomfield experiments, in 1910. The records of the F_5 generation consisted of the number of leaves of only 31 plants. From among these individuals two plants were selfed to become the mothers of the F_6 generation. Since no dependence can be placed on the F_5 distribution by reason of the few plants and since it is not absolutely certain that the mother plants of F_6 had 20 leaves each, the selection really began in 1911 with the F_7 generation. There is a difference between the minus strain and the plus strain in 1911 and 1912,—0.5 leaves the first year and 1.3 leaves the second year,—however, so that one may assume the possibility of a slow shifting of the mean in both directions.

The data on Family No. 73 are shown in Table XIII. This family came from a 28-leaved plant, one of the highest of the F_5 generation. The F_6 progeny of this

TABLE XIV

Frequency Distribution of Number of Leaves in Family 27, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total.	A.	S. D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(27–1)–1	F_7	1912	22	1	0	8	12	44	63	69	61	37	16	2	3	...	316	25.9 ±.07	1.75 ±.05	6.76 ±.18
(27–1)–1	F_7	1911	22	...	...	1	4	10	32	71	64	22	7	2	1	...	214	26.3 ±.06	1.32 ±.04	5.01 ±.16
(27–1)	F_6	1910	25	...	1	5	12	23	31	50	65	29	22	12	4	...	254	26.5 ±.08	1.94 ±.06	7.32 ±.22
27	F_5	1909	29	...	...	2	2	11	33	67	109	46	20	9	1	...	300	27.8 ±.06	1.40 ±.04	5.04 ±.14
(27–2)	F_6	1910	28	...	3	7	23	39	55	45	31	16	3	...	...	...	222	25.2 ±.07	1.63 ±.05	6.47 ±.21
(27–2)–1	F_7	1911	28	...	1	1	2	35	47	58	39	27	12	...	...	...	222	26.0 ±.07	1.50 ±.05	5.78 ±.19
(27–2)–1	F_7	1912	28	...	5	14	38	51	73	75	29	14	5	0	0	1	305	25.0 ±.06	1.67 ±.05	6.68 ±.18

TABLE XV

Frequency Distribution of Number of Leaves in Family 82, Grown at Bloomfield, Conn.

No.	Generation	Year Grown	Number of Leaves of Parent	Number of Leaves per Plant													Total	A.	S. D.	C. V.
				20	21	22	23	24	25	26	27	28	29	30	31	32				
(82–2)–1	F_8	1912	30	...	1	5	6	13	21	48	60	43	20	3	3	2	225	26.7 ±.08	1.80 ±.06	6.74 ±.21
(82–2)–1	F_8	1911	30	...	...	...	2	11	35	53	62	37	12	4	1	...	217	26.6 ±.06	1.40 ±.05	5.27 ±.17
(82–2)	F_7	1910	28	1	0	2	4	21	31	41	36	30	22	13	3	...	204	26.6 ±.09	1.95 ±.07	7.33 ±.25
82	F_6	1909	30	...	...	...	7	15	38	73	91	60	16	1	1	...	297	26.6 ±.05	1.37 ±.04	5.08 ±.14

individual showed a mean of 26.9 ± .06 leaves, and from among them plants having 25 and 29 leaves, respectively, were selected to start the minus and the plus lines. These two mother plants gave F_7 populations alike as to mean, but differing by one class as to mode. The minus line had the higher mode. The extremes of this generation used in carrying on the experiment differed by 8 leaves, and the resulting progenies apparently followed the selection. The means are 25.6 ± .07 and 28.2 ± .09 leaves. Whether these shifted means represent a permanent change or not we are not prepared to say. The minus mean is probably somewhere near the correct figure for in the F_9 generation it was practically the same, but in the F_9 generation of the plus strain the mean dropped from 28.2 ± .09 leaves to 26.7 ± .13 leaves. This is a slightly lower point than that of the original F_5 distribution, but it was calculated from only 76 individuals. A conservative estimate of the significance of the results would probably be as follows: the mean of the minus strain has shifted slightly but permanently and is now fixed, while the mean of the plus strain has not changed but has shown evidence of some heterozygosis in one generation.

We come finally to consider Families No. 27 and No. 82, the data on which are listed in Tables XIV and XV. Two generations of both plus and minus selection were recorded for Family No. 27, but only plus selections of Family No. 82 were grown. There is no necessity for considering either in detail because a simple inspection of the tables shows that selection has accomplished nothing.

CONCLUSIONS

The cumbersome and no doubt dry details of the experiments to the close of the year 1912 having been described, let us give a brief résumé of the conclusions that we believe may reasonably be drawn from the data that have been offered. There can be no doubt that the original "Halladay" type of tobacco, isolated and propagated by Mr. Shamel and Mr. Halladay from the cross between "Havana" and "Sumatra" tobaccos, arose through the segregation and recombination of the Mendelian factorial differences of the two plants, and not as a mutation. It is simply a union of the factors that stand for leaf size and height of plant in the "Havana" variety with the factors that bring about leaf shape and high number of leaves in the "Sumatra" variety. It happened that the somatic characters of these varieties account for all the characters of the hybrid. At the same time one must remember that strains were obtained by selection that averaged higher in number of leaves than did even the "Sumatra" parent. We can only conclude from this fact that the difference between the "Havana" and the "Sumatra" varieties in leaf number is greater factorially than somatically. Besides certain factors common to the two varieties, the factors for leaf number in "Havana" tobacco might be represented by the letters *AA*, and those of "Sumatra" tobacco by the letters *BB, CC, DD, EE*. By recombination, this would give plants with a smaller number of leaves than the "Havana" variety and plants with a greater number of leaves than the "Sumatra" variety. Both combinations were obtained; and further, the theory has been shown to be correct by the results of other crosses where both types appeared (Hayes, '12). It is probably unwise to suggest too concrete a factorial analysis of the cross, yet the factorial difference assumed above will account for all of the facts obtained, by simple recombination. We assume a factor in the heterozygous condition to account for the production of one leaf and a factor in the homozygous condition to account for the production of two leaves. The mean of the "Havana" variety is about 20 leaves and the mean of the "Sumatra" variety about 26 leaves. Somatically there is a difference of 6 leaves or three factorial pairs for which to account. But in order to have the theory coincide with the facts there must be at least one (possibly two or three) factorial difference that does not show in the two varieties. The meaning of this statement can be shown best by an illustration. The 20 leaves of the "Havana" variety and the first 20 leaves of the "Sumatra" variety are represented by 10 pairs of factors, of which nine are the same and one different in the two strains. The "Havana" variety is nine leaf factors plus *AA*, the first 20 leaves of the "Sumatra" variety are nine leaf factors (the same as those in the "Havana") plus *BB*. The additional leaf factors of the "Sumatra" are *CC, DD. EE*. With these assumptions, the recombinations of a tetra-hybrid will represent our facts fairly accurately. But, as was stated above, it does not seem wise to take this interpretation of the facts too literally. That some such factorial combination will represent our facts superficially there can be no doubt, but in reality if one could grow hundreds of thousands of individuals and follow the behavior of each he would likely find himself constrained to represent his breeding facts by a much more complex system. There would probably be gametic couplings and factorial differences whose main effect would be on some entirely different character or complex of characters, but which would have some slight jurisdiction over leaf determination. To become diagrammatical, the unit characters of a house are its cornices, its windows, its floors and what not, but a collection of these components is not a house. We may even exchange dormer windows with our neighbor, but we can exchange them only if they fit. Again, we may put on a coat of paint, a color unit, but this color unit affects the appearance of many other parts that are just as truly units.

The essential part of our conception of the origin of this hybrid type is that recombinations of characters quantitative in their nature can be expected and predicted in crosses in exactly the same manner as is done with qualitative characters. On the other hand, it must be borne in mind that here was a hybrid type that appeared to be breeding true to the general characters that we have described, in the F_4 generation. That it was not breeding true is clear from the results of the selection experiments, yet out of the small number of F_5 and F_6 families taken under observation at least two were found to be breeding true for all practical purposes in the F_5 and F_6 generations. We were able to reproduce the "Havana" type by continued selection in Family 77 and were able to produce strains breeding approximately true to 30 leaves or so by the selection of mother plants in several families. But can we say that any of our families are now fixed so that no progress can be made by selection? We can not. But we can say that some of them are so constant that it would be a loss of time for selection to be continued for economic results. It is important to know whether plant or animal populations can reach such a state of constancy by inbreeding that no profitable results can afterwards be obtained by the practical breeder. We believe it demonstrated by even these few data that such a state, a homozygous condition, occurs in a definite proportion of F_2 offspring, and can be propagated commercially at once if a sufficient number of families are grown to be relatively certain of including the desired combination.

As to the problem of theoretical importance, the question of the true constancy of homozygotes generation after generation, we believe it to be fair to conclude that a state so constant is reached, that even for the theoretical purposes of experimental genetics it may be assumed as actually constant. Further experiment and larger numbers may show that selection can always cause a shift in the mean, but will necessarily be a shift so slight that it can be detected only by a long-continued experiment and enormous numbers. Assuming for the purpose of argument that this is the case, the matter would affect only the question of the trend of evolution. It may come to be believed, from evidence now unknown, that evolution may progress slowly in this manner, but if it does, its course can hardly be demonstrated experimentally beyond a reasonable doubt. The problems of experimental genetics can be attacked, however, from the standpoint that experimental evidence of the shifting of the mean of a homozygous population by selection is negligible.

Mutations may occur. We have shown the origin of one family by a very wide mutation. In this particular case it was not difficult to show that a constitutional change took place in a single germ cell of the mother plant. It was only by a lucky chance that this fact could be demonstrated, for with smaller changes such proof would be impossible; but there is no reason to believe that this phenomenon is unique or even rare. It is much more reasonable to assume that mutations usually arise in single gametes than that the same change occurs simultaneously in many germ cells. One should expect the somatic result of a mutation in an hermaphroditic plant —the sporting plant itself—not to breed true, therefore, but to behave as an F_1 hybrid between a mutating and an unchanged germ cell. It is true that the mutations observed by DeVries in *Œnothera Lamarckiana* are supposed to have bred true, but this is sometimes questionable even from DeVries's own data. The Lamarckiana "mutants" that did breed true are much more reasonably explained as segregates from complex hybrids. They can be interpreted by Mendelism with no essential outstanding facts, but if they are to be interpreted as mutations, several discrepancies between what actually occurred and what should be expected on DeVries's own theory must be explained. It must be shown why the changes took place in numerous germ cells,—in both the male and the female gametes,—and why these germ cells always fused at fertilization; for the changed germ cells must have fused with each other because many *Lamarckiana* plants were produced by the same mother plants that produced the mutations, while the mutations are supposed to have bred true. On the only other possible theory of mutation, that the change occurred in the developing zygote after fertilization, one would have to explain why the mutants did not often appear as bud variations, instead of these being much rarer than the supposed mutations, as is actually the case.

We do not deny the theory of mutation as modified to assume only that constitutional changes usually occur in the germ cells, but on this belief the sporting plants must often be F_1 hybrids, and the plant breeder must resort to selection to isolate his pure mutation. And by the same reasoning one gametic change may produce many new creations, for there is a chance to recombine it with all the known gametic differences in the species.

No one can say how often mutations arise. It is likely that changes other than the one observed took place in our tobacco experiments, but it is not likely that they are sufficiently numerous to base a system of selection within a pure race on the possibility of their occurrence. The fact that no changes ensued that could be detected in several of our selected lines is an argument against it. The comparatively large jumps are the ones likely to have the greatest economic importance, and these are easily detected without refined methods of procedure. Small jumps can be economically important only if they are numerous, and, as there are absolutely no data to show either that they are numerous or that changes can be produced rapidly within homozygous pure lines through any other cause, it seems unwise to recommend that the practical breeder expend time and money to bring about results that either can not be expected at all or that are so slow and so trifling that they can not be detected in carefully planned and accurately executed genetic investigations. On the other hand, the results of the last decade show that important economic results can be obtained easily and surely by selection from artificial hybrids or from the natural hybrids that occur in cross-fertilized species by the recombination of Mendelian factors. We believe, therefore, that the isolation of homozygous strains from mixtures that are either mechanical or physiological, that are either made artificially or are found in nature, offers the only method of procedure that the practical plant breeder will find financially profitable.

Finally, we should like to call attention again to the practical importance of determining the duration of the period in the course of which particular plant characters are responsive to the action of environmental influences. The character complex that has been the basis of this study is a striking illustration of how results from such investigations may be applicable to farm practise. One may plant a portion of the seed from a self-pollinated tobacco plant on poor soil or on good soil and the average number of leaves per plant and the general variation of the plants in number of leaves will remain nearly the same in both cases.[2] But seed selected from *mother plants* grown on the good soil will produce plants averaging slightly higher in leaf number than the plants coming from seed on mother plants whose environment is poor. Consequently, it is better to select seed from well-developed mother plants—mother plants whose environment has been good—than from mediocre mother plants. There is no question here of the inheritance of an acquired character or of continuing to raise the number of leaves by cultural treatment. One simply takes advantage of the fact that during seed formation there is a period of mobility at which time the potential number of leaves of the young plant are practically fixed. Pending the end of this critical period, the number of leaves can be influenced by external conditions within the limit of fluctuating variability.

In the same connection, the effect of time of planting on the tobacco plant should again be mentioned, as this also emanates from environmental change. The actual number of leaves is, of course, practically fixed at the time of setting the plants in the field, but this is not true of the number of leaves that will have a commercial value. For example, a seedling with 26 potential leaves is planted. If it is planted when about four inches high, the general physiological disturbance due to transplantation is negligible and the plant continues its normal cycle of development without a pause, bringing to maturity

---

[2] Garner's (:12) results on Maryland Mammoth are an exception to this statement because this variety is indeterminate in growth.

about 22 leaves. If planting is delayed until the seedling is eight or ten inches high, there is a different state of affairs. Development is arrested, the plant pauses to adjust itself to the change. It soon recovers and continues its normal ontogeny, but the period of reduced growth has left an ineffaceable record. Several of the leaves—among them the more valuable leaves—have been so affected during this readjustment, that they develop to only a fraction the size that they should attain because the internodes between them are so short, due to the constricted development that normal metabolism does not occur. Thus there is a loss of one or two leaves, which on several acres of tobacco may make the difference between profit and loss. Hence, the grower should not delay setting his plants in the field until they have become overgrown in the seed bed.

March, 1913

LITERATURE CITED

Davis, B. M. Genetical Studies in Œnothera, III. Amer. Nat., 46: 377–427. 1912.

East, E. M. Inheritance of Flower Size in Crosses between *Nicotiana* Species. *Bot. Gaz.*, 55: 177–188. 1913.

East, E. M., and Hayes, H. K. Inheritance in Maize. Conn. Agr. Exp. Sta. Bull. 167: 1–142. 1911.

Garner, W. W. Some Observations on Tobacco Breeding. Ann. Rpt. Amer. Breed. Assoc., 8: 458–468. 1912.

Hayes, H. K. Correlation and Inheritance in *Nicotiana Tabacum*. Conn. Agr. Exp. Sta. Bull. 171: 1–45. 1912.

Heribert-Nilsson, N. Die Variabilität der *Œnothera Lamarckiana* und das Problem der Mutation. *Ztschr. Abstam. u. Vereb.*, 8: 89–231. 1912.

Jennings, H. S. Heredity, Variation and Evolution in Protozoa, I. *Jour. Exp. Zool.*, 5: 577–632. 1908.

———. Heredity, Variation and Evolution in Protozoa, II. *Proc. Amer. Phil. Soc.*, 47: 393–546. 1908.

———. Assortive Mating, Variability and Inheritance of Size, in the Conjugation of *Paramecium*. *Jour. Exp. Zool.*, 11: 1–133. 1911.

Johannsen, W. Uber Erblichkeit in Populationen und in reinen Linien. Jena, Gustav Fischer, pp. 1–515. 1903.

Pearl, Raymond. Inheritance of Fecundity in the Domestic Fowl. Amer. Nat., 45: 321–345. 1911.

Shamel, A. D. New Tobacco Varieties. Yearbook U. S. Dept. Agr., 1906: 387–404. 1907.

Tammes, Tine. Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung. *Rec. Trav. Bot. Néerl.*, 8: 201–288. 1911.

ORLAND E. WHITE

STUDIES OF TERATOLOGICAL PHENOMENA IN THEIR RELATION TO EVOLUTION AND THE PROBLEMS OF HEREDITY

1. A STUDY OF CERTAIN FLORAL ABNORMALITIES IN NICOTIANA AND THEIR BEARING ON THEORIES OF DOMINANCE

Presented in Partial Fulfillment of the Thesis Requirement for the
Degree of Doctor of Science at the Bussey Institution of
Harvard University, 1913

Reprinted from the AMERICAN JOURNAL OF BOTANY **1**: 23–36. *text figs. 1-4.* Ja 1914.

[Reprinted from AMERICAN JOURNAL OF BOTANY, Vol. I, No. 1, January, 1914.]

STUDIES OF TERATOLOGICAL PHENOMENA IN THEIR RELATION TO EVOLUTION AND THE PROBLEMS OF HEREDITY

I. A STUDY OF CERTAIN FLORAL ABNORMALITIES IN NICOTIANA AND THEIR BEARING ON THEORIES OF DOMINANCE[1]

ORLAND E. WHITE

When Mendel's law was rediscovered, dominance was considered as essential and as important a principle as segregation. Further investigation soon demonstrated the phenomenon of "imperfect dominance," and still later studies led to a substitution of the "presence and absence" factor hypothesis for Mendel's conception of contrasted character pairs. De Vries (1902), Bateson (1909), Davenport (1910), Castle and others look upon dominance as an attribute of the factor or determiner, and according to the last two investigators, variation in dominance, at least in part, is the result of variable potency, or variation in the power of a determiner or factor to express itself in ontogeny. De Vries held the racially older characters to be dominant over the younger, a conception which the last ten years of experimental investigation has not upheld. On the other hand, East (1912) and Emerson (1912) think of dominance as a result of the activities of one or more specific factors, plus the modifications produced by the whole factorial organic complex (all the other factors concerned in the organism's heredity) and by the external environment (climate, soil, etc.). In other words, under identical genotypical and external environments, the factor A would always give the same expression, no matter how often the experiment was repeated.

The chief value of the data which I have to present lies in its bearing on this important question of dominance. The abnormalities concerned are three in number, viz., petalody and pistillody of stamens and that peculiar form of corolla doubling to which de Vries and others

---

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University. Brooklyn Botanic Garden Contributions, No. 7. Read at the Annual Meeting of the Botanical Society of America, Atlanta, Ga., 1913.

apply the term catacorolla. The data on each are given in some detail, followed by a short discussion and summary.

The work was done in the Laboratory of Genetics, Bussey Institution of Harvard University, under the direction of Prof. E. M. East, for whose kindly interest and criticism, I wish to express my appreciation.

The material was obtained from various pure line cultures of *Nicotiana* species, which had been under observation for several years. All pure species used in this study bred comparatively true and no abnormal variations appeared in them, except in *Nicotiana langsdorffii grandiflora*, which was subject to petalody, and gave evidence of being a hybrid as it was heterozygous for yellow and blue pollen, the true form according to Comes (1899) having only blue pollen.

1. PETALODY

This teratological character is an extremely common feature of garden flowers, and, as usually found, is variable even among the stamens of the same flower, *i. e.*, one stamen may possess it, or it may be present in two, three, four or all of them. On one stamen, the petal-like outgrowth from the filament, which constitutes the character, may be very small, while another filament in the same flower may show an anomalous enlargement from three to ten or twelve times as great. It presents its extreme form in the common double-flowered races of *Dianthus*, *Rosa*, *Prunus* and *Ranunculus*. The majority of gardeners as well as many scientists believe that such double-flowered races can be *created* from single-flowered varieties by selection. A very excellent treatment and historical résumé of this subject is given by de Vries (1906, Chap. 17) in which he produces historical proof that many of our common double-flowered races arose suddenly and in full possession of their peculiar character. His experimental studies led him to assign doubleness because of its variability, to the category of "ever sporting" characters. In many of our cultivated races, double-flowered plants quite faithfully reproduce themselves if they are fertile at all. The majority of these races have arisen as mutations, the causal factors of which are largely unknown. Among horticulturists the belief is prevalent that intense cultivation is responsible for the anomaly, but there are no data from controlled experiments to support such a belief. Peyritsch (Goebel 1900, I, p. 195) induced all degrees of doubling ~~in~~ the floral organs of

Cruciferae by artificial parasitization with *Phytoptus*, and, according to Hus (1908), Molliard caused the formation of double flowers by mechanical irritation. From these facts, one may conclude that double flowers may result from many different causes.

In *Nicotiana*, petalody arose in at least two dozen plants of four or five hybrid families on which observations were being made for other purposes. The pure species from which these hyrbids were derived, while under observation for five years, never developed petalody. Further, this abnormal condition was never observed in F_1 hybrid generations, although thousands of flowers were examined.

Two of these abnormal plants were self-fertilized, and the progeny, grown under approximately the same environment as the mother plant, reproduced the character, showing it to be a hereditary and not an induced phenomenon. One of the races was derived from an F_2 segregate of *N. langsdorffii* × *N. forgetiana*. The expression of the character in the stamens was very variable. Table 1 gives a general idea of the extent of this variability among the different flowers of the mother plant. The progeny, over 100 in number, all possessed the abnormality. The throats of the corolla tubes in some plants were, however, almost packed with anomalous stamens; while in others, perhaps only a single stamen was malformed. An examination of the progeny plant by plant for differentiating characters showed that segregation in flower color, habit of plant, leaf shape, etc., had occurred, indicating that the mother plant was heterozygous for a large number of factors.

TABLE 1

Number of affected stamens per flower........	1	2	3	4	5	Total
Number of flowers..........................	1	14	4	6		25

The other race of these anomalous stamen-bearing plants was derived from selfed seed of a plant which appeared to be *N. langsdorffii grandiflora*. The variability of the abnormal character is shown in Table 2. In 1912 under the same field conditions, 70 plants were grown from selfed seed of this mother plant. The inspection of these 70 plants showed the parent to have been homozygous in all its

TABLE 2

Affected stamens per flower..................	1	2	3	4	5	Total
Number of flowers..........................			1	20	4	25

grosser morphological features, excepting pollen color. Habit, foliage, height and floral characters were in all plants practically of the same type and no evidences of a difference in genotypical constitution were to be observed except for the case mentioned. The anomaly expressed itself to about the same degree in all 70 plants, and had I desired to begin selection work toward securing a double-flowering *Nicotiana*, one plant would have been as good a starting point as another.

Summarizing these facts, one finds that where the anomalous race was heterozygous in many characters, the expression of petalody was extremely variable; while in the race largely homozygous, practically no variation in the abnormality was noted.

2. PISTILLODY

This anomaly consists of the presence of small pistils in connection with the anthers. Sometimes these little pistils amount to no more than a style and a stigma; at other times, the anther or pollen-sacs may be partly changed into carpels and rudimentary ovules produced. Occasionally such ovules are fertile and produce seeds. An examination of the literature on the subject shows the character to be neither common nor rare. Usually it is so small and inconspicuous that it passes unnoticed, but in the opium poppy, it is showy and characterizes a distinct horticultural variety. *Papaver somniferum* var. *monstruosum* or var. *polycephalum*, as it is sometimes called, affords the material for a very interesting chapter on pistillody in "Species and Varieties, their Origin by Mutation" (de Vries, 1906, Chap. 13). The writings of Masters, DeCandolle, and Hofmeister also contain valuable information on this subject. Masters considered the anomaly to be an accidental phenomenon, while DeCandolle in his Prodromus described pistilloid wall flowers as a distinct variety. The pistilloid poppy is at least a century old, and was grown as a field crop in Europe, being especially valuable because its anomalous condition did not allow the capsule to open and scatter the seed. De Vries (1906, pp. 369–99) found these poppies, in respect to their chief peculiarity, very sensitive to environment, especially during the first two to five weeks of their seedling stages. By manipulating the soil conditions at the proper time, he was able to increase and decrease the anomalous expression. Plants almost normal and those extremely abnormal were produced in this manner. Selection had no permanent effect on its expression. De Vries classified it as an "eversporting" variety. Although it was possible almost to destroy the character or inhibit the expression of its hereditary elements by modifying the environment, it was never absolutely eliminated by this treatment. In addition to the action of the external surroundings, internal factors must have had some part in making this an extremely sensitive character, because poppies, like corn, are cross-fertilized, and hence are more or less heterozygous, and, while the external conditions are no doubt very important for the characteristic development of the anomaly, the eversporting condition one may ascribe at least partially to the effect of segregating genes.

FIG. 1. *Nicotiana* flower showing pistillody.

The race of pistilloid *Nicotianas* with which I experimented originated from the guarded seed of a single anomalous mutant which was discovered among the segregates of an F_2 generation from *N. langsdorffii* × *N. alata*. Two or three hundred of these F_2 plants from the same cross were grown, but no other pistilloid mutant was found among them. The plant was designated (-2-1A) and in all subsequent experiments will be known under this number. Over 110 of its flowers were examined, all of which showed the character in each stamen, although there was considerable quantitative variability. No semblance of an ovary in connection with the pistilloid stamens was found in these -2-1A flowers, although this occurred in its descendants. Cuttings of the mutant were made, and selfed seed procured from which 90 offspring were obtained, 72 of which reproduced the character in all faithfulness, and were in all apparent respects like the parent. Eleven of the progeny developed flowers with only two or three or at most four pistilloid stamens, and in these, the anomalous pistils were much smaller than those of the original (-2-1A) or of its 72 offspring. Seven of these offspring entirely lacked pistilloid stamens. At first, such a state of affairs was very puzzling, as the possibility of technical error was not taken into consideration. However, there were sap-colored flowers among the progeny, which was

FIG. 2. Stamens from a single flower showing pistillody in detail.

very surprising, inasmuch as the hybrid family had contained only cream and white-flowered plants even to the grandparental generation. Table 3 shows the ratio of white to colored plants and their stamen character.

TABLE 3

Color	Pistillody	Pistillody not fully expressed	Normal	Total
White	71	10		81
Colored	1	1	7	9
	72	11	7	90

When I found that some of the progeny with sap-colored (magenta, etc.) flowers possessed pistilloid stamens, I was more puzzled than ever, because I had already found it to be completely recessive in the crosses I had made. When the conception of dominance and recessiveness as characteristics, not of the unit "character" or factor alone, but of the latter plus the effect produced upon it by its internal (genotypical) and external environments, was brought to bear upon the problem, the explanation was simple, especially as 90 F_1 and 381 F_2 progeny of a cross between -2-1A and 321 (*N. alata*) had given nothing but white-flowered plants. During the winter I had been working with many colored-flowered F_2 segregates of *N. forgetiana* (314) × *N. alata* (321) and had not been careful enough about cleaning my pollenizing tools before selfing the flowers on the cuttings of the original (2-1A) mutant, and, as a result, a few hybrid seeds were produced. Pistilloid stamens in the colored-flowered plants were due to dominance, complete in one case and partial in the others, of the anomalous condition over that of the normal. In the other 7 progeny with colored flowers, the expected condition, *i. e.*, the dominance of the normal, prevailed. Probably all 18 progeny belonging to the normal and intermediate classes were hybrid. Further experiments are in progress to determine this. The change in dominance is not thought to have any special connection with the color factors, but is interpreted in the same manner as the anomalous results secured in some of my unpublished studies on fasciation, viz.: the modifying influence of other factors. The 18 plants which were causing confusion had, in the majority of cases, a very different and distinct habit from the original pistilloid mutant, and this was especially true of the plants with colored flowers. The 72 or more pure abnormal (2-1A) progeny were very similar in habit, flower color and other characters, so much so that I inferred that the parent plant (2-1A) had been largely homozygous in its genotypical constitution.

From the cross referred to above (2-1A × 321), 90 F_1 progeny were grown, all of which were intermediate in both habit and in size of floral organs, but *absolutely* normal as regards pistillody. Two of these were selfed and F_2 progeny grown. The results are tabulated in Table 4.

TABLE 4

Pedigree	Normal	Abnormal	Total
(394 × 321) — 2 — 1A × 321 — 1	103	82	185
(394 × 321) — 2 — 1A × 321 — 2	152	42	196
Total	257	124	381
Expected	285.75	95.25	381
Deviation	—28.75	+28.75	

One family (-2) gave a fair approximation to the 3:1 ratio, but the other had a large excess of abnormal segregates, which I am at present unable to account for, because the two families were grown from the same grandparental stock, and under the same external environment. Many other characters of a structural nature had segregated in this F_2 generation, and the variation in the expression of the anomaly was large. Many plants were as abnormal, and many much less so than the grandmother. Other abnormalities appeared, both in pistilloid and normal segregates. Split corolla tubes and 3- to 4-loculed ovaries were not infrequent. Some of the segregates, as well as a number of the pure line (?) progeny, possessed flowers with pistilloid anthers containing numerous small ovules. Where these occurred, the pollen-sacs were deformed, sterile, and usually the ovules were exposed, owing to hypertrophy of the anther-sac walls.

3. CATACOROLLA

This is not an uncommon anomaly, and hereditary races of it have long been known, *e. g.*, hose-in-hose primula, and a garden variety of gloxinia, first described by Prof. E. Morren (see Masters, 1869, pp. 451–52, figs. 213–14). Catacorolla has been exceedingly well described by both Morren and Masters, so I shall not take the space here for a general detailed description, but confine myself to the form it takes in the particular race with which I worked. This race (4-1A) is descended from a single plant which possessed the catacorolla peculiarity to a more marked degree than any other one of the 15 anomalous plants which appeared in a family of 50 F_2 segregates from a cross between *N. langsdorffii* × *N. alata.* In fact, this hybrid family was derived from the same grandparental cross as that in which the pistilloid mutant occurred. Instead of a bud mutation occurring shortly after fertilization, as was probably the case with the homozygous pistilloid character (2-1A), this catacorolla mutant (-4-1A) must have originally arisen as a change in the gametes of one or the other of the grandparental types or in the cells concerned in their ontogenesis, if we are to interpret the succeeding experimentally obtained results in accordance with our general knowledge of heredity. In the F_2 generation grown from guarded F_1 seed from a cross between two normal individuals occurred a segregation of 15 anomalous and 35 normal plants, making a ratio of 7 normal to 3 abnormal or 2.33 : 1. Supposedly the abnormals would have all bred true, for the one plant (-4-1A) which was selfed produced 20 progeny all of which faithfully repeated the parental peculiarities in respect to catacorolla, habits of growth, character of foliage, size and color of flowers, and color of pollen. It is not supposed that only one "altered" egg cell or pollen grain was necessarily produced in attempting to explain the place in ontogeny at which this mutation arose. Possibly many were formed as the result of a prematuration mutation, but if such were the case, and if they united with unaltered gametes, the resulting seeds possibly were not planted, or if planted, only one F_1 plant of this sort chanced to be included in those selfed for further propagative purposes.

Catacorolla in this race is typical of the anomaly as it appears in other plant species. Petalloid segments are produced outside the ordinary corolla, and partially adhere to it, these segments having colored outer and plain green inner surfaces. In other words, the normal corolla appears to have been separated at some time during its ontogeny into five segments. Later when these fused to produce the normal gamopetalous *Nicotiana* flower, the union appears not to have taken place through the careful growing together of the edges of each segment, but on the contrary, to have been brought about in such a manner as to leave a seam like that made by a tailor. At the point of union of two segments, there is a slight waste of material, and it is this which is reflexed back in the mature flower and gives the catacorolla effect. The segment then is really a piece of left-over petal. In some flowers, the petaloid segments are not united with the normal corolla except at their bases, and, in such cases, other factors have interfered and effected a distinct separation. The anomalous character, then, is the result of imperfect fusion of the corolla segments in ontogeny. This theory is further supported by the relation that exists between the number of normal corolla lobes and the number of extra-corolla segments. Table 5 shows the character of this relationship in 28 flowers taken from the original parent (4-1A).

FIG. 3. "Catacorolla." *Nicotiana* flowers from the parent plant of the -4-1A race, showing variation in the expression of the anomaly.

TABLE 5

Number of segments per flower	1	2	3	4	5	6
Number of flowers	3	2	6	9	5	3

A more extended investigation from the standpoint of anatomy and morphology is necessary before such a theory can be demonstrated as a truth. The fact that six extra corolla segments are sometimes present can be explained by supposing that two segments sometimes result from a single "seam." The size of these segments varies from a slender, thread-like structure to one as broad as the normal lobe. In some flowers they fuse and produce a supernumerary corolla. This variability is characteristic of the race as a whole, *i. e.*, some plants are not more variable than others, so that the character may be said to be eversporting only in the sense that a single plant may possess both very abnormal and slightly abnormal flowers.

FIG. 4. Flowers from F_1 hybrids between catacorolla and normal races, showing variation in expression ("dominance and recessiveness"). Each flower represents the typical expression in a single hybrid plant.

Several series of hybridization experiments are in progress, but they have reached only the F_1 stage. The most interesting of these experiments relates to a study of the dominance and recessiveness of catacorolla. In addition to the selfed seed produced by the parent

(4-1A) plant, a large amount of "open field" seed was gathered from it. Thousands of hybrid F_2 segregates of various crosses such as *N. forgetiana* × *N. alata* and *N. alata* × *N. langsdorffii* were grown in the same field, and in the same year as the 4-1A parent. These were all normal in respect to catacorolla, excepting the 15 plants already mentioned. Cross-fertilization was more favorable to the production of seed on this one (-4-1A) selection than self-fertilization. This means that the open field seed would produce largely hybrid F_1 plants. One hundred and sixty-two plants grown from this seed gave 43 homozygous 4-1A progeny and 119 hybrid F_1 progeny, the latter representing almost as many different F_1 combinations as there were individuals. As a consequence, they were extremely variable in almost every taxonomic feature,—in habit, height, foliage; in flower color, size and shape; in pollen color, and in many other less prominent characters. Sixty of the 119 were colored, and 59 were white. Some of the flowers were as small as those of *N. forgetiana*, while others were as large as those of *N. alata*. Fig. 4 is an attempt to show something of these differences in flower size, as well as in the variability of the catacorolla character. Each flower represents a single plant. The F_1 variation in the expression of the catacorolla was remarkable. Supposedly each of the 119 plants represented a different genotypical complex, and hence one would, on the conception of dominance supported by East, expect a great deal of variability. Table 6 shows the results of classifying the whole 162 progeny by color and by their expression of the anomaly.

TABLE 6

Color	-4-1A Pure Homozygote	Hybrids Intermediate	Hybrids Normal	Total
White	43	33	26	102
Colored		11	49	60
	43	44	75	162

Those classified as normals showed absolutely no expression of the character.

Guarded crosses were made between the -4-1A and -2-1A strains. The genotypical constitutions were very different, as each had a distinct growth habit, leaf size, etc. About 150 F_1 plants were grown in the same field and under approximately the same conditions as the other "catacorolla" cultures. In this cross, the F_1 expression of catacorolla was intermediate, with a fluctuation towards complete dominance of the normal, although never approaching that state. The pistillody was absolutely recessive.

4. Discussion and Summary

1. *Nicotiana* plants showing petalody were selfed and progeny grown from them. In one race the abnormal character was extremely variable, some plants showing a large expression, other plants showing it only to a slight degree. This race varied in many other characters, proving the mother plant to have been very heterozygous. In another race, the abnormality was reproduced in all the progeny to the same degree as in the mother plant. With the exception of pollen color, no variation in other characters occurred in this race.

2. Pistillody originated as a discontinuous variation and was inherited in the same manner, crosses with the normal in one case giving in F_2 a progeny closely approximating a simple 3 : 1 ratio. In two hybrid F_1 families, it was completely recessive, while in what appears to be another hybrid F_1 family, it is wholly dominant. The first two families differ from the last family in a large number of characters, as the ancestry of the latter involves another species.

3. The catacorolla race of *Nicotiana* originated from a discontinuous variation. When crossed with normal races, the F_1 progeny were either intermediate in character or absolutely normal, though the individual F_1 progeny from each cross showed no variation among themselves. Great variation existed between the different pollen parents of many of these F_1 individuals.

As a whole, the data secured from hybridizing races of normal plants with those possessing the three abnormalities discussed above support the view that dominance and recessiveness are not in any way attributes of the factor or "character" in itself, but are the result of the factor expression plus the modifying influence of the environment, whether genotypical or external (soil, climate, etc.). The variability in the expression of catacorolla in the 119 F_1 plants of -4-1A crossed with the 119 different normals is strong supporting evidence that this conception of dominance is the most tenable of those recently advanced by geneticists.

LITERATURE CITED

Bateson, W. Mendel's Principles of Heredity, Cambridge Univ. Press, pp. 1–396. 1909.

Castle, W. E. The Origin of a Polydactylous Race of Guinea-pigs. Contrib. from Zool. Lab. of Mus. Comp. Zool., Harvard Univ., No. 176, pp. 17–29. 1905.

Castle, W. E. Heredity in Relation to Evolution and Animal Breeding. New York and London, pp. xii +1–184. 1911.

The Inconstancy of Unit Characters. Am. Nat. **46**: 352–362. 1912.

Clos, D. Essai de Tératologie Taxinomique. Toulouse, pp. 1–80. 1871.

Comes, O. Monographie du genre *Nicotiana*, Naples, pp. 1–80. *pl. 14.* 1899.

Davenport, C. B. Inheritance of Characteristics in Domestic Fowl. Carneg. Institution Pub. No. **121**: 1–100. *pl. 1–12.* 1910.

DeVries, H. Die Mutationstheorie, Leipzig. 2 Bd. 1901–1903.

Species and Varieties, their Origin by Mutation. Open Court Pub. Co., Chicago, pp. 1–847. 1906.

The Mutation Theory. Open Court Pub. Co., Chicago. 2 Vols. 1909–1910.

East, E. M., and H. K. Hayes. Inheritance in Maize. Conn. Agr. Exp. Bull. No. 167 and Contrib. Lab. of Genetics, B. I. H. U. No. 9, pp. 1–142. *pl. 1–25.* 1911.

The Mendelian Notation as a Description of Physiological Facts. Am. Nat. **46**: 633–655. 1912.

Emerson, R. A. Inheritance of Certain "Abnormalities" in Maize. Rpt. Am. Breed. Assoc. **8**: 385–399. 1912a.

Goebel, K. Organography of Plants. Clarendon Press, Oxford. 2 Vols. 1900–1905.

Hus, H. Fasciations of Known Causation. Am. Nat. **42**: 81–97. 1908.

Johannsen, W. The Genotype Conception of Heredity. Am. Nat. **45**: 129–159. 1911.

Masters, M. T. Vegetable Teratology. London, pp. xxxviii + 534. 1869.

White, O. E. The Bearing of Teratological Development in *Nicotiana* on Theories of Heredity. Am. Nat. **47**: 206–228. 1913.

Überreicht von dem Verfasser

Sonderabdruck aus der

Zeitschrift für induktive Abstammungs- und Vererbungslehre

1916 Bd. XVI Heft 1/2

Verlag von Gebrüder Borntraeger in Berlin W 35

ORLAND E. WHITE:

Studies of Teratological Phenomena in their Relation to Evolution and the Problems of Heredity.

Studies of Teratological Phenomena in their Relation to Evolution and the Problems of Heredity.

II. The Nature, Causes, Distribution, and Inheritance of Fasciation with Special Reference to its Occurrence in *Nicotiana*[1]).

By **Orland E. White,**
Brooklyn Botanic Garden, Brooklyn, N. Y., U. S. A.

(Eingegangen 1. Juli 1914.)

Contents.

---

[1]) Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University. Brooklyn Botanic Garden Contributions, No. 11.

A. Introduction.

The present paper is the outcome of an extended series of studies on the phenomenon of fasciation in plants. The first part consists largely of compiled date on its occurrence and classification, together with a review of the researches of de Vries on this anomaly. In the second part, I have described in some detail, a series of hybridization experiments, in which a mutant variety of *Nicotiana tabacum* breeding true to fasciation was crossed with several distinct normal varieties of this same species, as well as with several strains belonging to markedly distinct species. In the course of this account, I have tried so show the necessity of dispensing with the latent character conception of the morphologists and of being more precise in our use of terms. Particular emphasis has been laid upon the fact that a character always is the result of both internal and external factors and hence non-existent as a continuous entity in the germ-plasm of two or more successive generations of organisms. Characters are either present or absent and never latent. Characters morphologically indistinguishable, and present in the same species of organism, may be entirely unrelated when viewed from the standpoint of cause. Such facts have a very important bearing on the numerous morphological studies of evolution which the last half century has brought forth. Many of the morphological studies concerning the origin and relation of various plant and animal groups must be reinvestigated from this standpoint before the final word as to their place in the evolutionary scale can be said, for it is obvious that a plant with a character caused by a combination of a certain protoplasmic material with a certain environment is not necessarily even remotely related to an organism with the same character produced by a different kind of protoplasmic material in a different or perhaps even the same environmental medium.

The character of my material has made possible a tabular presentation of data which will give one an unprejudiced picture of the actual results from a study of the inheritance of fasciation. The meristic nature of this character makes such results a I have obtained more nearly free from the personal element than those involving studies such characters as colors. Further studies of this particular character are in progress[1]).

The major portion of this investigation was carried on under the direction of Prof. E. M. East, to whom much credit is due, for helpful criticism and encouragement. I wish also to express my appreciation for the helpful suggestions and criticisms given me by other members of the biological faculty of Harvard, and to Director J. H. Maiden, of of the Sydney Botanic Gardens for the compilation of data on the occurrence of fasciation in Australia. I have drawn on the papers of several investigators for text illustrations and for these I have given proper credit in connection with the legends.

B. Definition, occurrence and distribution.

Fasciation, as commonly defined, is a flattened, strapped-shaped or ribbon-like expansion of the main axis or axillary organs of a plant; at the base it is generally cylindrical, at the apex, combed (truncate), or diffusely branched in "witch-broom" fashion. Its presence in a plant may alter the arrangement of both foliar and floral leaves, and increase their number. Under classification, detailed information concerning both morphological and physiological aspects of this anomaly are given.

Taxonomically, fasciation is a very widely distributed anomaly, largely confined it would seem to the vascular plants, as I have been unable to find records of typical cases occurring in the lower groups. Hus (1908, p. 83) cites its presence in fungi, but gives no descriptions or references to where such data may be found. More or less typical fasciations have been recorded from 102 of the 290 families into which Engler (1909) divides the living vascular plants. These 102 families are listed in alphabetical order in Table A. According to this table, less than two fifths of the total number of families have contained

---

[1]) The greater part of this study was presented in 1913, in partial fulfillment of the thesis requirement for the degree of doctor of science of the Bussey Institution of Harvard University.

fasciated individuals. In a consideration of the potential ability of all plants to become fasciated, this fact is only negative, and hence largely valueless evidence. Table A is necessarily incomplete. Owing to the scattered nature of the literature on the subject, records which would add other families to the fasciated column probably have been overlooked. One must also remember that many families are small, inconspicuous and limited in their distribution, facts which would often make them inaccessible to observers. From my own studies, I would conclude that there is no evidence for believing that the individuals of any particular family may always be exempt from fasciation, but on the contrary, it would seem reasonable to adopt the view that all vascular plants under the "right" conditions may become fasciated. Sorauer (1906, p. 334) practically holds this opinion, while de Vries (1910; 2, p. 502) believes

Table A. List of plant families from which fasciated individuals have been recorded.

Acanthaceae
Aceraceae
Aizoaceae
Amarantaceae
Amaryllidaceae
Anacardiaceae
Anonaceae
Apocynaceae
Aquifoliaceae
Araceae
Araliaceae
Asclepiadaceae
Berberidaceae
Betulaceae
Bignoniaceae
Borraginaceae
Bromeliaceae
Cactaceae
Campanulaceae
Capparidaceae
Caprifoliaceae
Caryophyllaceae
Casuarinaceae
Celastraceae
Chenopodiaceae
Clethraceae
Combretaceae
Compositae
Convolvulaceae
Cornaceae
Crassulaceae
Cruciferae
Cucurbitaceae
Cyatheaceae
Dioscoreaceae
Dipsacaceae
Droseraceae
Epacridaceae
Equisetaceae
Ericaceae
Euphorbiaceae
Fagaceae
Gentianaceae
Geraniaceae
Gesneraceae
Goodeniaceae
Gramineae
Guttiferae
Haemodoraccae
Halorrhagaceae
Iridaceae
Labiatae
Lauraceae
Leguminosae
Liliaceae
Linaceae
Loranthaceae
Lycopodiaceae
Lythraceae
Malvaceae
Meliaceae
Moraceae
Myrtaceae
Oenotheraceae
Oleaceae
Orchidaceae
Orobanchaceae
Oxalidaceae
Palmae
Papaveraceae
Phytolaccaceae
Pinaceae
Piperaceae
Plantaginaceae
Plumbaginaceae
Polemoniaceae
Polypodiaceae
Polygonaceae
Primulaceae
Ranunculaceae
Resedaceae
Rhamnaceae
Rosaceae
Rutaceae
Salicaceae
Sapindaceae
Sapotaceae
Saxifragaceae
Scrophulariaceae
Simarubaceae
Solanaceae
Sterculiaceae
Tamaricaceae
Taxaceae
Thymelaeaceae
Tiliaceae
Umbelliferae
Ulmaceae
Valerianaceae
Verbenaceae
Violaceae
Vitaceae

the character to be entirely absent from some plant "groups", but present in the individuals of the majority of them in a latent or inactive condition. Moquin-Tandon and Godron (1871—72) state it to be more common in dicotyledons than in monocotyledons, and several present-day students, including de Vries, have expressed the same opinion. Differences exist between the various families, genera and species as to the frequency with which their members become fasciated. According to Masters (1869, p. 20) the anomalous character is especially common in certain species of *Delphinium*, *Cheiranthes*, *Matthiola*, *Brassica*, *Cichorium*, *Campanula*, *Euphorbia*, *Celosia*, *Fraxinus* and *Fritillaria*. Records of its occurrence in the *Oenotheraceae* and *Compositae* are extremely numerous. These data, however, as I hope to show later, are not to be taken as evidence that under the "right"[1] conditions, any one species is more capable of producing fasciations than is any other.

Examples of this anomaly have been recorded from trees, shrubs, vines, and herbaceous plants. In the first two divisions, the branches are most frequently fasciated; in the latter, the main stam is usually altered. Annuals, biennials and perennials are subject to the monstrous condition. De Vries secured the best developed examples in biennials, such as *Crepis* (see Fig. 5), but among annuals, *Celosia cristata*, when cultivated properly, produces magnificent specimens.

Halophytic and hydrophytic environments do not seem favorable to the production of fasciations, as I can find no evidence of such plants in species characteristically growing under these conditions. Xerophytic surroundings do not inhibit the creation of this class of anomaly, as is shown by the frequency of its appearance in the hedge cactus, *Cereus marginatus* (Starr 1899) of the dry Mexican plateau, and in the desert loving genera *Cereus* and *Epiphyllum*.

Celosia cristata does not lose its prominently çombed inflorescence under artificial drouth conditions. *Sedum* is characteristically a xerophytic genus, but a well known fasciated variety of *Sedum cristata* has existed in Europe for two centuries. *Nicotiana tabacum fasciata* still retains its flattened stem when grown in dry, impoverished soil. Fasciated plants may be produced in xerophytic species and persist under such conditions, but an environment of this sort is not favorable

---

[1] "Right" conditions may signify many different sorts of environment, as environment favorable for the production of fasciation in one species may prove altogether unfavorable in the case of other species.

to their maximum development. Among mesophytes, the anomaly is common and in this type of plant attains its greatest degree of expression.

Geographically, fasciation may be said to be known from almost every botanically explored region of the torrid and temperate zones. The largest number of records, as one would expect, refer to examples in old settled countries, but these are by no means the most interesting. *Phyllocladus glauca* often produces fasciated male cones. New Zealand's especially beautiful tree-fern, *Hemitelis smithii* has been recorded as fasciated. A marvellous specimen of *Araucaria cunninghamii* Ait., 79·3 dcm. high, about 18 years old and possessing huge combed-branches is pictured in "Pines of Australia" ([R. T. Baker & H. G. Smith 1909] See Fig. 1).

Frequency of fasciation in wild and cultivated plants compared.

The data on the occurrence of fasciation do not appear to support the commonly accepted notion that teratological variation originate more frequently under artificial conditions than in nature. This anomaly has been recorded many times in wild plants.

According to de Vries (1894, 1906) wild fasciated plants of *Crepis biennis*, *Aster tripolium*, *Geranium molle*, *Taraxacum officinale*, *Oenothera Lamarckiana*, *Raphanus raphanistrum* and *Pedicularis palustris* are common in Holland. Hus (1908) mentions the frequency of fasciation in *Erigeron canadensis.* Often it takes on the character of a disease, and sweeps over a locality, affecting only plants of certain species. Instances of this kind have been recorded in connection with *Rudbeckia hirta*, *Ranunculus bulbosus*, *Taraxacum officinale* and *Lepachys columnaris.* Conrad (1901) in the first case reports the occurrence of fasciated *Rudbeckia* plants by the hundreds in a field near Hainesport, N. J. in 1899. A similar outbreak occurred in *Ranunculus* in a meadow near Haddonfield, N. J. in 1893. Mr. C. T. Brues informs me that several years ago he noticed large numbers of plants of *Lepachys* in the fields around Austin, Texas, were affected. Dandelions *(T. officinale)* are often fasciated, both in wild and man-made environments. Sometimes they are numerous, 20 or more plants being noted by M. Brévière (1881), near the village of Saint-Saulge, France; in other cases, only two or three individuals have been found.

There are only a few of the large number of observations on fasciation in wild plants that might be cited, but they are believed sufficient to indicate the especial frequency of its appearance in nature. A complete list would probably contain examples, in some cases by the dozen, from very nearly all the families listed in Table A.

On the other hand, records of the anomaly in cultivated plants, though more numerous, afford no proof that it *originates* more often in

Fig. 1. Fasciated tree of *Araucaria cunninghamii,* Ait.
(Drawn from a photograph after Baker and Smith.)

domesticated races than in wild forms. This statement is based on the following facts: First, cultivated plants are much more accessible to observation than those in nature, and secondly, when the hereditary form of this variation occurs, it is more likely to be perpetuated, both as a homozygote and heterozygote, than were it subject to natural selection. In view of these facts, the more frequent appearance of the anomaly in cultivated plants may be erroneously credited to repeated origin, when it is only a case of hereditary transmission (see Emerson 1912b).

Among field crops such as sugar beets, corn, peas, sweet potatoes and pine-apples, fasciations are often extremely numerous. These anomalous individuals are commonly found growing beside the normal plants in the same field and under apparently the same environment. Blodgett (1905) reports a case of a field of peas *(Pisum sativum)* where not over 10 per cent of the vines were unfasciated. Conard (1901) finds the sweet potato so commonly fasciated in all parts of the United-States where it is an important crop, that he concludes it to be a hereditary phenomenon. M. T. Cook (1906) mentions a variety of pine-apple ("Smooth cayenne'') which gives over 25 per cent abnormal fruits of a fasciated nature. Other pine-apple varieties such as „Puerto Rico'' also produce fasciated fruits, but not in large numbers. Sugar beet plantations and cornfields both yield a plentiful supply of fasciated material, the former of the stem, the latter of the female inflorescence (ear). I doubt if there is any corn-grower who has not observed these occasional flattened ears in his field. East, Hayes and Emerson have each isolated pure strains of such plants. Recently I have observed fifty or sixty extremely fine examples of fasciation among a couple of hundred hybrid *Rosa Wichuraiana* plants planted along a Boston parkway. Other species of cultivated plants in which the anomaly is common are *Lilium speciosum album corymbiflorum, Evonymus japonica, Rubus* sp., *Tetragona expansa, Helianthus annuus, Cucurbita melo* (all de Vries); *Cotoneaster macrophylla* (Worsdell, 1905); *Prunus* sp. (Maiden, 1913, White, 1912).

C. Classification.

Variation may be viewed from two angles; the strictly morphological, which takes into consideration external form, color, anatomical structure, and other physical features, or the physiological, which involves a study of the conditions necessary to produce the character, its transmission from generation to generation through seed, its vegetative propagation and the factors favorable to its minimum and optimum development.

1. Morphological.

Fasciations, on the basis of changes which they bring about in the external form of the stem, may be divided into linear (the ordinary form), bifurcated, multi-radiate and ring categories.

The first is the commonest type, the second has been observed by de Vries to be a variation of the first, and often associated with it. The third is also a variation of the first, in which the inflorescence or affected structure separates at the apex into three or more short branches. De Vries (M. T. 2: 497—8, 1910) figures this type for *Amaranthus speciosus*. Quadri-radiate fasciations have been found by the same investigator in *Digitalis lutea* and *Celosia cristata*, in the case of the latter on a branched individual. Tri-radiate fasciated heads are common in the *Compositae*.

Ring fasciations are quite distinct morphologically from the other forms and are not very common. Typical cases are found in the hereditary fasciated race of peas. *Pisum sativum umbellatum* and not uncommonly in *Veronica longifolia* and *Taraxacum officinale*. In *Veronica*, according to de Vries, they are less than a centimeter long, while in *Peperomia maculosa* (M. T. 2, p. 496, 1910), they are sometimes a decimeter in length. Typical ring fasciation differs from the ordinary linear form in that the main axis becomes distended into a funnel-shaped structure, with the inner cavity somewhat freely exposed to the atmosphere. De Vries calls these annular fasciations because the vegetative cone is transformed into annular wall. I have observed a case or two comparable to ring fasciations in *Nicotiana*. In *Pisum*, the character is strictly hereditary, my statement being based on the observation of over 300 plants grown in 1912. This type of fasciation appears to be common in legumes, as it is also the form described by Blodgett (1905) for *Pisum*. De Vries is inclined to separate it from the ordinary type because of its morphological and anatomical peculiarities, but Knox (1908) says all the various forms are related to each other, the difference being morphological, not physiological. Possibly the dissimilarities in anatomical structure in some species and genera bring about the distinctive character of the ring type, at least in those species where it occurs as the usual type form as would appear to be true in certain legumes.

According to an earlier, but somewhat more detailed system of classification (Godron 1871—72), fasciations were grouped on the basis of the special part of the plant which they altered. In some fasciated plants, the inflorescence is often entirely inhibited (e. g. *Oenothera biennis L.*), while in others no modification of this structure may take place. In this manner, Godron sorted out six different morphological types. Recent physiological studies on this anomaly have shown, however, that all of these types may occur within the same species or even on the same plant.

In order to understand thoroughly the nature of the changes caused through fasciation, a somewhat detailed description of the monstrous variations produced in the different plant organs is necessary. Those structures which call for special attention are roots, underground stems, main stems, branches, leaves, inflorescence, flowers, fruit, and incidently, seedlings.

Roots. Braun (Worsdell, 1905) described fan-shaped aerial roots in the cactus, *Epiphyllum hookeri.* J. C. Costerus and J. J. Smith, Jr. (1896) mention the same anomaly in *Saccolabium blumei (Orchidaceae).* Other orchids in which anomalous roots have been observed, are *Aërides crispum* and *Phalaenopsis schilleriana* (Gard. Chron. 1874, p. 703) (Fig. 2). In the former, the roots are usually contracted into flattened masses, irregularly plaited, and give rise to contorted ramifications.

Fig. 2. Fasciated potato (Photographed from an drawing in the Gardener's Chronicle).

Underground stems. Fasciations of these structures occur in *Spiraea sorbifolia* (de Vries, M. T. 2, 1910, p. 505), *Solanum tuberosum* (Gard. Chron. 1885, pp. 80—81) and *Oxalis crenata* "Oka" (Hus, 1906). In the latter case the tubers transmitted the character.

Main stem. This is the plant structure most commonly altered by fasciation. The variation in form this takes has been adequately described in the preceding pages and in a former paper (White 1913).

A more detailed account of the linear type as it occurs in *Nicotiana* is given under "materials" in the part devoted to a special study of *Nicotiana tabacum fasciata.* Often the main stem is the only organ altered, and the degree of this alteration in plants of the same pure line¹) may vary from a perfectly normal to an extremely abnormal condition. De Vries states this variability to be true of all of his "eversporting" fasciated races. "Ring" and „linear" are the two main morphological types, but probably "witch-brooms" should also be classed as a form. Very generally (and this is true especially of fasciation in woody plants) the surface of the stem is striated by the prominence of woody fibers (Fig. 3). Fasciated branches or main stems, owing to more rapid growth on one side than on the other, are not infrequently curved, presenting an appearance that may be likened to a shepherd's crook.


(a) (b)

Fig. 3.

(a) Fasciated branch of *Acer rubrum.*

(b) Fasciated stem of *Erigeron canadensis.*

Branches. Branches may remain unfasciated, even though it is expressed in the main axis. In *Pisum* and *Rubus,* both are altered; in *Nicotiana,* egnerally only the latter. In cases representing Godron's fourth class, a small branch may be the only part of the plant affected. Examples of this kind are common in trees and large shrubs.

Leaves. Leaves are usually modified by the presence of fasciation only through their relation to the main axis. Changes in number and position are common, changes in size and shape uncommon. Alterations in number and position are exceedingly irregular in character

---

[1] The term "pure line" as used in this paper refers to the descendants of a single self-fertilized ancestral plant, and does not refer in any way to the degree of homozygosity of this descendant population.

as illustrated by *Nicotiana tabacum fasciata*, in which the phyllotaxy is distorted and the number of leaves in extreme cases is increased from the normal 24 to 160, the fluctuating arc for the fasciated race being from 28 to 160. Occasionally fasciated plants of *Nicotana* produce from the same point on the stem, two leaves, which have the appearance of resulting from a post-genital fusion. J. C. Costerus and J. J. Smith (1896) describe a fasciated plant of *Hymenocallis senegambia* which produced all gradations between single normal leaves, partly fused leaves, and two independent leaves attached to the same point on the main axis. The leaves on fasciated stems may be smaller than those of normal stems, if there has been a very great increase in number. In clovers and other pinnately-leaved plants, the presence of the anomaly may increase the number of pinnae (Kajanus 1912).

Inflorescence. Fasciation may express itself in this organ of the plant by greatly increasing the number of flower-bearing twigs or by suppressing the production of flowers altogether. In the former case, if the twigs (pedicles or peduncles) remain unfused, a "witch-broom" effect is produced, such as occurs in *Erigeron*, *Nicotiana,* and some plumose types of *Celosia cristata.* When the floral twigs are shortened, and the main floral axis is broadened out into a fan-shaped, truncate structure, a "combed" type is produced such as is found in the dwarf races of cockscomb and in *Phyllocladus glauca.* All gradations exist between these two main types of inflorescence. In either type, bifurcated and multi-radiate crowns may occur. Inflorescences have also been observed in which the anomaly expresses itself very slightly, perhaps only in the "apparent" fusion of two or more of the terminal pedicles.

Flowers. Flowers borne upon fasciatad stems are usually, although not necessarily, altered in structure, as is evidenced by the normal floral organs of *Pisum s. umbellatum.* Alterations commonly take the form of a repetition of parts that may extend even to the locules of the anthers, in linear arrangement of parts, and in hypertrophy and atrophy. In the first case (polyphylly) repetitions may occur that include any one or any combination of the four whorls of organs. The lowest whorl (calyx) is most likely to be modified, and the likelihood of alteration of the other three follows in the order of their axial attachment. There is, however, no close correlation between the increase in number of parts in the separate whorls, as far as I was able to observe in *Nicotiana.* The repetition in *Geranium molle fasciatum* de Vries, is said to represent a series of duplication of whorls, the normal flower being 5-parted, the abnormal having approximately 10, 15 and 20 lobes. Such a series is no present in *Nicotiana*, irregularity in number being characteristic of all increases in the number of parts to its whorls.

Alterations in flowers expressed in a linear manner or as a single plane are usually confined to the gynoecium. The other whorls generally retain their normal shape, unless rendered impossible through changes in the form of the gynoecium.

Hypertrophy and atrophy are commonly present. The former expresses itself as an increase in size relations, the latter as abortions of organs. Atrophy associated with fasciation frequently takes the form of abortion of gynoecial and androecial (contabescence of anthers) structures, producing either partial or complete structural and functional sterility.

Fig. 4. Fasciated pineapple fruit with 71 crowns.
(After M. T. Cook.)

Many minor alterations in the character of each whorl may be associated with fasciation. Petalody of sepala (calycanthemy) and stamens, pistillody of stamens, adhesion and cohesion of the different floral organs, synanthy, syncarpy, and dialysis are somewhat common attendant phenomena. One may rightly infer from the preceding account that in the floral organs, the expression of this anomalous character very often reaches its maximum, and produces its greatest alterations.

Fruits. The term "fruits" is used in a general sense and not in its strictly technical meaning. The seed capsules of *Nicotiana t. fasciata* are frequently distorted, hypertrophied and atrophied structures, always having an increased number of locules. Pasciated medlar fruits (Owen 1885) have been recorded which are curved like a ram's horn and possess 40 instead of 5 calyx teeth. Ferhaps the most striking example of the effect of fasciation on fruits, may be found in certain varieties of the pine-apple, *Ananas sativus.* The "pine-apple" of course is a multiple fruit, in reality a mature inflorescence, so that properly, this example should be described as fasciation of the inflorescence. Cook (1906) describes the following variations of the anomalous pine-apple fruits: fruits with 2 separate crowns, with two united crowns, with 3, 4, 5, 6, 7, 8, 13 separate and compound crowns; flattened fanshaped compound fruits enlarged by a more or less continuous series of crowns. A specimen of the latter character, weighing 18 pounds, and containing 71 crowns, was observed (Fig. 4). Conard (1901) mentions the occurrence of large fasciated fruits on the commercial variety of strawberry "Clyde".

Seedlings. Seedlings of fasciated dicotyledonous plants not infrequently posses more than the normal pair of cotyledons, but even in such hereditary races of the anomaly as *Nicotiana tabacum fasciata* and *Celosia cristata,* the great majority of the young plants are normal.

a) Morphological theories.

Two theories regarding the morphological nature of the fasciated organs have been advocated, each by a famous botanist. Moquin-Tandon holds that fasciation is the result of the flattening (enlargement) of a single growing point. Linné, on the other hand, held it to be the result of an increase in number of buds that, owing to their crowded quarters, subsequently fused. A discussion of the arguments for and against each theory is given in Masters' Vegetable Teratology (1869), Masters himself, concludes in favor of the opinion advanced by Linné. Recent investigators on the anatomical structure of fasciations are inclined to agree with Moquin-Tandon, as the internal vascular structure does not appear to uphold the "concrescence theory" of Linné. Compton (1911) on the basis of detailed investigation of ring fasciation in *Pisum s. umbellatum* concludes the anomaly to be the enlargement of a single growing point; although he advances a suggestion which would explain the manner in which the peculiar anatomical features could be produced through the fusion of several normal stems.

Knox (1908) from an investigation of the anatomical features of fasciated *Oenotheras* also concludes in favor of Moquin-Tandon's deduction. She finds no evidence of fusion of stems in the growing region and calls attention to tho fact that ring fasciations may break on the side and develop the linear type. According to this author all types are the result of the enlargement of a single growing point.

Church (1905) and Worsdell (1905) favor a very modified form of the concrescence theory of Linné. Worsdell believes fasciation to be the result of a compromise between two inherent ancestral tendencies, and rarely a case of real mechanical fusion in the Linnean sense. Two opposed forces are operating in the organism, — one inducing integrity, the other producing plurality of parts. Fasciation in higher plants is a reversion to the ancestral branching character of the lower plants, such as lycopods, ferns and algae. In other words, this anomalous character in a morphological sense is a case of the congenital fusion of an unusual number of branches. The reason advanced to account for the fusion in one plane is the ancestral or primitive branching character, — algae, ferns, etc. being said to branch primarily in a single direction[1]). In this sense, Worsdell's hypothesis of congenital fusion and increase in number of parts is a modification of the "concrescence" theory.

The morphological aspect is mainly descriptive and gives but little insight into the real or perhaps more fundamental nature of fasciation. On the other hand, physiological investigation, though increasing the complexity of the problems involved in a study of fasciation, gives at least deeper descriptive knowledge of its nature and the causes which produce it.

2. Physiological.

a) General considerations.

Variations of any kind, from the standpoint of physiology, may be placed for all practical purposes into two main categories, those inherited (germinal) and those uninherited (somatic). This statement

---

[1]) Braun as far back as 1859, advanced a somewhat similar view (see Roy. Soc. Publ., London).

implies that such a classification is very simple, which is very far from the case as the following pages will abundantly testify. Characters, as we have come to use the term, are definite morphological realities. We divide a plant or animal up into parts, more or less arbitrarily, using function, origin, form, or some other criterion as a basis, depending on the special phase of biology in which one is most interested. A horn, a pattern, an organ, become, through continuous familiarity with this thought, absolutely definite entities, entirely separated, in our minds, from the remainder of the organism. In this way, we come to think of the brown eye in man, not as two or more separate character-entities, but as one distinctive character, whereas from the standpoint of genetics, the color and the remainder of the eye must be considered separately. As systematists, it becomes hard for us to adopt the physiologist's or perhaps the chemist's basis of classification, founded as it is upon experimental evidence, the methods and nature of which we find rather strange. We are prone to think of the inheritance of characters as though they were actually handed on from cell generation to cell generation, a conception very foreign to fact, for the character is the combined expression of a bit of protoplasm and a specific environment.

In dividing characters into hereditary and non-hereditary classes, I realize I am adopting an arbitrary classification which represents but a part of the whole truth. But it represents that phase of the question in which I am most interested in a clear manner. As I understand the term, heredity simply implies that a given material under a given specific condition or environment presents certain physical phenomena which we describe as characters. We start with a standard material, and if other material under the same conditions does not present this character phenomena, we hold it to be absent, but if under other conditions it can be induced, we call it an environmental effect, and contend that it is not inherited because under its normal (usual) conditions, the offspring will not reproduce it.

Looking at the character fasciation from this standpoint, it becomes comparatively easy in many cases to distinguish between the inherited and the non-inherited form, but in certain cases, the difficulties of classification are very greatly increased through our general ignorance of the nature of the material and the various combinations of material and environment necessary to produce fasciation. Environmental and hereditary effects are apparently hopelessly mixed.

Take, for example, the investigations of de Vries upon this anomaly, the results of which were partly responsible for his formulation of the conception of "eversporting characters". This investigator defines an eversporting race of plants as one in which the „character" under observation is inherited by all the individual progeny, but only expressed (somatically) in part of the individuals. In other words, some of the progeny possess the character fasciation and some do not. This percentage could be and was increased by selection in a plus direction, but the permanency of the increase was always subject to the caprice of the environment. Even in a homozygous pure line, de Vries looks upon this anomaly as inconstant, although its transmission to all the progeny is said to be perfect. In some of de Vries' cultures, this character was so inconstant that often over half the individuals of one of these races were normal, although the race was held to bre edtrue

Fig. 5. Fasciated rosette of *Crepis biennis*.
(After de Vries.)

to fasciation as far as transmission was concerned, for seeds of self-fertilized normals produced progeny in which the percentage of fasciated individuals was nearly as high as that from seed of self-fertilized abnormal plants. Some fasciated races were poor as regards somatic expression, others were rich, and a race producing few anomalous plants could not be induced by selection to give a higher percentage of them. *Rubia tinctorum* and *Pedicularis palustris* are typical examples of the former, in cultural trials producing the anomaly in very few individuals, even under what appear to be the most favorable environmental conditions (de Vries, 1906, p. 410). These poor races are technically known as half races.

On the other hand, the rich races (eversporting or "middle" races) often gave as high as 50 per cent fasciated progeny.

Crepis biennis (fasciated) is a typical example of the latter and I will recount its history in the Amsterdam garden as it is related by de Vries.

Crepis biennis is commonly fasciated in Holland and de Vries found two such plants growing among hundreds of normal plants in a meadow near Hilversum in 1886 (Fig. 5). From the normals, he collected ripe seed and from this seed grew about 100 plants in 1887—88, 12 per cent of which were fasciated. Seed from fasciated plants of this generation gave 120 plants, of which 40 per cent showed fasciated rosettes the first year. The remainder were destroyed. Of the 40 per cent fasciated individuals, three of the finest fasciated plants were selected and used as seed parents for the next (4th) generation, which gave 30 per cent fasciated plants. The fifth generation gave 24 per cent; the sixth was very rich in the anomaly, although no exact figures are given. The seventh generation produced only 20 per cent fasciated progeny, only rosettes of the first year being counted. The eighth generation was sown on a small scale and no percentage is recorded. The hereditary constitution of this race is said to be fairly constant under normal conditions and the average percentage of fasciated individuals fluctuates between 30 and 40.

Out of 350 plants raised from seed of isolated normal (atavist) individuals of the *Crepis biennis fasciata* race, about 20 per cent were fasciated. Again in 1895, 41 individuals of *Crepis biennis fasciata* were abundantly manured with horn meal. Under these conditions, the number of fasciated individuals rose to 85 per cent, the race under ordinary conditions at this time, producing 20 to 40 per cent. In the manured culture, the plants stood close together, or, says de Vries (M. T. 2: p. 516) "I should probably have succeeded in inducing the anomaly in every one of them."

No sharp limit, according to de Vries can be drawn between the normals (atavists) and the fasciated individuals, and he again uses the *Crepis* race to support his statement. From an isolated group of 3 fasciated plants of this race, seed was saved from the one most abnormal and 150 progeny raised under the most favorable conditions. The following results were obtained:

Stems without fasciation	33
„ slightly fasciated at top	9
„ fasciated along whole length . . .	108
Total	150

or, altogether, about 80 per cent were fasciated. The breadths of the 108 fasciated stems were tabulated by classes and a curve plotted, 0 indicating the group of the 33 normals (atavists). Transitions between normals and fasciated individuals occurred, but are said to have been relatively rare. Two pure types were produced then, as shown by the two peaks of the curve. Practically the same results were secured in all the numerous fasciated races with which de Vries experimented, and even the cockscomb, *Celosia cristata*, belongs to this category of eversporting hereditary varieties, although in its case, "complete atavists are very rare". (M. T. 2: p. 519.) De Vries (see 1906, p. 401, also M. T. 2: pp. 525—526) summarizes his conclusions regarding fasciated eversporting varieties as follows: (Nos. 7 and 8 are a free translation).

1. "Races always consist of fasciated individuals and atavists" (normals).
2. "The proportion of the former varies greatly, often amounting to only 40% or less, but not infrequently to more (*Geranium* and *Crepis* with 65% and 85%; *Celosia cristata*)."
3. "The fasciated individuals are connected by transitional forms, which are, however, rare; and the statistical curves representing them have therefore 2 apices."
4. "These proportions are to a large extent dependent on external conditions of life, which can transform atavists into fasciated plants and vice versa. This transformation obviously takes place during the plastic period in youth, before the character in question is actually developed."

5. "The atavists, as well as the selected individuals, produce fasciated offspring, and often in proportions very little lower than those in which the selected individuals produce them."
6. "Between the broadened specimens and the atavists there is no essential or fundamental difference, in spite of the great difference in their external forms."
7. Fasciation is due to some internal hereditary quality, which though often latent, becomes active in response to external conditions. Its wide distribution causes one to assume that it arose in some common ancestor of the forms which now possess it. Hence, phylogenetically, it must be very old.
8. Poor races and rich races both may be strengthened or weakened by selection and treatment, but the limits between races are never transgressed. A poor race cannot become a rich one through selection. The external conditions being the same, the hereditary factor must be variable.

The de Vriesian conception of eversporting hereditary characters has burdened the science of genetics with an extremely complex interpretation of a set of facts that may be given a much clearer and simpler explanation, and certainly more in accord with the modern strict use of the term heredity. De Vries has urged the need of much more research upon anomalies, and gives his results and conclusions rather as suggestions than unquestionable facts. Further discussion of eversporting races is given at the conclusion of this review.

b) Inherited (germinal) form of fasciation.

Pisum sativum umbellatum Mill., *Celosia cristata, Nicotiana tabacum fasciata,* and some races of *Zea mays* L. are well known examples of hereditary fasciated races. With the exception of *Nicotiana*, nothing is known concerning the manner in which they originated or the genetic character of their immediate parents. Numerous observers vouch for the absolute constancy in the transmission of this character by seed. *Pisum s. umbellatum* is figured in Gerarde's Herball as a separate species. Lynch, (1900) Körnicke and Rimpau have grown this race for a number of years, and all three regard it as perfectly constant in its transmission of the fasciated character. My own observations have led me to adopt the same view. Goebel grew *Celosia cristata*, and found, contrary to de Vries that it was absolutely constant as regards fasciation.

Races which are suspected of being hereditary, but about which little is known genetically, have been from time to time recorded as variants of *Cirsium* (Moq.-Tand.), *Reseda* and *Myosotis* (de Vries), *Curcurbita pepo* (Mazzani and de Vries), *Oxalis crenata* (Kuntze and Hus), *Ipomoea batatas* Poir. (Conard) and *Ananas sativus* Schult. (M. T. Cook).

There is another class of fasciation commonly present in woody and herbaceous plants, which appears to be transmitted asexually. There is no experimental evidence that they are germinal variations, but the fact that the anomaly reappears in every season's renewal of growth, is regarded by some observers as proof that it is a hereditary phenomenon. In *Abies* (Fig. 3) de Vries describes a fasciated condition that reappeared year after year in every season's growth of wood. Hus (1906) gives similar facts regarding a specimen of *Rhus diversiloba.* Repeated annual fasciation is a charactistic of a specimen of *Sophora secundiflora* (Vasey, 1887) described from Texas (Fig. 6). *Rheum moorcroftianum* (Worsdell, 1905) plants at Kew send up a number of fasciated shoots each year. The sweet potato[1]) regarded by Conard as a constant fasciated race, has been propagated entirely asexually and in this manner, the anomalous character is said to have been so widely distributed, that in many areas unfasciated plants are difficult to find. Numerous instances of a similar nature are recorded in connection with other woody and herbaceous plants.

Fig. 6. Fasciation in *Sophora.* (After Vasey. Photographed from a drawing in the Bot. Gazette.)

Unless the situation were considered carefully, one might conclude prematurely that in these plants the anomalous character is reproduced through seed, but no one so far as I know has demonstrated this to

---

[1]) One may consider fasciation in this case a bud sport and account satisfactorily for its wide distribution asexually.

be a fact. On the other hand, there is some circumstantial evidence that certain of these cases may need the services of a pathologist rather than those of a geneticist in order to determine the nature of their ailment. I have no doubt, that in some instances, the presence of fasciation in woody and herbaceous plants is a strictly hereditary character. In other instances, some of which have come directly under my own observation, I believe the anomalous condition to be due to perennial fungi or to bacteria. I have no other proof than circumstantial evidence for this statement, but several perennial fungous diseases of economic importance, such as those resulting from the presence of several species of *Exoascus*, are known to be capable of bringing about marked modifications in the character of the host-plant structures. As a rule, they do not affect every individual plant of a group to the same extent on their first appearance, even though these plants may all belong to the same variety. Often only a few branches show the anomaly, the disease in some years gaining, in others, losing ground. Some species of *Exoascus* produce "witch-brooms", which in the matter of increasing the amount of woody tissue through stimulation, is comparable with what takes place in the production of a fasciated branch.

c) Uninherited (somatic) form of fasciation.

De Vries and others regard heredity as a matter of degree. A single fasciated plant appears in a normal culture of a species, and the next year, seed from this plant produces another large culture with perhaps a single fasciated plant or perhaps three or four present. The per cent is small and cannot be increased by selection. It is designated as a poor race. Rich races produce larger numbers of the anomaly. In order to show that the value of heredity as a conceptional term will be decreased if a sharp line cannot be drawn between non-inheritance and inheritance of characters, it seems to me necessary to emphasize the importance of this point, and I shall go into greater detail here than the subject would otherwise warrant. Somatic fasciations may be classified under several heads on the basis of difference in causal factors, although these factors, from a physiological standpoint, function in producing the character in the same manner. Fasciations may be caused by insects injuring the young embryonic tissue, by mutilation through the agencies of frosts, higher animals and man by abruptly increasing the supply of nutriment, either by checking the plant's ability to use it or by an actual increase, perhaps by fungi and bacteria, and other unkown factors.

Insects. Knox (1908) has shown the moth *Mompha* to be the cause of fasciation in several *Oenothera* species (Fig. 7). Injuries were inflicted

Fig. 7. Fasciated plant of *Oenothera parviflora*. (After Knox in Carneg. Publ.)

on the initial meristem of the growing point and could only be detected microscopically during the earliest growth stages. The greatest number of fasciations were produced under optimum conditions, showing increase of nutriment in an abrupt manner to be the real cause, though this abrupt increase was made possible through crippling the metabolism of the plant by the insect. Knox's investigations are the most extended, but other observations on other plants support her conclusions.

A specimen of *Hieracium vulgatum* with a broad flattened stem was found in relation to a gall of *Aulax hieracii* (de Vries, 1901, p. 291). Below the gall the stem was normal, above, it was fasciated. Hus (1908) figures fasciated specimens of *Erigeron canadensis*, containing larvae of *Cecidomyia erigeroni.* Other specimens contained larvae, and though abnormal, were not fasciated. In all the specimens examined, the fasciated and abnormal modifications began only above the gall-like swellings. Molliard (1900) found coleoptera larvae at the base of fasciations in stems of *Raphanus raphanistrum* L. and lepidopteran larvae occupied the same position in fasciated *Picris hieracioides* individuals. In the former case, a score or so of affected plants were examined and the larvae were present without exception. In the latter example, the relation between the insect and fasciation was not so clear. More recently, the same investigator has shown that a relation exists between the presence of fasciation in *Senecio jacobea* and certain insect larvae inhabiting their roots or the bases of their stems.

Branching palms are not uncommon in India and are classed by F. Scott of the Agri.-Hort. Society of India as of the nature of fasciation. A particular case is given on the authority of Dr. Beaumont (Gard. Chron. 1874), which is unique. This is a specimen of the „common date palm with 22 branches, 18 of which rise vertically, and are so closely packed that it was not possible to give a clear idea of them in the picture". S. Pulney Andy (1869, p. 661), commenting on these branched palms, states that the intelligent native farmers, give insect depredations, particularly beetles which bore into the growing point, as the cause of this condition, especially as found in bifurcated trees of *Cocos nucifera.* Petch (1911) states that the fasciations frequently present in young trees of *Hevea braziliensis* are probably due in some cases, to insect and fungous attacks, although these factors will not account for the presence of the anomaly in every cases.

Fraxinus excelsior and *F. ornus* are often affected with "fasciations" which are sometimes "so abundant that it looks as if the trees had been sown with them", according to Kerner and Oliver (1902, p. 549), These "fasciations" are caused by a gall-mite *Phytoptus*. Judging from my own observations, and from pictures, these are not typical fasciations, such as really occur in ash trees at times. The typical linear fasciation illustrated in Fig. 119 (*Fraxinus excelsior*, see Kidd 1883) may occur in connection with these hypertrophied inflorescences, but as to this I have no information. Cases of fasciation which may be and have been interpreted as the result of insect mutilation are numerous, but definite information is absent from these observations in the majority of cases.

Natural elements, higher animals and man. The examples of traumatic response to injuries from these sources are numerous, but not always accompanied by desirable details. *Cereus marginatus*, under the name of "Organo" is largely used as a hedge plant in Mexico. A hedge of these plants (Starr, 1899), (Hus, 1908, Fig. on p. 86) which were partly injured, probably because cuttings were taken from them for planting, showed numerous fasciations: Krasan (Klebs, 1903—06, p. 134) observed fasciations induced by loss of foliage through the action of June beetles or spring frosts. According to Sorauer (1906, p. 334), a fasciation in *Tecoma radicans* was brought about through appression to a wall, the parts above the wall also showing the anomalous character. Lopriore (Hus 1906) however, did not succeed in producing this condition in *Vicia* roots through prolonged pressure. An asparagus grower (Hus, 1906) in California, claims fasciated shoots of his crop are more common among those plants which first pierce the ground, especially after a cold winter. Fasciations (Hus, 1906) were very frequent in wild and cultivated plants at Berkeley, California, within a week after a heavy rainfall at a most unusual time of the year (September, 1904). Other teratological phenomena were also common. Dandelions from time to time appear on lawns, along sidewalks and in fields in a fasciated state. Hus believes these to be the result of mutilation.

M. T. Cook (Letter, 1912) writes me that Cuban planters believe mutilated pine-apple stock will produce malformations (fasciation included) and that his own observations tended to confirm this belief. Richly nourished, but uninjured individuals of *Weigelia* (Goebel, 1900) sometimes produce fasciated shoots.

Experimental production. Sachs (1859) was one of the first to produce fasciations experimentally. By cutting off the chief axis above the cotyledons in such plants as *Phaseolus multiflorus* and *Vicia faba,* the axillary shoots frequently became fasciated. Double leaves and changes in phyllotaxy appear not infrequently on individuals thus treated. Lopriore (1904), following Sachs' methods, cut off the root tips of seedlings of *Vicia faba* and obtained fasciated roots in a large number of cases. Goebel (**1**: 1900, p. 190) calls attention to the production of "fasciations artificially by causing the 'sap' to flow rapidly and with great intensity into a lateral bud which otherwise would only obtain a small part of it". This is his explanation for the common occurrence of fasciated suckers and stool shoots. An intentional slight injury of the growing tip produced fasciation in *Ibervillea sonorae* (Knox 1907). By crushing young stems of *Viola tricolor,* var. *maxima,* fasciated shoots were produced (Blaringhem, 1904—5). By removing the main stem of *Agrostemma githago* (de Vries M. T. 2, p. 501) just above the cotyledons, the axillary buds, which as a rule do not develop, grew out under this treatment, and frequently became fasciated. Mutilation of the main stem and branches of *Barkhausia taraxacifolia,* induced more or less fasciation in the branches and inflorescences of this plant, according to Lamarlière (1899).

Hus (1906) was able to induce fasciation by the use of the following method: 'Plants, just previous to flowering time were subjected to the environments described below':

> "About the time of the appearance of the first flower, the plant is kept as dry as possible, only enough water being given to prevent wilting. As a result, the flowering period will be comparatively short, and in an indeterminate inflorescence, the buds near the end of the spike remain undeveloped. If at this time, the plants are abundantly irrigated daily, occasionally with manure water, numerous fasciations will make their appearance. But it must be remembered that this result is usually reached only with plants which throughout their existence have been well nourished and well cared for generally. For no apparent reason, one plant will fasciate; while the next one, belonging to the same species, remains normal."

During 1905 fasciations were obtained by this method in *Antirrhinum majus, Actinomeris squarrosa, Solanum lycopersicum "Magnus", Lythrum virgatuma, Oenother Lamarckiana* and *Collomia grandiflora.* Experiments with *Solanum pseudo-capsicum, Capsicum annuum, Solanum nigrum* and *Abutilon avicennae* yielded no fasciations.

Fasciations (perhaps produced in this manner) of *Solanum lycopersicum*, *Antirrhinum majus*, *Echeveria glauca* and others have been propagated by cuttings at the Missouri Botanic Garden (Hus 1908).

Reed (1912) induced fasciations in seedlings of *Phaseolus multiflorus* through the removal of the plumule when it was about an inch long. Shoots were thus caused to develop from the axillary cotyledon buds, and many of them showed fasciation. The removal of the apical buds from these shoots caused still more fasciated and twisted structures to delelop. Through this treatment, the hypocotyl also often became fasciated. *Vicia faba* and *Pisum sativum* under the same treatment as *P. multiflorus* produced only a few slightly fasciated structures.

Epigeal types such a *Phaseolus vulgaris*, *Lupinus douglasii*, *Ricinus communis* and *Cucurbita pepo* have fleshy cotyledons, and hence a large supply of reserve food. When subjected to the same treatment as *P. multiflorus*, no fasciations were produced. Epigeal-type seedlings were given a plentiful supply of nitrogenous manures, and some were mutilated. Although the checks were vigorous in their growth, the mutilated individuals did not produce any fasciated structures.

Daniel (1904) induced fasciation in the common European pear by a method of pruning called "à onglet complet", which consists of removing all the buds, the terminal included, from a branch, and allowing this branch to remain on the tree.

D. Discussion and summary of Parts B and C.

All characters, whether somatic or otherwise, may be regarded as the resulting expressions, in an organism, of stages in the development of a factor (gene, or germinal unit) plus the modifications of this expression brought about through the presence in the organism of other factors, and through the action of external environmental conditions such as soil, climate, insect depredations, etc.

Fasciation, on the basis of this conception of a character, may be caused by many diverse and unrelated combinations of internal factors and external conditions. Hence, to speak of it as latent, when it does not exist as an observable entity, is an absurdity. If one holds to such a vague form of interpreting certain facts, the furniture dealer is justified in speaking of chairs being latent in mahogany trees or of the latency of office desks in oak trees. The fore-going data show us beyond all doubt that many factors, both internal and external, are responsible for fasciation. Mechanical injury, sudden arrest of growth, insect and fungous depredations, injury due to climatic factors (frosts, increased humidity), poor seed associated with richly fertilized soils and intensive cultivation are probably only a very few of these numerous environmental conditions. But the internal factor or factors are just as important as the external ones, as shown by the results obtained in attempting to produce this phenomenon experimentally. All plants, even of the same species or of even closer taxonomic affinity, when subjected to apparently identical environmental conditions do not respond in the same degree or in the same manner. This is amply illustrated by the results obtained by Hus, Reed and others. *Cucurbito pepo* seedlings did not become fasciated with Reed's methods, but fasciated plants of this species are recorded by de Vries. Fasciated races never bred true with de Vries, although he tested out many fasciated individuals belonging to numerous diverse species, by growing large numbers of their progeny. Even the old established horticultural varieties of cockscomb proved to be inconstant in his cultures, as far as the character fasciation was concerned. On the other hand, Goebel found the cockscomb to be absolutely constant in his cultures even when they were grown in sterile sand. Fasciation is also known to be an absolutely constant character in several races of plants, as the hundreds of individuals comprising several generations that have been raised under controlled conditions, testify. Normal strains of these same fasciated races are also common, and in the case of peas, have bred true to absence of fasciation for at least a quarter of a century. Are we to believe that the character fasciation is latent in these normal strains, or are the facts more clearly expressed by looking upon it as absent? From the standpoint of genetics, the latter interpretation is by far the more preferable, because it more clearly expresses the facts in the case, as we know them. There are undoubtedly constant hereditary races of fasciated plants. — races, in which every plant derived from the seed of a self-fertilized fasciated parent, is fasciated, if both parent and progeny are grown under identical environments. There are also constant normal strains of these same species, which breed true to normalness, when all are grown under the same environment as their fasciated relatives. There are still other races of plants in which fasciated individuals are common and the percentage of these abnormals vary greatly as in the case of the *Crepis* with which de Vries experimented. Progeny grown from such fasciated races under the same conditions as the constant normal and constant fasciated races continue to remain inconstant, even though they may all be grown from seed of a single self-fertilized plant. Such races are usually plants which are naturally cross-fertilized and hence may be heterozygous in many internal factors. The segregation of these factors, even in the germ-cells of a single selfed plant, may produce a very diverse progeny. As the development of one factor may be hindered or helped by the presence or the absence of others, one may conclude that part of this eversporting condition is due to the segregation that takes place in each generation. Further, more than one primary factor may be involved in producing fasciation in some races of plants. In attempting to explain the eversporting character of de Vries' fasciated races, one must not forget the prevalence of the various external factors, which especially in an old settled country, are always on hand to commit depredations. When these external factors operate in the form of an insect, they are very hard to trace, as has been shown by Knox and others. My own experience with *Oenotheras* has shown me how hard it is to guard against such factors. I grew 200 seedlings from two very fasciated wild plants of *Oenothera biennis*, which were obtained for me through the kindness of S. M. Blake of the Gray Herbarium. They were grown under conditions generally held to be favorable to the development of fasciation, and on ground only a few rods from which in former years, many fasciated *Oenotheras* had been observed. Of the 200 seedlings only one was fasciated and that only to the extent of a small twig. It is obvious that in this case, fasciation was not hereditary in the sense in which we ordinarily use the term, yet had I previously believed such characters to be inherited in this inconstant manner, I would have never considered the true cause — insect mutilation.

Summary of Parts B and C.

1. The character fasciation is widely distributed in the plant world, both in wild and cultivated plants. Sufficient data have not been collected to prove that it is absent from any taxonomic group.

2. Certain ecological conditions are favorable to its development, but these conditions are not necessarily essential.

3. The character fasciation may occur in almost any part of the plant. Morphologically, it appears to be an enlargement of a single growing point, so that considering the fasciated plant as a whole, the amount of tissue is greatly increased over that of its normal relatives.

4. Very numerous, diverse internal and external factors operate singly or in combination to develop fasciation. If these factors are largely internal, and the race is naturally cleistogamous, the character is generally hereditary and constant. If the factors are largely external (insect depredation, mutilation, etc.) the character fasciation is neither hereditary nor constant. If the fasciated race, to begin with, is not genotypically homozygous, as is not the case when the individuals of a species are naturally cross-fertilized, the character fasciation may be hereditary, but present in only part of the progeny, owing to the segregation of the primary internal factors for fasciation or to the segregation of numerous other internal factors which may modify in some manner the expression of those factors especially concerned in the production of fasciation.

E. Review of previous Mendelian studies.

1. *Pisum sativum umbellatum* Mill. is the only race of fasciated plants which has been fully tested as to the discontinuous nature of its inheritance in crosses with the normal race (Fig. 8). The fasciated character of this plant was one of the original seven Mendelian character-pairs. Mendel (Bateson 1909) found that crosses of fasciated × normal in F_1 gave complete dominance of the normal condition. In F_2 the ratio of abnormal to normal was 3·14 : 1, Bateson and Punnett (Bateson, 1909, p. 25) repeated this experiment, but secured intermediates in F_2.

Fasciated (terminal inflorescences) . . .	207
Normal (axial „) . . .	651
Total	858

Mendel's experiment was again repeated by Lock and later by Darbishire. Lock hesitatingly confirms Mendel's results. The hesitancy is caused by the variation in the fasciated character. Normal × fasciated in F_2 gave Lock (1908) approximately a 3 : 1 ratio, but many of the fasciated F_2 segregates expressed their anomalous character in a much slighter degree than the fasciated grandparent ("Irish Mummy"). Some of this modification in expression was ascribed to crowding and to other unfavorable growth conditions, since the fasciated F_2 segregates "had to compete with thrice their number of normal sister plants, but it did not seem likely that this would account for the whole difference". 'Seeds of very slightly fasciated plants were sown and the resulting F_3's grown under optimum conditions. All the plants thus produced were in every case fully fasciated, almost, if not quite as much as the original grandparent.' The slight variability of the character was therefore ascribed by Lock to environmental influences. F_1 plants grown at the Bussey Institution from seed ("Irish Mummy" × "Chinese Native") furnished by Darbishire, gave absolute dominance of the normal condition.

2. *Zea Mays* L. De Vries, East and Hayes, Emerson and Hus have all experimented with races of maize which produce fasciated ears.

De Vries (1894) finds this character to belong to the "eversporting" class. Cultures that were grown by him contained 40 per cent abnormal plants. Hus and Murdock (1911) secured results similar to those obtained by de Vries.

East and Hayes (1911) found an ear of this fasciated type in a culture of field corn which had been selfed for three generations. The seed was grown and 34 abnormal and 12 normal-eared plants were produced. Another fasciated ear appeared in the F_2 generation of a cross between two normal strains, one of which had been recorded as throwing abnormal-eared plants. This ear produced 62 abnormals: 23 normals. The normals appeared to breed true, and the abnormal condition is regarded by them to be dominant. The character itself fluctuated between very abnormal and (superficially) almost normal states.

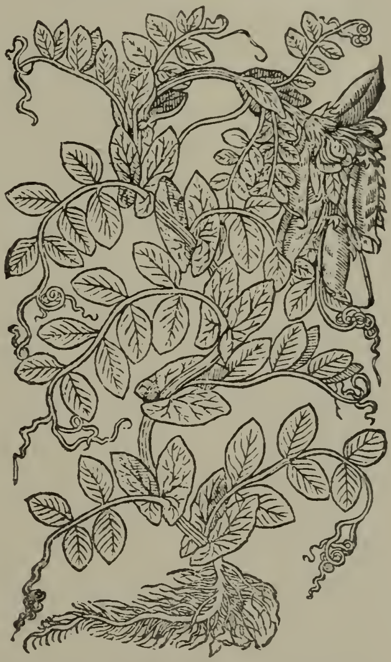

3. *Pisum umbellatum.*
Tufted or Scottish Pease.

Fig. 8. *Pisum sativum umbellatum.* (After Gerarde.)

The most extensive investigations on the inheritance of fasciation in maize have been made by Emerson (1912). In his cultures, the degree of fasciation varies much even between the different ears of a single plant, some ears being very broad-tipped, while others are only

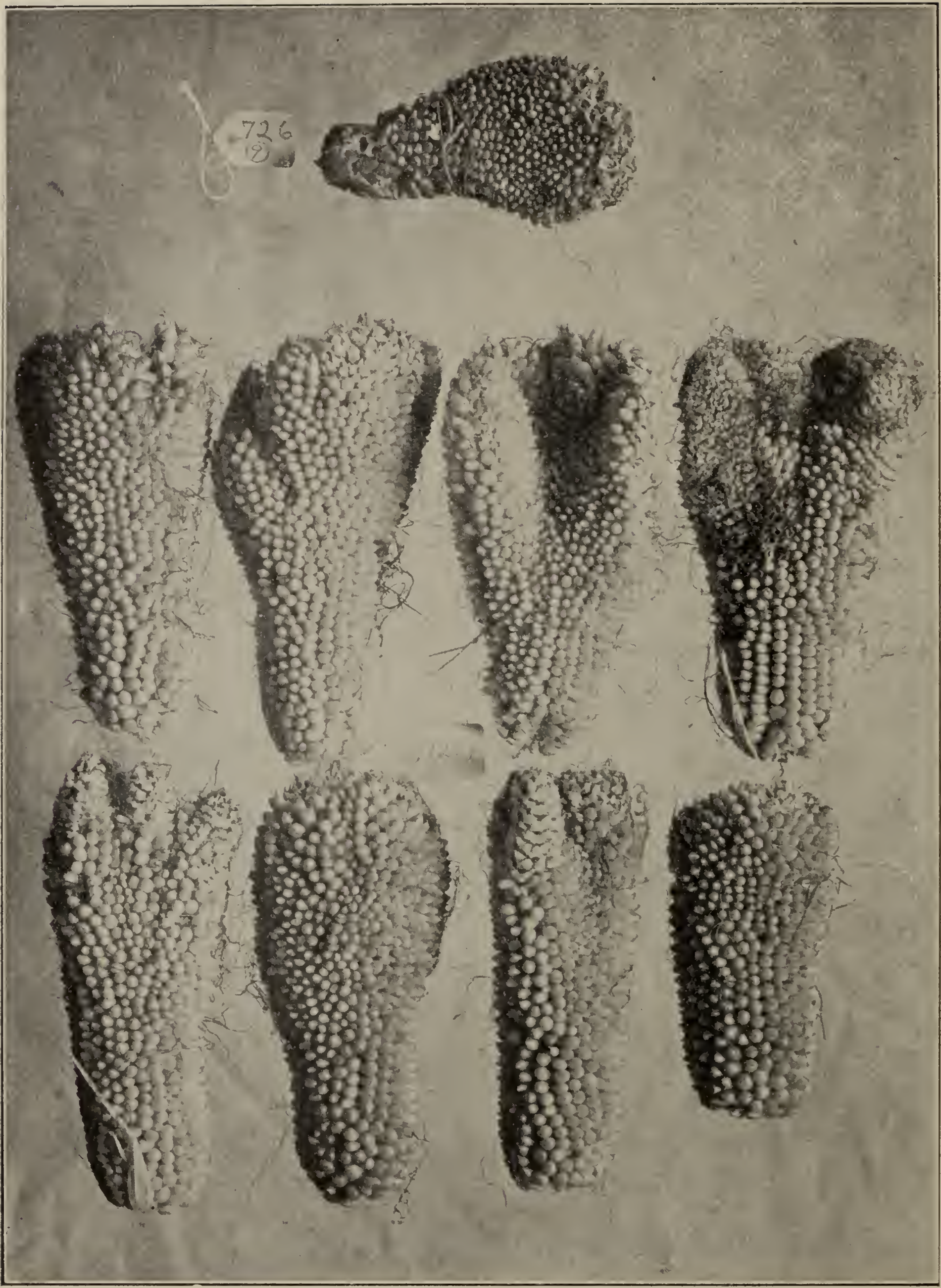


Fig. 9. Fasciation in *Zea mays*, illustrating constancy of the fasciated character in this strain. The horizontal ear is from the parent plant of the plants producing the vertically placed specimens. (Photograph by Emerson.)

slightly flattened. The opinion is expressed that different degrees of fasciation may be inherited.

One of Emerson's corn families shows an extreme type of fasciation, not present in any of the others (Fig. 9). 'From a 1910 family of popcorn that contained both normal and abnormal ears, four fasciated ears were selected and used as parents of 1911 families.' The results obtained were as follows:

		No. of Plants grown	Character of Ears.
1911	Ear 1	18	All strongly fasciated.
	Ear 2	46	All strongly fasciated.
	Ear 3	15	12 more or less fasciated. 3 perfectly normal.
	Ear 4	28	Strongly abnormal, normal and all intergrades making classification impossible.

From one of the first two families, I examined and collected ears, and found very little variation in the expression of the anomalous character. Another family grown from a fasciated ear gave a proportion of 32 plants with more or less fasciated ears, and 35 plants with apparently normal ears, though some of the latter may have been slightly flattened. The parent of the above family was also crossed with an 8-rowed dent corn plant. The F_1 generation contained 63 plants, all producing perfectly normal ears. In other crosses (1912) between fasciated and normal races, the F_1 was also perfectly normal. About 25 per cent fasciated plants occurred in some F_2 families, while in other crosses even less than 25 per cent were fasciated. Emerson believes soil and climatic conditions to have considerable influence on the expression of fasciation in maize. In some strains, he thinks perhaps two Mendelian factors are involved. The suggestion is also made that 'interaction between a single fasciation factor' and the diverse characters present in the different strains, may provide just as good an interpretation for the complexities in the results as the postulation of more than one factor.

F. Special study of fasciation in Nicotiana.

1. Problems.

Chief among the problems involved in this particular study, is the effect of diverse and unrelated genetic factors in their ontogenetic expression upon that of the fasciation factor. Owing to the historical data extant concerning the origin of this fasciated race, one is almost justified in saying that in this particular case, through comparison with its normal parent, and through crossing, an isolation of a factor has been accomplished. If to some, this statement is not justified by the data which is to follow, I feel that at least, I have found ideal material to serve as a standard with which to compare the variation in expression which takes place when this race is crossed with other races, and thus better appreciate the true nature of the phenomena of dominance. Other problems more or less associated with this main problem are: the nature and causes of dominance, the ability of selection to modify a unit factor, the relation between fasciation and environment, the nature of Mendelian segregation when two abnormal hereditary characters are combined through crossing, the appearance of mutations in controlled cultures, and the fidelity with which pure homozygous F_2 segregates breed true in later generations.

It is realized, however, that the data secured on the problems of selection and the modification of unit factors, are too few to be of more than suggestive value.

2. Materials and methods.

The material upon which the study is largely based is a fasciated race of *Nicotiana tabacum*. In connection with the hybridization experiments, cultivated and wild species and varieties of *Nicotiana*, which have been tested in controlled cultures for at least two years were used. These types were obtained by Dr. East from Prof. W. L. Setchell, from Mr. J. S. Dewey, from Prof. A. Splendore and Prof. O. Comes through the kind offices of Mr. D. Fairchild. To all of these gentlemen the writer wishes to express his grateful thanks. *Nicotiana* is an excellent genus on which to conduct investigations, and of the numerous species it contains, *Nicotiana tabacum* is one of the most favorable from a genetic standpoint, because of its large number of distinct subspecies and varieties, the majority of which are practically cleistogamous, hence, yielding races which are at once almost natural pure lines. Varieties and species in this genus in many cases are fertile inter se, and the seed produced by one flower furnishes an abundance of progeny, thus helping to eliminate the arduous technique of making crosses. The species and varieties which were used in this study are described by number.

a) Description of material-species and varieties.

300—309 *Nicotiana tabacum fasciata* (Fig. 10). Mutant derived from "Cuban" variety of *N. tabacum*, J. S. Dewey, 1907. This race was obtained from selfed seed of a mutant found growing in a field of Cuban tobacco in the district of Partidos, near the town of Alquiza, Cuba in 1907. J. S. Dewey, who was connected with the company on whose plantation the discovery was made, describes the original plant as follows: 'Stem fasciated; leaves 152, not over 8 cm. long when dry, flowers abnormal, very little seed produced.' Owing to the cleistogamous nature of *N. tabacum*, the strain from which the mutant arose was probably a natural pure line, the characters of which were largely homozygous. The isolation of pure true-breeding lines ot Cuban tobacco from a mixed population by Hasselbring (1912) seems to substantiate such a claim. And if this be true, hybridization had no part whatever in producing the mutation. As only one fasciated plant occurred in the field, so far as is known, and as this plant was homozygous and bred true upon selfing for the abnormal character, the actual place in ontogeny at which the change from the normal to the abnormal took place must have been shortly after fertilization. If it had occurred later in ontogeny, the fasciated character would have appeared first as a bud-sport. If it had taken place before fertilization as the result of a disruption in one of the cells involved in the maturation of the egg or sperm, a double mutation would have been necessary (i. e., a similar single mutation in both egg and sperm ancestry) in order to account for the homozygous condition of the original mutant. In the latter case, the element of chance is so great, that it is very improbable, even had such mutations occurred, that it would have been possible for them to unite, and had all the germ-cells of a whole plant changed, more than one abnormality should have appeared. One may say, of course, that on its first appearance, it was heterozygous and that the single plant found was a representative of an F_2 or possibly of a backcross. But it is hardly probable in a crop so closely attended and scrutinized as is tobacco, and with so prominent a change in character as the original mutant showed, that additional abnormal plants would have escaped unnoted. The heterozygote (Aa) produces plenty of seed under even

Fig. 10. Fasciated *Nicotiana* plants growing under shade in Connecticut.

unfavorable conditions, so its scarcity would not account for the presence of only one plant. So many mutations are coupled with maturation phenomena at the present time that it seems worth while to call attention to cases that one may feel tolerably certain did not arise as a consequence of reduction or maturation phenomena disturbances.

The morphological differences between the normal Cuban (402) and the mutant (300—309) which constitute the somatic character called fasciation, will be described in detail, beginning with the grosser structures such as stem and inflorescence, and concluding with a description of the changes brought about in the reproductive organs. Special care will be observed in the description of the leaves and floral parts because of the variability in number produced by the presence of this character.

Seedlings. Generally normal; tricotyls rare.

Stem. Cylindrical base, gradually developing the characteristic flat, ribbon-shaped, fasciated condition. Grooved or ribbed by fine vascular strands. Linear width, 1·25—5·5 cm. Some stems more flattened than others. Fasciated part of stem not the same throughout its whole extent. Variable, often slightly curved owing to irregularities of growth. Usually unbranched except for the cluster of small twigs constituting the inflorescence. Pith an ellipse in cross section. Anatomical preparations give no support to the "concrescence" theory.

Leaves. Phyllotaxy very irregular. Double leaves and leaves with broadened apices not uncommon. Great increase in number as compared with normal parent race. Many normal-sized leaves and many smaller than normal (402). Variation in number of leaves correlated with size and character of main axis. Variation in number per plant ranges between 28—152 as taken from records of over 200 plants grown under five different environments and during five seasons. Normal as regards form. (See Table 2.)

Inflorescence. Bifurcate, multiradiate, rarely "annular" or funnel-shaped, often single main axis, abruptly terminated by a number of small twigs. Flower-bearing twigs small, densely clustered into 'witch-broom'-like bunches or irregularly distributed along the sides and apex of the stem.

The floral structures were deformed in a large number of ways, the most prominent being the increase in number of parts to each whorl per flower. This numerical increase is not of a constant nature, in the sense of a variation from one definite number to another, a statement also true of the change in phyllotaxy and leaf number. Nor does it at all substantiate de Vries' notion of a duplication in number such as is said to occur in *Geranium molle fasciatum.* In a figurative way, one may compare the variability of *Nicotiana tabacum fasciata* to that of an arc made by a pendulum, provided there was a force behind the device to change the rate of its swing and the size of its arc when affected by things external to itself. Tables 3 and 4 give a better idea than mere description, of the extent and nature of this variability, the former as regards the variability of the race and the latter as regards the range per individual plant. By inspection of Table 3, the average number of parts per whorl of a flower is seen to show a progressive increase in the expression of the fasciation factor. This may be expressed in tabular form by subtracting the normal number of parts per whorl (5 for the first three and 2 for the gynoecium) from the average for the number of parts per abnormal flower. In order to compare the first three whorls with the gynoecium, their differences should be divided by 2·5* as there are 2·5 times as many petals, sepals and stamens to a flower as ovary-locules. The results for families 301—1 and 303—1 are thus:

Table C.

	301—1 Average No. of floral parts above normal	*	303—1 Average No. of floral parts above normal	*
Sepals	1·74 +	0·69 +	2·03 +	0·80 +
Petals	2·65 +	1·06 +	3·24 +	1·29 +
Stamens . . .	2·70 +	1·08 +	3·47 +	1·39 +
O.-locules . .	1·93 +	1·93 +	2·86 +	2·86 +

The calyx is thus seen to be the least, and the gynoecium the most affected. The latter is almost three times as abnormal as the former in 301—1, and more than three times in the case of 303—1. This progression in the manifestation of abnormal condition is in accordance with the observations on other parts of the plant. The seedlings appear to be normal; the first few leaves are not deranged as to phyllotaxy, and the whole stem remains normal, even in the most fasciated specimens for a foot above ground. The linear expansion increases in extent and the leaves in number as the plant approaches maturity. At maturity, the apex of the stem shows the greatest linear expansion, and sometimes becomes so abnormal that the whole inflorescence is partially inhibited in its development. The greatest alteration in phyllotaxy and the largest increase in number of leaves is characteristic of this terminal portion of the main axis. Owing to the fluctuation in expression of the factor, the stem may not always show the linear expansion throughout its whole length, but in all cases it shows in the inflorescence.

In addition to the increase in number of parts, the floral structures are subject to many minor abnormalities. The first flowers to bloom on a plant are much more abnormal than those appearing later. Because of this, all data on the abnormal flowers of a family have been taken as nearly as possible at the time when all the plants were approximately in the same blooming stage. These early flowers were often so split (dialysis) and deformed as to lose all semblance of belonging to any regular-flowered family such as the *Solanaceae*. The later flowers, though generally possessing as many floral leaves as the earlier ones, were usually as symmetrical as those of the normal 402 (Fig. 11).

a b

Fig. 11.
a *Nicotiana* 300—309 (fasciated).
b *Nicotiana* 402 (normal).

A detailed study of the various whorls disclosed many more anomalous characters. The calyx, in addition to being irregular, sometimes possessed a sepal attached to the outside of the regular whorl (Fig. 12). Sepal lobes were irregular in size, and occasionally one would occur with a slight reddish color on the tip (calycanthemy). Calyx and corolla whorls not uncommonly were present as one spiral whorl („speiranthie"). Two flowers were sometimes fused and enclosed in a continuous calyx (adhesion). Once or twice, a flower was found consisting of only a corolla and a few stamens, growing on the side of and fused with the main corolla (synanthy). Instead of an increase in flower parts through a multiplication of whorls (pleiotaxy) the increase takes place through a multiplication of the number of parts per whorl (polyphylly). All four whorls are increased in the number of their parts in this manner. Polyphylly of the androecium increases the number of stamens per single flower, the range of variability being 4—25. Filaments are fused to each other (cohesion) and to the walls of the corolla (adhesion). The anther-sacs are sometimes split at the end into

Fig. 12. Stems and flowers of the fasciated (300—309) and normal (402) races of *N. tabacum.*

two segments; in other cases an actual increase in number occurs and a single stamen may have as high as six. Petalody and pistillody of the stamens are rarely present. In the former case, the petals are very slightly developed; in the latter, three or four rudimentary pistils occur, developing from almost any point on the anther-sac. In an examination of thousands of flowers of this race, I have found petalody, pistillody and calycanthemy only in a dozen or so cases. Abortion of pollen (contabescence) is common as well as various distorted conditions of the anthers.

The pistil frequently was wholly or partly incapable of functioning, owing to various forms of distortion, including proliferation, staminody, pleiotaxy, and meiophylly of the style and ovary-locules. The increase in number of locules ranged between 2 (rarely) and 21, the mode being about 4. The style was often shortened and twisted. Ovary-locules were so crowded at times, owing to polyphylly that many were abortive, resulting in a much distorted capsule. From 2—4 pistils (pleiotaxy) were often present in the same flower, sometimes all capable of functioning; in other cases, all but one abortive. Sterility was present, but in the majority of cases, examination of a mature capsule demonstrated fertility to be almost perfect.

Cytology. In a preliminary paper, the normal conditions were briefly described for both this abnormal strain and the normal (402). The chromosome number was 48, reduced in the germ-cells to 24. Cytological variations in the normal (402) were rare, either as to chromosomes and their number or in other structures. Many anthers of the abnormal race when examined cytologically were entirely normal in all their maturation phases. Others showed evidences of almost total sterility through premature breaking down of the archesporial tissue, while still others were only partially sterile. Abnormal variation in the rate of progress of maturation stages was often characteristic of the abnormal anthers. Atrophy and disintegration following physiological abnormalities causes the not infrequent appearance of only a very few mature pollen grains in the mature anther. This breaking down of the pollen mother-cells began in the early prophases of the first division, and persisted as late as the prophases in the second division. Abnormalities were not as common in the second reduction division as in the first. Deformed nuclei were common in the first maturation division. The nucleoli and chromatin were not infrequently clumped together as though overheating on the slide had taken place. Nuclear fragmentation was common. Great variation in the staining properties of the preparation was noticeable, this probably resulting from physiological abnormalities. The chromosomes of a mother-cell were either increased in number by abnormal division or nuclei divided and never separated. In one case 51 chromosomes were counted in a reduction phase, and from the manner of their occurrence, it would seem there was no other interpretation than of increase in number through a division of only part of the chromosomes of this cell. The cell was in a state of disintegration. Other cases occurred in which there were 30 where only 24 should have been counted. Irregular divisions and lagging chromosomes were not infrequent. The chromosomes of *Nicotiana* are small, though very distinct in the maturation stages, but in cases where abnormal conditions prevailed, one could not always be certain they were counting heterotypic or homotypic chromosomes or both, owing to premature division of some of the heterotypic chromosomes. Increases in number were rare, but many of the other abnormalities mentioned were common. Supernumerary pollen grains such as occur in *Hemerocallis* were never found. Divisions of chromosomes in somatic cells on account of their size, were studied with difficulty, and gave no data. Cytological observations on maturation in the gynoecium were only superficial as compared with those of the anthers. No special abnormalities in the reduction divisions were noted in the few sections examined, but a small percentage of the embryo-sacs appeared to be abortive.

From data taken in connection with the floral leaf counts, I should judge the contabescent anthers to be from 4—5 per cent, but such data probably gives too low an estimate, because one cannot be always certain that an anther, externally normal, represents the same internal state.

Summarizing, one may say that although these abnormal cellular conditions are strictly inherited, their morphological aspects closely resemble the cytological changes produced in plants through external stimuli, such as fungi, insects and chemicals, after the manner in which these have been described by Molliard (1897), and others. Gregory (1905) described similar phenomena in the case of the abortive anthers of sweet peas, though in this case as in *Nicotiana*, the phenomenon was of strictly hereditary nature.

Fasciation in *Nicotiana* is comparatively rare, as somewhat extensive search through the literature brought to light only a few cases of floral fasciation in *Nicotiana affinis (alata)* (de Vries).

The relation of this race to different environmental conditions and the nature of the variability in expression of the fasciation factor will be further discussed under "selection and environment".

402. *Nicotiana tabacum* L., var. "Cuban" (Fig. 13). (13—29 U. S. Dept. of Agr.) Grown in controlled cultures for at least three years. Remarkably constant in all its characters. As contrasted with 300—309, it is normal in all the organs altered in that race by the fasciated character. A possible exception to this generality is found in the rare occurrence of an extra sepal or petal. Stem cylindrical, number of leaves per plant 18—24 with mode of 20, ave. 19·65, based on counts made by East and Hayes on 124 plants grown at Bloomfield, Conn. in 1911; inflorescence branched, flowers pink, three whorls 5-lobed, gynoecium 2-loculed. Number of parts to androecium and gynoecium practically constant. Plants in our cultures, uniform in height and other gross morphological features. Same variety as that from which

Fig. 13. Enlarged view of the inflorescences of *Nicotiana tabacum*, races 300—309, 402. (Photographs from F_2 segregates of 304 × 402.)

300—309 was derived, but obtained from a different source. Maturation phenomena in the anthers normal. No contabescence.

353. *N. tabacum,* var. *fruticosa* Hook. fil. U. S. Dept. of Agriculture, 1908. Orig. from Portici, Italy. General description given in Comes' Mon. (1899, p. 8) Sp. 1, var. 1. Comes' var. *fruticosa* not that of Hook. fil., according to Setchell (1912). Inbred for three years, constant for characters noted in crossing experiments. Low, shrubby, profusely branched plants, height ave. (1912) from 9 plants, 14·55 + dcm. Lvs. petioled, non-auriculate, leaf count made on main axis from 9 individuals (1912), ave. 12·33 + leaves per plant. Range in variation 10—14, but method was very unsatisfactory and results are only approximate. Flowers normal, occasionally 6-sepaled or 6-petaled, 100 flowers examined (1912) were all perfectly normal, slightly darker pink than 300—309, deeply lobed corolla, petals acuminate, slender throat and tube. Sepals long, acute, and reflexed at tips.

373. *N. tabacum*, var. *havanensis*, (Lag.) Comes' Mon. (p. 16), angustifoliae, vern. Loemodjang. Comes' 1908 (See S. & P. Int. Inv. No. 14, p. 40) U. S. Dept. of Agr. 22164. When first grown, variable in leaf and flower characters. Selected by East for constancy in corolla shape and leaf characters. Race from selfed seed, constant for two years in characters here noted. Hght. 17·54—19·06 dcm., ave. 18·3 dcm. in 1912. Unbranched main axis, lvs. in number 18—21, ave. (1912) 19·33 +, auriculate, sessile; inflorescence spreading, flowers dark red, inflated throat, corolla pentagonal, varying toward subrotund lobing, normal as to number of parts, no 6-sepaled or 6-petaled flowers being noted. Fertile. See Comes' Mon. (p. 16) for general description.

396. *N. tabacum*, var. *fruticosa hybridae, fruticosa* × *macrophylla purpurea.* Hort. *N. calyciflora* Caille. Comes' Mon. (p. 10). From Portici, Italy. Same as *Nicotiana tabacum* var. *calycina* of Setchell (1912, p. 6) (Fig. 14). Race from inbred seed, constant for two years or more, except in characters noted as otherwise (See Setchell on constancy of this variety). Low, shrubby, profusely branched, 353-type of plant. Hght. constant in inbred stock, except for the appearance of a single nana plant in 1912. Ave. hght. from 24 (396—1) individuals, 13·84 + dcm. Lvs. sessile, auriculate, ave. no. per plant 11, with range of 9—12 [count includes 24 plants determined from observations on main axis (unsatisfactory)]. Inflorescence normal; flowers reddish pink, subject to splitting of corolla tube and other morphological irregularities. Sepals, petals and stamens fluctuate between 5 and 6 per flower. Filaments not infrequently fused to corolla tube (adhesion). Three or four of the sepals are always roseate colored in whole or in part (calycanthemy). This character is variable and the anomalous sepals usually are longer than the non-colored. The peculiar crinkled effect shown in Fig. 6 is also characteristic and constant when even the calycanthemy does not appear. Gynoecium normal. Fertility 100 per cent, and especially noticeable. Corolla is usually irregular. The constancy of the anomalous character is perhaps better shown in Table 5. Table 5 gives an individual record of 25 flowers of plant 396—1 (1911), together with six of its progeny grown from inbred seed. 24 other 396—1 progeny were grown in the same row and their range of variability was approximately the same as the six plants on which the table is based. Masters (p. 384—85) says teratological coloration of sepals is especially common in gamosepalous flowers and cites numerous cases.

Calycanthemy usually means simply a change in color, but may not infrequently be accompanied by structural changes, and this is said to be especially true in cases where displacement of organs has occurred. In the 396, as grown in our cultures, structural changes were always present in some form and degree. Splitting of the corolla tube and the formation of and adherence of an extra petal were especially common. Coloration in at least one sepal and usually three was characteristic. The dwarf (mutant?) mentioned differed from the race only in height, not in number of leaves nor in type of flowers.

Fig. 14. *N. calyciflora*, Caille. Note the calycanthemous sepals.

Other Species.

324. *N. bigelovii* Watson. U. C. Bot. Garden 1909. Answers to Comes' (p. 43) description, except in floral characters. Sepals, petals and stamens vary between 5 and 7, per flower, 6 being very common. The race breeds nearly true to a 3-loculed ovary. Sp. 25. (See Setchell 1912, p. 25).

327. *N. glutinosa* L. U. C. Bot. Garden 1909, Comes' Mon. (p. 24) Sp. 3. Constant from selfed seed for 3 years.

331. *N. paniculata* L. U. C. Bot. Garden 1909, Comes' Mon. (p. 25), Sp. 4. Constant from selfed seed for 3 years.

332. *N. sylvestris* Speg. et nob. (Nova. sp.) U. C. Bot. Garden 1909. Comes' Mon. (pp. 34—35). Sp. 19. Constant.

b) Number of plants grown.

This investigation of the inheritance of fasciation in species of *Nicotiana* is based on data from studies of about 5,000 plants, grown over a period of five years, and under several distinct physiological and geographical environments. A nearly complete list of the different species, races, families and hybrids, together with the exact number of each grown, the year and the environment are given in Table 1.

c) Methods.

All plants used in these experiments were grown as nearly as practicable under the same external environmental conditions. Plants for comparative study were often grown side by side. After each operation in making crosses, all instruments were carefully cleansed in 95 per cent alcohol. Pollen was used only from unopened flowers. The technical work was always personally looked after. The methods used in the cytological phase of this investigation are described in an earlier paper (White 1913).

Tabulation. Data were collected on each plant and tabulated separately. The character on which most of the studies were made were: — extent of fasciation in the main axis, number of leaves per plant, number of floral parts per whorl. 25 flowers from each plant were taken and the number of parts per whorl for each flower was recorded separately, and in such a manner that all the whorls per single flower remained identifiable and their correlation could be shown. Minor abnormalities of all kinds, such as calycanthemy, pistillody of the stamen, united filaments (cohesion), abnormally distorted anthers, petalody of the stamen, deformed styles and stigmas, cohesion or fission in leaves, were recorded for each flower and plant. In presenting in tabular form, the mass of data thus accumulated, two types of frequency tables are used, each of which shows the variability of the fasciated character expressed in terms of numerical-plant-organ alterations, as for example, one flower may have 8 sepals, 10 petals, 12 stamens, and

5 ovary-locules, while another may be altered from the normal 402 condition by having 10 sepals, 10 petals, 12 stamens and 4 ovary-locules.

One type, such as Table 4, gives the frequency distribution of floral parts (sepals, petals, stamens, etc.) per flower, and shows the fluctuation of the character fasciation per plant in a whole family. The second type of table such as No. 3 disregards the individual plant entirely, and gives the frequency distribution of the number of parts per flower and leaves per plant for the family as a whole. The first type is especially useful in comparing the individual inconstancy of the character in two different races. The second is only valuable as a basis for the comparison of the average variation of different races. In order to show the variation in the organs of a single plant, when affected by fasciation, tables of records of typical individuals have been used (See White 1913, pp. 212—13). The race 402 is at all times accepted as the normal, and a basis for comparison as to what constitutes an abnormal *Nicotiana tabacum* deviation.

3. Fasciation and Environment.

In order to study accurately the manner of the inheritance of a "somatic" character, it is first necessary to thoroughly understand its reaction toward its particular environment, and this is especially true of such a character as fasciation, as has been repeatedly emphasized by de Vries, Knight (1822) and a host of seedsmen and florists. De Vries found the influence of conditions surrounding the parent seed plant to be a factor that must always be taken into consideration in studying anomalies. In his work, plump seeds gave the plant a better start in life and as nutriment and good care are very essential to producing large fasciations, such seeds, he says, should be selected. Seed from branches favorably situated should produce more anomalies than seed from 'poorer' flowers and weaker branches (considering the latter to be atavistic or more normal structures), but in his experimental work, this expectation bore but little fruit.

De Vries has very often called attention to the relation between plant vigor and the production of anomalous variations, — "the stronger a branch is, the more liable it is to flatten out". Biennials and perennials when allowed to fasciate the first year gave but very small expressions, and in some cases, a heritable race would show no sign of its fasciated character. On the other hand, high percentages of individuals with beautiful comb-like expansions were secured the second year. Time of sowing, according to de Vries (1909—10), (M. T. 2, p. 498) is also a factor in the production of fasciated individuals. In Holland, sowings of *Crepis* in April and May gave 30—40 per cent fasciations, sowings at the end of July 20 per cent, and those made in September, none at all. The same results were obtained with *Taraxacum officinale.* Apparently early sowing gives the plant time to make a strong rosette before winter stops growth. Crowding, pruning, and nutrition are important factors. Crowding is said to lessen the percentage of fasciated individuals, and increase the atavists in a hereditary race. Pruning diverts the sap rapidly into lateral branches, and this, according to de Vries and Goebel, arouses the latent character to somatic expression. Nutriment is very important as evidenced by the remarks on crowding, selection of seeds, etc. For the reason that fasciated branches are often somewhat weakened by growth expansion, de Vries thinks atavistic (normal) branches may perhaps produce the best seed for continuing the race. By the same method of reasoning, absence of fasciated branches on a fasciated main stem, which is very common, are explained. Briefly then, in order to favor the expression of such characters as fasciation, even though the character is said to be strictly hereditary in a race, it is necessary, according to de Vries, to take into consideration, environment of seed parents, character of seed (weight, plumpness, etc.), climatic conditions, time of sowing, crowding, pruning, and other methods of diverting sap or increasing the food supply abruptly, and nutriment (soil, water, fertilizer, etc.).

Growing in sterile sand decreases, while richly manured soil increases the percentage of fasciations in a hereditary race, and the finest specimens are produced by pot culture, rich soil and subsequent transplantation (de Vries, 1899, M. T. 2, p. 501).

Nicotiana tabacum fasciata furnishes especially favorable material on which to test out some of these ideas and throw further light on the interpretation of the facts, for in this race, there are so many structures on which reaction-phenomena can be noted. The experimental cultures of this race have nearly always been grown beside the normal 402 race, and it is understood that both races (300—309 and 402) under all the environments tested, constantly show the differences noted in the preceding descriptions.

Commercial growers of tobacco fan their seed, sowing only the heaviest. In my work, unselected seed was planted in seed pans, containing moderately rich soil. Often these pans were crowded with young plants, but they did not remain in such quarters long enough to become stunted. In pricking out plants, naturally and unconsciously, the best seedlings were selected, though this was not always the case, especially when seed was scarce. Variation between the plants became greatest after they had been pricked off into flats, and when final transplantation time arrived, there were some more or less stunted individuals, but all were usually planted. The normals (402) were always subjected (in my own work) to the same treatment as the fasciated race. Plants were grown in a variety of environments, and in order to show the constancy of the race under these environments, Table 2 was constructed. The number of leaves per plant is extremely variable, as evidenced repeatedly in a leaf count of the progeny of a single selfed plant, when all had been grown under the same conditions. 124 plants from selfed seed of a single 402 plant, grown under shade in Connecticut in 1911, gave an average of 19·65 leaves per plant, with a range of variability between 14 and 24, and a mode of 20. In 1908, under about the same conditions, 99 plants from selfed seed of the original mutant were grown, and leaf counts made by J. S. Dewey, gave an average of 69·7 leaves per individual, with a range of variability between 30 and 133 and a mode of 57. Included in Table 3 are abnormal segregates, but these as far as I can judge, are indistinguishable from the pure abnormal race. The range of variability in the number of leaves in different years is well shown in Table 2. 301—309 consisted of 148 progeny grown at Bloomfield, Conn., from selfed seed of nine of Dewey's 1908 plants. 301—1 and 303—1 were selections from the 1909 cultures, the progeny of which were grown under field conditions at the Bussey Institution in 1910. X is the progeny of a single selfed plant of Dewey sport (genealogy lost) grown in the Bussey greenhouse, the winter of 1909—1910. The 1911 selections were all grown under the same environment at the Bussey Institution. The same is true of the 1912 cultures, except that the five 301—1 plants were neglected before transplantation, and given poor soil in field cultures. These data are subject to the criticism that in a study of environmental effect on plants, seed from the same, instead of from different plants, should be used. But this criticism is probably invalid here, because the fasciated race is a pure line upon which selection (White, 1913) seems to have no effect. So for purposes of comparison, seeds of different individuals of a pure line have the same value whether from the same plant or generation or different plants in different generations. The tent-grown plants in Connecticut had a higher average number of leaves than the plants of the 1910 culture at the Bussey Institution. 1911 was an especially favorable year for fasciations. After transplantations in June, a drouth ensued through which the plants barely lived. July followed with much rain and excessive heat. 1912 was a fair year for field cultures. A June drouth was followed by rain in July, but the change was not so abrupt nor so extreme as in 1911.

From the table. it is apparent that this race shows very decided variation in the number of leaves in the different families, and if I am correct in considering the variability as not due to a mixed population, the only other alternative is to admit the effect of environment. And yet environment does not affect the expression of this character in *Nicotiana* to the degree claimed by de Vries for his fasciated races. In all my field cultures and those reported by Mr. Dewey and Dr. East (aggregating 694 plants grown over a period of five years in four distinct environments) the fasciated character has bred very true in the sense that its somatic expression always showed to some extent in the stem, in leaf number, in the character of the inflorescence and the floral organs, and that this development never fluctuated toward the normal sufficiently to make classification even remotely questionable. No so-called atavists have appeared at any time.

Another experiment was inaugurated in the winter of 1912 to test further the constancy of the fasciated character under different environments. Cultures of normal and abnormal plants were started in February by sowing seed of these strains in ordinary sterilized soil. Germination was excellent, and the young plants were kept in their seed quarters for about four months. No additional food was supplied them, and a struggle for existence ensued. As a consequence, the survivors do not represent more than one tenth of each original "pot" society. From these 5·08 and 10·16 cm. pots (orig. seed quarters) the survivors were removed, with all of their soil, to 15·2 cm. pots and fed once a week with a solution made up as follows:

2 pt. superphosphate
1 pt. sulphate of ammonia
1 pt. potash
1 teaspoonful to 7·57 litres of water.

Table D.

Effect of environment on the expression of the factor A.

Designation	Survivors	Somatic Appearance	Hght. in dcm.	No. of leaves	Flowers	Remarks
301—1—8	18	Abnormal	7·63—9·2	42—51	Abnormal	[1]) One plant with no fasciation.
301—1—32	13	„	7·63—9·2	62—77	„	One plant with extreme fasciation.
303—1—13	16	„	—	1 plant, 80	„	Stems characteristically flat.
402—1	9	Normal	4 plants, 9·2	20—22	Normal	
(304 × 402)—1—28	10	„	3·05—9·2	17—22	„	
(304 × 402)—1—8	14	Abnormal	3 plants, 9·2	76—80	Abnormal	Stems all fasciated.
(304 × 402)—1—31	18	Normal	5 plants, 9·2	19—	Normal	
Total	98					

When the text photographs were taken (Fig. 15), the plants were 6 months old, having passed 2 months in the 15·2 cm. pots. In the course of these two months many died, and the remainder had bloomed and matured seed. Many of their leaves were yellow and the bottom four to seven leaves had fallen. Table D gives their pedigree, the number of survivors to each pot, their height and character. The flowers were as large and as unaffected as though the cultures had been given the best care. The normal flowers were in all respects similar to those of field-grown plants. The leaves were reduced to a fourth of their normal area, but as shown by the table, their number remained unchanged. The main plant stems were very small, but flattening was as characteristically expressed, though in 'baby-ribbon' dimensions, as that of field plants.

While other characters such as leaf size and plant size are modified in expression by adverse conditions this does not seem to be true of fasciation as it appears in *Nicotiana*, except through its relation to other characters, such as size of stem. Not one single individual of the whole 61 surviving abnormals but what could very easily be

---

[1]) Stem so small in diameter that inflorescence fasciation would be difficult to determine through casual observation.

distinguished from the normals grown under the same conditions. So far as this race is concerned "atavists" in the de Vriesian sense do not exist. And when abnormals and normals are grown under certain specific identical environments, my experience gives me reason to believe there will always be the same decided features by which to distinguish them.

Fig. 15.

4. Fasciations and selection.

In a former paper (White, 1913) the statement was made that the fasciated character of the 300—309 race did not seem any more amenable to selection than the race of cockscombs with which de Vries worked. In other words, from two generations of selection for normalness, no effect seemed to be apparent, so the attempt for the time, was given up. The exact data on which this conclusion rests were by no means conclusive. The results obtained were clearly enough interpreted, but the experiment was not of long enough duration, nor detailed enough to furnish any but indicative data. In 1909, East selected one of the most abnormal and one of the least abnormal plants of the *fasciata* race cultures grown at Bloomfield to be selfed. 301—1 is the pedigree number of the least abnormal, and that of the most abnormal plant is 303—1. Both the parents were shade-grown plants raised by Dewey. The parent of 301—1 had 64 leaves, that of 303—1, 133 leaves. East took no definite data on the number of leaves of 301—1 and 303—1, but remarks in notes that 303 was the most abnormal of all the eight families grown in 1909. The leaf count varied between 40 and 100. The plant selected as 303—1 was one of the most abnormal of its family. Plants from selfed seed of these two strains were grown in 1910 side by side at the Bussey Institution. Table 4 shows the individual variation of each plant in the number of its floral parts while Table 2 gives this same information for the number of leaves. Table 3 is a summation table showing the frequency distribution in number of flower parts per flower for the race. Adding together the total number of flower parts of all the flowers from all the plants of each race examined, and dividing this sum by the total number of flowers examined a constant is obtained by which to more accurately compare the difference between the two races (301—1 and 303—1). Thirty three 301—1 plants with a total of 825 flowers, gave a constant of 6·509+, while 303—1 with a total of 850 flowers from 34 plants, gave 7·152+, the difference in abnormalness being 0·643+ in favor of the 303—1 race. This difference in abnormalness is apparent in the averages calculated for all the flower parts, and is also true of the stem-flattening and the number of leaves. The average number of leaves per plant for 32 of these same 301—1 plants is 34·18+, while that for 36 (303—1) plants is 45·52+ leaves per plant. Table 4 gives the range of variation in flower parts per flower for each plant of the two races. The range in individual plant variation is about the same for the two races with a slight advantage in favor of 303—1. The modes for the variation in number of parts per flower are also the same, with the exception of the ovary-locules, 303—1 having almost one more locule per average flower then 301—1. Selection so far seemed to be producing results, so four plants were selected from the progeny of 301—1 and 303—1 and selfed. These were 301—1—2, 303—1—14, 301—1—29 and 303—1—12. The two former were approximately the least abnormal progeny of their respective families grown in 1910, while the two latter were approximately the most abnormal. The extent of their abnormalities in floral structures may be noted in Table 4, and changes in leaf number in Table 2.

Selfed seed of these four selections was grown in 1911 and the plants matured under about the same environment as surrounded the 301—1 and 303—1 cultures of 1910. Time did not allow me to make an elaborate examination of the 239 plants thus produced, nor of the 303—1 and 301—1 plants that grew beside them, serving as checks. However, by going through them at maturity, I was able to classify them roughly by the extent of their stem-fasciation into slightly abnormal and abnormal classes (see Table E).

Slightly abnormal simply means that stem fasciation only appeared in the region of the inflorescence. This was the stem condition of the parents 301—1—2, 301—1—29 and 303—1—14. Parent 303—1—12 had an exceedingly abnormal, bent flattened stem.

Table E.

Pedigree	Leaves of Parent	Selected toward	Slightly Abnormal	Abnormal	Total
301—1—2	33	Normal	22	44	66
301—1—29	34	Abnormal	9	60	69
303—1—14	40	Normal	3	36	39
303–1—12	69	Abnormal	13	52	65
		Total	47	192	239

No plant in any of the four families was any less normal than the parents, and there were many more extreme abnormals in all the selections than were present in either of the 1910 families. Roughly 301—1—29 appeared to be more abnormal in stem-fasciation then 301—1—2, but this was not true of the families 303—1—14 and 303—1—12, although the two parent plants represented extreme conditions. If one may draw conclusions from such scant data, I should interpret these results as showing the ever-varying nature of the character, not ever-varying however, in the sense of de Vries. No plant ever approached the normal, and were it not for labels, I should have been unable to have distinguished the two 301—1 selections from the parent strain growing beside them. De Vries, too, after two or three years, found selection of little value, and this was especially true in his attempt to produce a normal cockscomb by selection from an abnormal race. The value of selection for the first two or three years in de Vries' cultures may be accounted for by the fact that his plants came from the wild, of whose immediate ancestry he was ignorant. His fasciated races were also plants which as a rule were cross-fertilized. Selection work on this *Nicotiana* race should be continued, and careful detailed records taken during many years before a dogmatic decision in regard to selection of an abnormal from a normal and a normal from an abnormal could be made. The material is ideal for such work, as it fills the conditions called for by the advocates of Johannsen's pure line theory admirably, and the objection of bisexual inheritance is not here applicable as in the case of animals. Starting with what is in all probability a natural pure line, made homozygous by thousands of generations of inbreeding, and making use of a character that acts very clearly as a single unit, it would seem that the question of the power of selection to modify this particular gene could be irrevocably settled.

5. Fasciation and hybridization.

The hybridization work with the fasciated race was the most important part of the investigation. Crosses between it and various normal species and varieties have been numerous, and one such hybrid family has been grown to the F_4 generation. Crosses were also made between it and a calycanthemous-flowered race, *N. t. calyciflora.* The F_1 progeny will all be described together; the later generations of all crosses, under their respective headings. All parents used in this hybridization work are typical plants of the forms described under materials. Where the individual record of any fasciated parent used is known, it may be found in Table 9. The number, place and year in which any cross was grown is given in Table 7. The factor for fasciation is designated (A), that of calycanthemy (B).

a) Fasciation × Normal.

F_1 progeny (Fig. 16 u. 17).

Eight successful species and varietal crosses were made with the fasciated race. The species hybrids were all sterile, while the varietal F_1 hybrids were all fertile. The species cross (331 × 301) was not grown in sufficient numbers to give valuable data. The others, though sterile, gave important data regarding the nature of dominance. Tables 6—12 give the frequency distribution of floral parts (sepals, petals, etc.) per flower per individual plant of each different hybrid family. Table 13 shows the frequency distribution of parts per flower for the family as a whole, and gives the mode, number of flowers and plants examined and the character of single average flower for each of the crosses.

Fig. 16. Expression of calycanthemy (B) in F_1 flowers from 396 × 342. Note the petaloid sepals.

Exceptions to uniformity in F_1. All the F_1 plants of a given cross and its reciprocal were alike in the characters under observation with two exceptions. One of these was probably a reversal of dominance in connection with corolla shape, possibly resulting from internal environmental changes. It occurred in a family of 36 F_1 plants of 301—1—5 × 373, and all its (Plant 17) flowers were deeply lobed, similar to those of the mother, rather than to the pentagonal corolla-shaped flowers of the pollen parent. Cuttings were taken and grown the next year in field cultures, with the result that both of the parental types of flowers as well as intermediates were produced on the same plant. Seed was not saved from these three kinds of flowers to determine if somatic segregation had taken place. Selfed seed from the original plant gave only an ordinary segregating F_2 population.

Fig. 17. Flowers of parents and F_1 hybrid (303—1—24 × 332). From right to left: 332, 301—24 × 332 and 4 flowers of 300—309 race.

The other exception was in the nature of a mutation. It occurred in a 304 × 402 F_1 family of 39 individuals grown in 1910. Its resemblance to a plant of the pure fasciated (300—309) strain was very striking (see Table 6, Plant 39) and I would have eliminated it as a stray contamination, without any hesitation, had I not found after repeated trials to secure selfed seed, that it was at least self-sterile. And as I recall, cross-fertilization was also attempted, but resulted in failure. The latter point is one on which I have no notes, so I am not absolutely certain that it was tried. Dozens of flowers were bagged and hand pollinated, but no seed ever resulted. One may call it a reversal of dominance, i. e., a change from the intermediate to the completely abnormal condition, but some internal disturbance of a mutative nature must have accompanied this change, in order to account for the sterility. Unfortunately, I knew so little concerning the nature of my material and problems at the time that neither cuttings, nor cytological material were secured. In the light of Digby's (1912) studies on sterility in *Primula kewensis*, a cytological examination of this case might have proved interesting.

Fig. 18. Flowers of parents and F_1 hybrid (300—1—5 × 373). Four center flowers belong to hybrid.

Flower variability on individual F_1 plants (Fig. 18).

The first flowers on a plant of the pure fasciated race were usually the most abnormal. Flowers on plants maturing large numbers of seed capsules were likely to be the least abnormal. Environmental disturbances generally affected the variability of these organs in either a plus or minus direction. And in order to compare the range of variability of the fasciated expression in different plants and different families, it was necessary to take their flower records during approximately the same blooming phase.

Table F shows a study of 88 flowers collected from the same plant at different intervals of time. The study is given here in order to show the fluctuation there may be in dominance when environmental factors enter, for the differences in the three lots are largely due to this cause.

Table F. Effect of environment on the expression of (A) in an F_1 hybrid plant.

1) Aug. 10, 1911	No. of Flowers	Floral leaf class range							F (v)	F (v) Number	Constant
		1	2	3	4	5	6	7			
Sepals	25					22	3		128	5·12	2·048
Petals	"					24	1		126	5·04	2·016
Stamens	"					23	2		127	5·08	2·032
Ovary-locules . .	"		22	3					53	2·12	2·120
2) Sept. 1911											
Sepals	37					23	14		199	5·38	2·152
Petals	"					26	11		196	5·29	2·116
Stamens	"					27	8	2	197	5·32	2·129
Ovary-locules . .	"		30	7					81	2·18	2·189
3) Feb. 1, 1912											
Sepals	26					19	7		137	5·27	2·107
Petals	"					13	11	2	145	5·58	2·230
Stamens	"					15	8	3	144	5·54	2·215
Ovary-locules . .	"		16	10					62	2·38	2·384

Variability of dominance. Table 13 is a comparison between the average abnormal condition of the F_1 flowers of the different crosses, the data from all, except the first and last resting on a study of 25 flowers from each F_1 individual of the respective hybrid families.

324 × 301 appears to be the most abnormal, followed somewhat closely by 303—1—24 × 332 and 304 × 402. The least abnormal F_1

---

1) Field.

2) Same field as Aug. 10.

3) Greenhouse (richly fertilized soil).

families were 353 × 301, 301 × 396 and 301—1—5 × 373. The cause of the high abnormal condition of 324 × 301 F_1 flowers is easily accounted for by the character of the 324 parent, as the flowers of this race are 5—7-petaled and almost constantly in possession of a three-loculed ovary. In all cases except the one just mentioned and 301 × 396, one parent is normal. My F_1 data on this subject would be more satisfactory if I had used only a single fasciated plant as the abnormal parent in these crosses. Personally, I believe the race to be a homozygous pure line, and if the factor A cannot be modified by selection, any one of the pure strain individuals would be similar to every other one, so that the flowers of an F_1 family grown from 303 × 373 should not be more nor less abnormal than those from a 301 × 373 culture, providing both were grown under the same environment. An experiment of this kind is in progress. Two or more crosses of the same kind, so far as my experiments have gone have always given similar data on dominance, leading one to infer that internal environmental differences of the normal races are responsible for the variability in the expression of A in each of these hybrid families (Fig. 19).

Fig. 19. Flowers of parents and F_1 hybrid (303—1—13 × 327). Three center flowers belong to hybrid.

Cytology. The maturation phenomena in the F_1 anthers of 304 × 402 was investigated, but as compared with the pure strain, the abnormal expression of A was small. Contabescent anthers occurred in this cross, as well as in all the others, but their number per flower or plant depended always on the degree of dominance expressed by the factor A.

F_2, F_3 and F_4 progeny.

F_2 generation from three different varietal crosses have been grown, these being 301—1—5 × 373, 301—1—1 × 353 and reciprocal, and 304 × 402.

N. tabacum fasciata (304) × *N. tabacum* (402) (Fig. 20).

The experimental results and data from this cross have been given in detail in an earlier paper (White, 1913). The F_2 population contained abnormals (AA), intermediates (Aa), and normals (aa) in the proportion of 1 : 2 : 1. All the apparent classes were easily and accurately separated. The abnormal segregates bred asolutely true in F_3 and F_4, while the intermediates continued to produce AA, Aa and aa progeny in these later generations. Such a population is represented by Tables 15—16. By glancing at it, one may see how sharply the three classes are differentiated, and this contrast becomes more marked when one sees the plants themselves rather than mathematical characterizations of them.

Table 14 shows the ration of AA, Aa und aa segregates among the progeny of six different selfed heterozygotes. In some cases, where the families are small, the actual and expected ratio are far from agreement, but in the case of (304 × 402)—1—34), one could not possibly expect a closer approximation between the two. The total ratio from all the heterozygous families also closely approaches that demanded by theory.

In this cross, so far as one could determine by observation, no segregation in other factors took place, and one would expect none to occur if the two races differ only by the genetic factor A, as I strongly believe.

Character of aa and AA segregates.

Table 17 shows the character of an F_3 population from a selfed AA F_2 segregate, while Tables 18—19 represent two families from selfed aa F_2 segregates. A glance at the latter may cast doubt upon my statement that pure aa segregates occur in F_2 and breed absolutely true, because these tables show there is a slight variability in the number of parts per flower. But the normal (402) itself, so far as casual observation can determine, also shows this slight variability, and in practically the same degree. In an omitted table, the frequency distribution of these variations of parts per flower and the number of the abnormal flowers to each plant were calculated. Out of 11·475 flowers collected from 459 normal segregate plants or their progeny, there were 11·079 normal to 396 abnormal, or over 3·5 per cent of the latter. These abnormal flowers, representing 240 of the 459 plants concerned, had 608 extra floral parts (sepals, petals, etc.) or about 1·5 part per flower. Their absence from the remaining 219 plants is of no significance, as each plant of the whole 459 was represented by only 25 flowers, and as abnormal ones are more common on branches just entering the blooming period, I might easily have overlooked them on some plants. Plants on which two or three such flowers had been found were selfed and their progeny grown, and from an examination of these, I concluded this variation was not heritable (Fig. 21).

Fig. 20. Young inflorescences of 304—1, 304 × 402 and 402. Photographed from herbarium specimens.

As to whether the flowers of the aa segregates, in respect to number of parts, are as normal as those of the 402 grandparent, is an

Fig. 21. The three types of F_2 segregates resulting from 304 × 402. Left to right, AA, Aa and aa.

important question theoretically, on account of its bearing on the theory of gametic contamination as opposed to that of gametic purity. My casual observations on the 402 race are not in a sufficiently definite form as yet to convince others than students of this same material that they are accurate. This being true, two interpretations can be placed upon my data. One may say, until proof to the contrary in a tabulated form is presented, that segregation of fasciation-determining material was not complete in the formation of the F_2 seed, and consequently slight abnormalities in aa flowers appear, the latter being evidence in favor of such a supposition. However, one may also say that these abnormal flowers occur just as frequently in the 402 race, that they are just as abnormal, and that their presence is the result of accidents¹) in ontogeny, in which case, internal character-materials have undergone absolute segregation and the F_2 aa plants are pure normals.

In order to prove the former contention, it must be shown that the F_2 aa segregates under the same environment as 402 plants, continuously produce flowers more abnormal than the latter. Further, if contamination is at all common, repeatedly back-crossing normal segregates with the pure abnormal (300—309) race, should eventually give one a pure abnormal race, and each generation of back-crosses should show some progress. In making such an experiment, one must first be certain that homozygous lines are being used as material, otherwise, if favorable, one might look upon its results as due to unconscious selection, for if one believes as does Castle (1912) in the creative power of selection, there is no apparent physiological reason why, through self-fertilization and selection, an abnormal race such as 300—309 could not be produced from these slightly abnormal-flowered F_2 segregates.

If one adopts the "fixed factor" conception of East (1912) the extra parts of normal flowers on aa and 402 plants are simply and plausibly explained as ontogenetical accidents. For all practical purposes, the aa segregates are as normal as (402) individuals.

Cytology. The maturation phenomena of the anthers were investigated. Cytological irregularities in AA segregates were similar to those of the abnormal grandparent; in Aa anthers, similar to the F_1

---

¹) The term accident is used throughout this paper in a very specific sense. In using it, I intend to convey the idea that is expressed when a very accurate technical device, such as a rotary microtome, misses cutting a section.

conditions; while in aa segregates, normal conditions prevailed as in the normal grandparental race. The proportion of contabescent anthers and the cytological irregularities which they contain fluctuates as the grosser alterations produced by the factor A vary. These facts are of theoretical interest, because of their possible bearing on the chromosome theory of inheritance (see White, 1913).

N. tabacum fasciata (301—1—5) × *N. tabacum havanensis* (373). Two F_2 families were grown (Fig. 22). Tables 20 a and b give the ratio of abnormal to normal segregates and the proportion of fasciate to non-fasciate-stemmed plants. It was impossible to accurately classify the heterozygotes, owing to the numerous modifications the character fasciation had undergone, as compared with its appearance in the pure strain and the 304 × 402 AA and Aa segregates. The small proportion of 1 fasciated stem to 5 normal one was perplexing, inasmuch as theory demanded three of the former to one of the latter. The individuals of this population did not vary much in height, but segregation of factors governing color, habit and leaf character had occurred. The leaf count per plant varied between 16 and 111; for those classified as normal, it ranged between 16 and 28 and for "possible heterozygotes" as low as 19 and commonly 20 to 25. Table 21 shows the character of an F_2 population, in terms of its flower variability and leaf number per plant.

Fig. 22. Two F_2 segregate plants (AA) from 301—1—5 × 373.

N. tabacum fruticosa (353) × *N. tabacum fasciata* (301).

Only two F_2 families of this cross were grown and the ratio of abnormal to normal plants may be found in Tables 20 a and b. The difficulties in classifying the three kinds of segregates were greater than in 301 × 373, heterozygotes very often being classed as normals, until repeated inspections had taught me to look the whole plant over carefully for abnormal flowers. Individuals with fasciated stems occurred in a proportion of about 1 F to 9 N, whereas one would expect 3 to 1. 353 differs very markedly in character from 301, and one might almost say dozens of these differences had segregated, so that the F_2 generation, owing to the many new factor combinations, represented an extremely variable population. Variation in height ranged from 10·7 to 24·4 dcm., and the leaf count from 13 to 212 leaves per plant. The relation between these characters is shown in Table 23. The segregate bearing 212 leaves was 17·54 dcm. high and had a very fasciated stem, while the one with 13 leaves was 16·8 dcm. and normal-stemmed (Fig. 23 and 24). Table G gives the frequency distribution of height in decimeters and number of leaves per plant for 24 apparently normal segregates.

a Fig. 23. b

a) F_1 plant with 18 leaves (301—1 × 353—3).
b) F_2 AA segregate with 100 leaves.

Table G.

Hght. in decimeters	12·2	12·96	13·72	14·48	15·24	16·00	16·76	17·52	18·28	19·04	19·80	20·56	21·32	22·34
Frequency	1				2	3	4	2	4	1	1	2	3	1
Lvs. per Plant	13	14	15	16	17	18	19	20	21	22	23	24	27	28
Frequency	1	3	3	2	4	2	1	3	1	1		1	1	1

Extremely abnormal segregates, judging from the records, have a leaf count as low as 24 and a height of only 12·2 dcm. A survey of the data in Tables 22 and G shows there is some correlation between height and number of leaves. In addition to the characters just mentioned, these segregates differed as to color, habit of growth (branching or non-branching), leaf characters, flower characters and many others not so easily noted.

Fig. 24. Abnormal F_2 segregate (probably AA) from (353 × 301—1). Note absence of fasciated stem.

b) Fasciation × calycanthemy and reciprocal.

This cross was especially interesting for two reasons; first, the segregation of two characters which were more or less associated in the same organs, and second on account of the numerous modifications of fasciation, even in AA segregates.

In the first case, both characters had given simple 1 : 2 : 1 ratios in an F_2 generation obtained by crossing each of them separately with the normal 402. (See Table H.) Both were partial dominants when heterozygous, hence in monohybrid crosses with 402, the Aa and Bb classes were always easily distinguished. In the dihybrid cross under discussion then, an F_2 ratio of 1 AABB : 2 AABb : 2 AaBB : 4 AaBb : 1 AAbb : 2 Aabb : 1 aaBB : 2 aaBb :

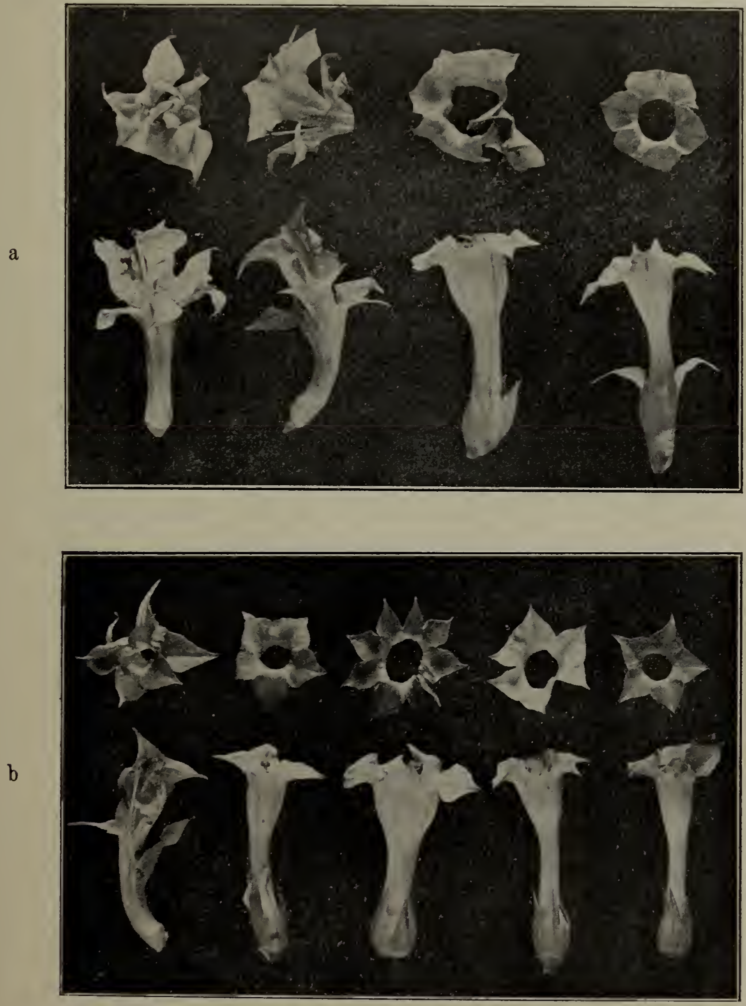


Fig. 25. Typical flowers from F_2 segregates of calycanthemy × fasciation, each flower representing one of the 9 somatic classes. Beginning at the top and left, they are (a) AABB, AaBB, AABb, AaBb (b), aaBB, aaBb, AAbb, Aabb, aabb.

1 aabb was to be expected, the 9 gametic classes all being identifiable (Fig. 25 and 26). The actual results obtained by growing 477 plants from three different F_1 individuals bore out these con-

clusions, but owing to complications caused by the segregation of numerous other characters, the classification was extremely difficult.

Table H. (396 × 402 F_2 generation.) (Calycanthemy × normal.)

Ratio	Classes of F_2 segregates			Total
	BB	Bb	bb	
Actual . . .	15	25	13	53
Expected . .	13·25	26·50	13·25	53

Some individuals could be assigned to their particular category with accuracy and speed, while others were so hopelessly modified that even after repeated trials and extensive study, they could only be placed by guess. This state of affairs was not a particular class characteristic, but true of all. In order to be as accurate as possible, three separate classifications were made; one early one involving only a part of the population, and two later ones in which nearly all of the plants were considered. Those not included, were either destroyed accidentally or were not yet in bloom at the time of the last inspection, and as they were few in number, the absence of data from them is of no significance. Table 23 gives the results of the three classifications. I consider that of the second the most accurate, as most of the plants were in full bloom when this was made. Count 3 was taken later in the season, when many of the segregates possessed few flowers, but

Fig. 26. Extremely abnormal flowers from F_2 AABB segregates of 396 × 402.

numerous maturing seed capsules. Under the latter conditions neither the character fasciation (in floral expression) nor calycanthemy are expressed typically. This is especially true of the individuals of the Aa and Bb categories. Table 25 gives the character of the individuals of this F_2 population, and enables one to note the fluctuation as regards each class. I consider the individuals of the classes AABB, AABb, AaBb, Aabb and aaBB to be the most accurately identified, and those of aaBb and aabb as probably the most inaccurately placed, as some of the former no doubt are AaBB and AaBb and some of the latter also are AaBb. But all the discrepancies between the actual and expected ratio cannot be accounted for by assuming preventable error to be the cause. The classes aaBb and aabb especially are too high to be explained in this manner, and in all counts the greatest discrepancy occured in the class aabb. But the factor B was not causing the distortion of the ratio, for in a population of 469 F_2 individuals, 351 were abnormal (BB or Bb) and 118 normal (bb)¹), a very close approach to the expected ratio. The factor A was causing the trouble as shown by the total number of abnormal (AA and Aa) to the total normal (aa) segregates. An examination of the whole F_2 population as regards stem-fasciation gives an added basis for my statement. Table 25 gives the total fasciate-stemmed plants to those with normal stems, the proportion being about 1 F to 8·5 N., whereas theory demands 3 F : 1 N, and at least *119 (*1 F : 2 FN : 1 N) plants fasciated enough in this structure to be easily distinguished, and twice that number with slightly altered stems. In making the observations, all plants showing the least indication of monstrous alteration in stems were included in the (F) class.

It is very evident in this hybrid population, that too many aa and not enough AA and Aa segregates were present to accord with theory. A glance at the nature of the characters present additional to those caused by factors A und B disclosed similar conditions to those found in the 353 × 301 and 301 × 373 populations. The two grandparental races differed by a large number of factors, and these were segregating. Height, leaf character, branched and unbranched habit, normal leaf number and numerous floral characters are a few of the more prominent, and as a consequence of this great shuffling of factors, the 477 segregates presented striking dissimilarities. Hardly two of the whole

---

¹) Note second count.

lot, but were distinguishable by some character difference, and this population was by far the most variable of all those which I grew. In Table 25, some idea of the striking differences in height may be gained. The range is: aa segregates, 12·2—20·6 dcm.; AA and Aa segregates, 10·7—24·4 dcm. In leaf count, the aa class varied from 10 to 17; the Aa between 10 and 33, and the AA, from 14 to 85 leaves per plant. Fasciate-stemmed segregates are not confined to any particular type, but are present in a large number of the different character combinations, among them being dwarf individuals (9·15 dcm.) with only 15 leaves, and extremely tall plants with either few or many leaves. The correlation between height and number of leaves per plant was not marked. Branched fasciated stems appeared for the first time. The branching type had come from the 396 grandparent and the fasciated stem character of the 300—309 race had spread itself out over the three or four main branches, expressing itself even in the little twigs. This was a distinctly new type, and not a bifurcate or multiradiate fasciation. Other well defined types with fasciated stems occurred, and one of these, especially distinctive, gametically AABB or AaBB, had a slender, unbranched, flattened axis bearing only 10 or 15 leaves. All types as described in Table 25, were selfed and much more light will be thrown on the subject by the F_3 generation. Pending the growing of this, the explanation given for changes in dominance of A in the various F_1 crosses, is presented to account for the unexpected distortion in the F_2 ratios.

Discussion.

From the results of these three varietal crosses, together with the data from 9 F_1 hybrid families, it would appear that other factors must markedly affect the somatic expression of the factor A. And this may be so much modified that the intermediate expression of dominance in the Aa segregate may be changed to complete dominance of the normal (aa) condition, provided certain other unrelated, but interacting factors were present in the zygote. If this occurred, more segregates somatically normal would be expected in F_2, because heterozygotes of this kind could not be distinguished from aa plants, except through the breeding test. The failure of the factor A to alter the normal appearance of the stem can be accounted for in the same manner. It is very evident from the F_2 results of the cross 304 × 402, that when two homozygous pure lines differing in a single factor are crossed, the F_2 individuals of each apparent class will differ but very little from each other, and this slight difference may be described as the difference in external environment. On the other hand, when two homozygous pure lines[1]) differing in numerous factors are crossed, F_2 individuals of each apparent class may express the character especially under observation in many distinct morphological forms, each of these changes in expression being the result of modification by other factor developments. Calycanthemy (B) is not so easily altered in its expression by changes in factorial complexes as is factor A.

6. Summary and conclusions.

The following conclusions may be drawn from this study:

1. According to the evidence already presented, the original plant which became the progenitor of this fasciated race, must have mutated from unknown causes, at or shortly after fertilization had taken place (somatic mutation in the embryo). For the reasons given in the body of this paper, the mutant is believed to have arisen in a homozygous condition as regards the factor A and upon self-fertilization to have bred true.

2. The Cuban variety of tobacco known as 402 in the B. I. of H. U. cultures is believed to differ from the *Nicotiana tabacum fasciata* race (300—309) only in the absence or presence of a single genetic factor (A). In all other respects, the two races in breeding tests give results that would lead one to believe them to be identical genotypes.

3. As a generality, *N. tabacum* varieties and races are held to be natural pure lines (as reported by Hasselbring) and to give uniform progeny in breeding tests of self-fertilized seed parents. Owing to cleistogamy and the consequent rarity of cross-fertilization, such pure lines, in the majority of cases, have bred true for thousands of generations. The sexually produced progeny of these *N. tabacum* homozygous pure lines, would differ in no way from the progeny that might be created by asexual methods such as cuttings.

---

[1]) In all the crosses of the fasciated race with normal varieties and species of *Nicotiana,* all the F_1 generation plants of a given cross were practically uniform in appearance (height, flower-shape, and color, foliage and stem characters, etc.). This fact indicates these normal parents to have been practically homozygous genotypes. (See Tables.)

4. The race (300—309) is such a homozygous pure line because it has been propagated from seed obtained by selfing a single (original) plant, which is believed to have arisen or mutated by a single factor A from such a homozygous pure line.

5. The factor A of this race, in expressing itself somatically, when surrounded by its original gene complex (402) affects a large number of important plant organs. Prominent among these may be mentioned the stem, the leaf number and arrangement (phyllotaxy), the inflorescence and the flowers. The nature of this expression is held to be ontogenetically progressive, as the seedlings and the early juvenile stages do not show any distinguishing *fasciata* features. As the plants of this race progress toward maturity, the factor more and more implants its distinctive morphological characteristics upon the various organs, so that those which develop last, exhibit the greatest alterations. Hence, the last flower whorl laid down in ontogenetic development is the most altered from its normal expression by the factor A.

6. The hereditary nature of the fasciated condition has been tested by breeding large numbers of progeny from the seeds of a single selfed plant. In all cases, the character is constant in the sense that its extreme fluctuations do not approach the normal (402) condition near enough so as to call forth any question as to which is which when the two are grown together. In other words, all the progeny of selfed plants of this race express the character fasciation, as described under "materials" to some degree. Its fluctuation is largely "inherent" and not the result of the "external" environments under which the experimental cultures were grown. As no "atavists" appeared, the character is not "eversporting" in the deVriesian sense.

7. The repetition in the number of organs, such as leaves, sepals, petals, stamens and ovary-locules is not a duplication of whorls (pleiotaxy) or of practically whole organisms, as the theories of some anatomists would seem to imply, and as deVries suggests in explanation of his data on *Geranium molle fasciatum*. No evidence of congenital mechanical fusions is given by cross-sections of the mature stem. The different whorls in the flower appear to vary somewhat independently of each other, as the correlation in number of parts between those of a single flower is far from perfect, though probably exceeding 50 per cent. The progressive expression of the factor in its ontogenetic development may entirely account for this.

8. Under five distinct geographical and topographical environments, the characteristic expression of the fasciated race has remained qualitatively, but not quantitatively constant. One of these environments was characterized by impoverished soil, general cultural neglect, and over-crowding, but the plants, though dwarfed in the size of their leaves and stems, had flowers and stems of the prescribed abnormal type. From comparisons in leaf number, between individuals grown under different field conditions, it is believed that environment, especially the factor weather, is able to change their variability in number per plant. The change in number of floral segments may also be associated with climatic factors.

9. The 300—309 race is probably not as well "adapted" to different environments, as is the parent race from which it mutated. The few seed set by the original mutant might indicate that had it arisen under natural conditions, its ability to persist would have been very problematical. In the Harvard University cultures, the race is very fertile, though falling short in this respect when compared with 402. This means, that on a basis of fertility, the latter would be the more successful competitor in the struggle for existence. The modifications produced by a combination of the factor A, and certain environmental conditions would further cause this variety to be a losing competitor in the struggle with the normal, as under extremely favorable environmental conditions (for the factor A) very few flowers would develop and mature seed. As far as roots and general plant vigor are concerned, when placed under ordinarily favorable tobacco growing conditions, one race is no better equipped for existence than the other. Under many tropical environments, I have no doubt that the race, as now grown, would persist and compete successfully with many other plants for existence, if selfed seed were sown in such places.

10. The results secured from the selection experiment are only indicative and possibly may be interpreted as favorable to the idea of the creative power of selection. I prefer to interpret them as indicating the inability of selection to modify the fasciated character, so as to produce eventually a normal. The data are not conclusive, however.

11. The data from crossing a fasciated plant with a normal (402) plant demonstrated in a clear manner that the two races apparently differed only in the possession of a single unit factor A. The F_1 was intermediate in character and the F_2 gave abnormal (AA), heterozygous (Aa), and normal (aa) segregates in the ratio of 1 : 2 : 1 or 3 abnormals

to 1 normal. The three classes were clearly recognizable and very distinct, the heterozygote always being an intermediate. No segregation of other factors, which might have been hypostatic (as in Bateson's sweet peas) occurred. The total progeny of 304 × 402 Aa plants gave an extremely close approximation to the theoretical expectancy.

Actual . . . 98 AA : 192 Aa : 103 aa; Total 393,
Theoretical . . 98 AA : 197 Aa : 98 aa; „ 393.

12. Four generations of the cross (304 × 402) have been grown and the F_2 segregates have all bred true to their respective character, AA plants producing always AA, Aa individuals always producing the original F_2 ratio of 1 : 2 : 1, and aa plants always giving rise to aa progeny. F_2 normal segregates and their F_3 and F_4 progeny have possessed two or three abnormal flowers. These, as pointed out in the body of the paper, may be interpreted by some biologists as evidence in favor of a theory of gametic contamination as opposed to that of gametic purity, because I have nothing better than casual observations to prove that the normal 402 plants have the same character in the same degree. This character is not hereditary in the strict sense, and upon the fixed unit factor conception, these slightly abnormal flowers may be explained as accidents in ontogeny.

13. The cytological investigations of the maturation phenomena in the anthers and ovaries of the pure abnormal (300—309) race showed numerous irregularities in the normal processes of reduction. Chromatin and cytoplasm were alike affected, and many of the pollen mother-cells were destroyed through the presence of factor A. Only a certain percentage of anthers and ovules are abortive, and this partial sterility is made good as far as seed production is concerned by the increase in the number of ovules and ovary-locules. In crosses with 402, the F_1 plants show the same irregularities, but to a lesser degree and in a lesser number of anthers. The cytological observations on the F_2 generation show that a perfect correlation exists between the gross morphological and cytological features of this fasciated race. The factor for fasciation then produces its abnormal effect even in the germ-cells, and this effect is subject to alteration in both somatic and germinal structures through changes in dominance. The same factor A expresses itself in the soma by altering the form of many of the characteristic organs, and in the germ-cells by destroying a certain percentage of cell materials, or by producing irregularities in their normal processes which ultimately cause their own destruction. Because of the F_2 ratio

of this cross, it is held that only one factor is involved, and if that factor is present in a chromosome, it is in duplex condition in each 2**n** cell and simplex in each **n** cell. All anthers and other organs are held to be gametically similar in such a race, and every cell, except for environmental modifications is identical with every other cell of the organism. Pollen mother-cells are identical as to factor composition and can differ from one another only in environmental modifications. Environmental conditions must be practically the same in the same anther and in all the anthers of a single bud. The questions then arise why the factor A is latent in some cells and patent in others, and why a certain definite percentage of each anther's pollen is not aborted rather than all of it, etc.[1]). From these data, one would find no support for the chromosome hypothesis of inheritance and in theory, there is directly opposing evidence.

14. Three other crosses were made, the F_1 plants of which were fertile. One of these (301—1—5 × 373) did not appear to differ much from 402 or 300—309 in factors affecting height, though in other respects the factorial complexes of the two varieties were very different. This was even more true of the varieties 353 and 396, as they were branching, shrubby, dwarf-statured plants. When crossed with 300—309 and the F_2 generation observed, it was very evident that the latter variety differed from the two former in an exceedingly large number of characters (factors). The crosses of 396 with 301 demonstrated the extreme extent of these differences, as hardly any two plants were alike among the whole 477 F_2 progeny, and many of their distinguishing features were sharp and clear-cut genetic characters.

15. The ratio of abnormal to normal plants in these three crosses was very confusing, as in all cases, there was excess of "somatic" normals and this divergence from the theoretical expectancy increased as the apparent character differences between the two grandparents became more numerous. In 301—1—5 × 373, the excess of normals above the expected was only 2·8 per cent; in 353 × 301—1, the excess rose to 4·8 per cent, while in 396 × 301 and reciprocal crosses, the increase in normals over the theoretical had mounted to 9·7 per cent

---

[1]) Attention is called to the similarity between the disturbances and modifications produced by the factor A, and that caused by certain parasite mutilations. All the experimental data are opposed to the theory that the factor A is an internal parasite foreign to the organism.

(second count) or 15·2 per cent on the basis of the third count. In each succeeding cross, the total number of F_2 progeny grown was larger and the discrepancies between the actual and the theoretical ratios should have been less in the case of 396 × 301 than greater. In addition to the discrepancies between the actual and theoretical ratios, the abnormal character was modified in its somatic expression to such a degree that it was very difficult to separate the three classes, AA, Aa and aa. Since going over my records, I think it would be impossible to classify them accurately except through breeding tests. Owing to the variable nature of dominance and recessiveness in these crosses, even the selection of the aa (normal) segregates became somewhat difficult, and no doubt the deficient number of abnormal plants (AA and Aa) in the actual ratio obtained, may be explained by my inability to distinguish properly between normal (aa) and Aa segregates. Variation in the expression of the abnormal character was extremely noticeable in all three of these crosses. The proportion of fasciate-stemmed F_2 segregates to those with normal stems was respectively 1—5, 1—9 and 1—8·5. Many abnormal plants (AA) then were not characterized by fasciated stems. In the case of the cross 304 × 402, all the F_2 AA segregates possessed the fasciated stem condition in varying degrees, but in some of the AA segregates of these other crosses, the stems were as normal as any normal tobacco plant's main axis well could be (Fig. 27). The explanation for this difference in the expression of the factor A appears to lie in the different nature of the gene complexes or genotypes. In 304 × 402, both parents appear to be genotypically alike except for the factor A, while in all the other crosses, it is evident that this was not the case. Factor A expresses itself as described under materials when in genotypical environment 304 and 402, but very differently under genotypical environments 373, 353, 396, etc., because it is modified in its somatic expression in all these environments. Taking 304 or 402 as the standard genotypical environment by which to compare the remainder and calling it X_1, the other environments may be referred to as X_2, X_3, or X_4, etc. Under X_1, factor or gene A always gives a certain typical somatic expression, while under any other X, that somatic expression may or may not remain the same. Under X_1 environment, no branched fasciations were produced, the ribbon-like linear expansion being characteristic only of the main axis, but in the cross 396 × 301, under X_n environment, segregate plants appeared expressing this anomalous condition in several of their branches. And of these plants, some may be homozygous in enough of the factors which transmit the branching habit, that a constant race could be obtained. Again, under X_2 genotypical environment, the factor A may not be able to express itself at all in the stem, and the abnormal floral and phyllotaxy conditions may be reduced, owing to the presence of modifying factors in this gene complex X_2, that were absent in that of X_1. Hence among the F_2 progeny of crosses 353 × 301, 396 × 301, etc., plants segregated out which, judged by the expression of the factor A under X_1 conditions, would be recorded as heterozygotes, yet they may be just as truly AA segregates, as any AA plants could be. Such a state of affairs causes extreme confusion in a study of

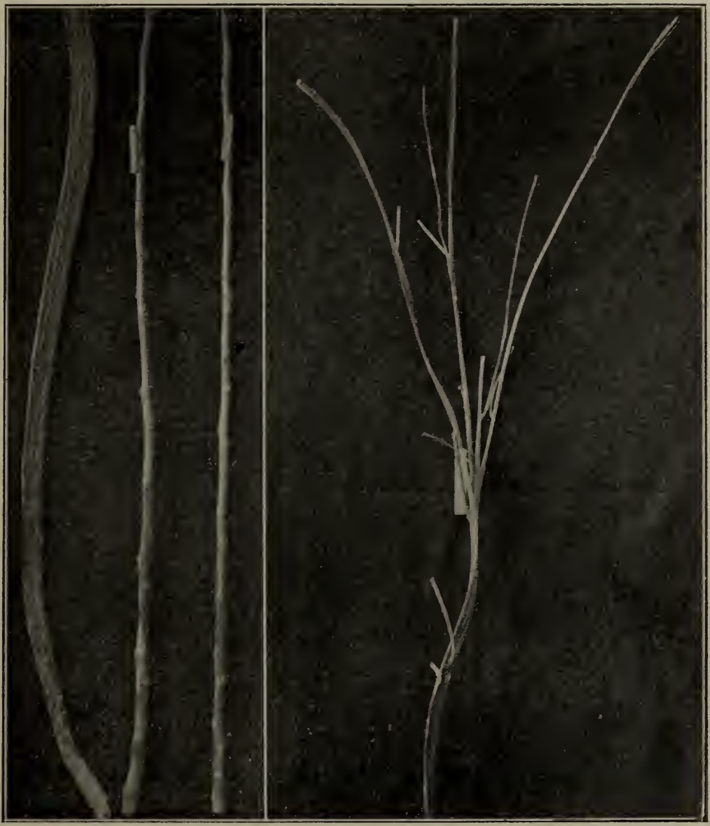


Fig. 27. F_2 types of stems resulting from crossing the fasciated race with normal-stemmed races of *N. tabacum*.

characters in heredity, but the phenomena are easily understood and more simply expressed when one can work with progeny, the male and female parentage of which is contained within the same plant. Under the conditions above mentioned, an F_2 population such as (396 × 301) — 12 may contain: —

AA segregates resembling AA plants of X_1 standard,
AA ” ” Aa ” ” ” ”
AA ” very nearly as normal as those aa plants of X_1 standard which have two or three abnormal flowers.
AA segregates which have numerous new modifications in the expression of the factor.

Such an F_2 may also contain:

Aa segregates resembling AA plants of X_1 standard,
Aa ” ” Aa ” ” ” ”
Aa ” ” aa ” ” ” ”
Aa ” with many new modifications.

One can readily see from this illustration the confusion which would ensue in attempting to classify such an F_2 progeny. The study of this factor A and its expression in the „soma” under differing genotypical conditions is exceedingly complicated because it is capable of expressing itself as a modification in so many of the important plant organs. The study of a color character is much simpler, as I shall soon indicate.

16. Dominance and recessiveness, being regarded as characteristics of the environment (both genotypical and external) are expected to show a large degree of variation in a series of crosses such as the present investigation involves. A study of the F_1 generation of four very distinct species crosses and three fairly distinct varietal crosses with the abnormal race (300—309) has fulfilled these expectations. All the species and varieties are normal as regards fasciation, except 324 and perhaps to a slight degree 396. When crossed with the abnormal (300—309) race, if other factors did not produce modifying effects, the F_1 plants from these different combinations should all show the same degree of dominance and recessiveness. Such is not the case, however; F_1 plants of 301 × 373, etc. are the most normal, followed by 353 × 301, 301 × 353, 301 × 396, 303 × 327 in the order named, through to 332 × 301 or 332 × 303, 304 × 402, and 324 × 301, which are the most abnormal. (Consult Tables 6—12.) The species crosses were all sterile. The F_2 generation of all the varietal crosses further substantiated this

interpretation of the variableness in dominance shown in the plants of the different F_1 families. It is not improbable that the F_2 progeny of some of these species crosses, if they were obtainable, would represent plants of the constitution AA, which would promote or allow a very much greater abnormal expression that that of the standard X_1 race (300—309). Theoretically, I should expect such segregates.

17. It is of interest to note the somatic effect when the factor A is present in simplex condition. Instead of a progressive increase in expression, as the plant approaches maturity, the factor seems to be unable to maintain its normal (under X_1) rate of development after the first one, two, or three floral whorls are laid down in morphogenesis. As a consequence, the gynoecium does not usually show the most abnormal expression of the factor A in the eight or nine different F_1 combinations grown. In 303—1—13 × 327, the greatest alteration occurs in the corolla, the least in the calyx and the next to the least, in the gynoecium. Practically the same relationship between the different floral whorls and the somatic expression of A, is apparent in all the other F_1 hybrid families represented in Table 13. The exceptions to this generalization are 324 × 301, 304 × 402 and 301 × 396. The first combination does not follow the floral organs (see materials). The second case, 304 × 402, is explained on the grounds of relationship, the gene complex in both races being extremely favorable to the normal expression of A. 301 × 396 shows only a slight deviation from the general rule and is possibly due to error resulting from the manner in which the data from it were collected.

18. The origin of factor A could be pictured as either a loss or a gain in actual protoplasmic substance. It was either a sudden dropping out of something essential to normal development (402) or it may have been an abrupt change in the germ-plasm. As Morgan and others before him have suggested, changes in chemical configuration (isomerism) of protoplasm may account for the origin of new factors and such a conception is preferable to the idea of an actual protoplasmic loss. The *Nicotiana* factor A is both discontinuous in origin and in inheritance. Whatever be its germinal nature, it arose as a unit and is transmitted intact.

19. Calycanthemy (B) in crosses is transmitted as a single unit factor, giving in the progeny of an F_1 Bb plant, segregates in the proportions of 1 BB : 2 Bb : 1 bb. When the calycanthemous and fasciated races are crossed, the resulting AaBb individuals show only

partial expression of the A and B factors. In F_2, the progeny are divisible into 9 gametic classes in the proportion of 1 AABB : 2 AaBB : 2 AABb : 4 AaBb : 1 AAbb : 2 Aabb : 1 aaBB : 2 aaBb : 1 aabb. These classes also represent the apparent or visible classes, because the heterozygotes are distinguishable from the homozygotes. In practise, accurate classification of the progeny into these classes was impossible, owing to the presence of modifying genes in the two grandparental races, which were also segregating in this F_2. The ratio of BB and Bb to bb individuals in this F_2 was as accurate as was to be expected, but a great excess of apparently normal aa segregates occurred. Some of these undoubtedly belong gametically to the other classes. Calycanthemy is only slightly altered by the presence of modifying genes or ordinary changes in external environment. This is to be expected, when such a character is compared with one much more fundamental (in that it expresses itself by such numerous and far-reaching alterations) in the organism's life cycle, such as is true of fasciation.

G. General discussion, showing the bearing of these data on some of the more general problems of evolution and heredity.

Under this heading, I wish to present certain general conclusions which my data, in my opinion, justify, The chief of these concerns the latent character hypothesis of the morphologists, in so far as it bears on problems of genetics and evolution. This conception, especially in the form presented by de Vries is not only confusing, but actually contrary to fact, as I have shown in the body of this paper. A further example will, I hope, make my previous contention clear. The character fasciation, as it occurs in *Pisum*, appears in at least two physiologically distinct forms. In *Pisum umbellatum* it is absolutely hereditary under the ordinary environments in which peas are grown. Lynch, Rimpau, Koernicke, Mendel, Lock, as well as myself, all vouch for this fact. Under these same conditions the ordinary varieties of peas do not possess this character. But in a case reported by Blodgett (Fig. 28), environmental phenomena induced this character in a variety of *Pisum* to the extent that not more than 10 per cent of the plants remained normal. This effect was distinctly an environmental one and was not hereditary in the absence of the inducing agent. Blodgett was not able to show this by experiment but after carefully considering the data he gives as to its extent and origin, I think there is but slight doubt that had experiments been feasible, the results would have proved the truth of this assumption. A comparison of the photographs in Blodgett's paper with those of fasciation in *Pisum umbellatum* (Fig. 29) show the two forms of the character to be morphologically indistinguishable. In the presence of such data, the question arises, are we justified in speaking of fasciation as being latent in the normal peas, such as those reported by Blodgett? It is far simpler, it seems to me, to regard it as hereditary in both forms, for under the same conditions, it is reasonable to suppose that this particular variety of *Pisum sativum* would always produce the phenomena Blodgett observed. The interesting point is that there is a hereditary difference between *Pisum umbellatum* and all other peas, when all are grown under ordinary environmental conditions. In neither case is a character latent, but rather absent, as a character is just as much an effect of a specific environmental medium as it is an effect of a bit of protoplasmic material. With appropriate material and appropriate environment, this effect can always be produced,

Fig. 28. Fasciation in *Pisum sativum* due to environment. (From photograph after Blodgett.)

if we are to believe what chemistry and physics teach us. A character is always the result, of a chemo-physical reaction and not a continuous entity existing from generation to generation. When a character is handed on from generation to generation, it is formed anew each time.

On this viewpoint, historical knowledge is the only criterion by which the newness or the oldness of a character may be established. Dominance has often been suggested (de Vries, Castle, etc.) as a means of distinguishing between old and new, progressive and retrogressive characters. But since dominance itself is an expression phenomenon, due to both environment and heredity, it must be dispensed with as a criterion. So that in the end, the primitiveness as well as the progressiveness of characters must be determined by palaeontological evidence and logic.

Fig. 29. Fasciated plants of *P. sativum umbellatum* arranged like Fig. 28 in order to show their close morphological similarity to those described by Blodgett.

This brings us to a still more important point, i. e., to the question of the validity of the work of many morphologists who have drawn deductions as to which characters in certain groups are primitive and which are progressive. These deductions are not infrequently made regardless of the very necessary support from evidence based on studies of fossils, and without paying due consideration to the effects of environment. For example, the character fasciation in peas, from the morphologist's viewpoint, is a single kind of character, for how are they to know, in the absence of experimental data, that there are, at least, two absolutely distinct forms of this character. Relatively speaking, perhaps these two forms of the fasciation character are even but remotely related. They differ as to cause and in behavior, but morphologically they are absolutely indistinguishable. If factors have a definite reality in the sense in which we think of the chemical atom, then probably a different combination of factors as well as of environmental phenomena are responsible for these two forms, just as the color, quality or character red, may be found in very distinct and relatively remotely related forms of mineral matter. And if the relationships of organisms cannot be judged by characters, how can one formulate a natural system of classification?

With the elimination of the latency conception from biological discussion, the various perplexing data on fasciation resolve themselves into an orderly and simple scheme.

From the standpoint of genetics, all fasciations may be divided into two classes; those inherited and those uninherited, the former due primarily to one or more genetic factors, the latter largely the result of external environmental conditions. The "half" and "eversporting" fasciated races of de Vries probably belong largely to the latter class. No necessity exists for and confusion results from maintaining the conception of "eversporting" fasciated races. Had the studies of de Vries been made at the present time rather than in the pioneer period of genetics, it is safe to say that this conception would never have arisen.

One may further deduce from this study of fasciation, certain conclusions regarding the phenomenon of dominance. Dominance and recessiveness in the case of the character fasciation is always dependent on the three elements held to be the basis of a character, — the primary factor or factor complex, the complex of all the other genetic factors constituting the total heritage of the organism, and the external environment. Changes in any one of these may give rise to a new character or modify an old one, the distinction between old and new being largely a matter of convenience, for, when a factor still retains its usual or common expression, except for slight modifications which do not alter its distinctive features, it may still retain its old name, but when these changes in expression are so complete as to make their relation to the same factor unrecognizable, it were better to describe them as new. This interpretation is opposed to that conception of heredity which implies dominance to be a possession of the factor or factors primarily concerned in the inheritance of a character. On the other hand, it accords with and supports in every way, the fixed factor hypothesis of East.

Literature Cited.

Baker, R. T. and Smith, H. G., The Pines of Australia. Techn. Educat. Ser. No. 16, Dept. of Publ. Instruction, N. S. W., Australia (see illustration p. 333), 1910.

Bateson, W., Mendel's Principles of Heredity. Cambridge Univ. Press, pp. 1—396, 1909.

Blaringhem, L., Anomalies héréditaires provoqués par les traumatismes. Compt. Rend. Acad. Sc. **140**, 378, 1905.

Blodgett, F. H., Fasciation in field peas. Plant World 8, 170—177, 1905.

Brévière, M., Extrait d'une Lettre de M. Brévière, de Saint-Saulge. Bull. de Soc. Bot. de France **28**, 5, 1881.

Castle, W. E., The inconstancy of unit characters. Amer. Nat. **46**, 352—362, 1912.

Church, A. H., On the relation of phyllotaxis to mechanical laws, III. Secondary growth phenomena. Oxford, 1905.

Clos, D., Essai de tératologie taxinomique. Toulouse, pp. 1—80, 1871.

Comes, O., Monographie du genre *Nicotiana*. Naples, pp. 1—80, Pl. 14, 1899.

Compton, R. H., The anatomy of the mummy pea. New Phytologist **10**, 249—255, Fig. 1—4, 1911.

Conard, H. S., Fasciation in the sweet potato. Univ. of Penn. Bot. Lab. Contrib. **2**, 205, 1901.

Cook, M. T., Teratologia de la Piña. Tomado del Primer Informe Anual de la Estaction Central Agronomica de Cuba, pp. 244—247, Lam. 43—46, 1906.

Costerus, J. C. and Smith Jr., J. J., Studies in tropical teratology. Ann. Jard. Bot. Buitenzorg, **13**, 97—118, 1896.

Daniel, L., Jardin **18**, 268—270, 276—278, 1904.

Darwin, C., Origin of Species, 6th ed. London, pp. 1—538, 1872.

— Variation of animals and plants under domestication, 2 vols. 1868.

Darwin, F., The life and letters of Charles Darwin, 2 vols. London, 1887.

Darwin, F. and Seward, A. C., More letters of Charles Darwin, 2 vols. London, 1903.

Davenport, C. B., Inheritance of characteristics in the domestic fowl. Carneg. Inst. Pub. No. **121**, 1—100, Pl. 1—12, 1910.

De Vries, H., Over de Erfelijkheid der Fasciatiën. Bot. Jaarboek **6**, 72—118, 1894.

— Sur la culture des fasciations des espèces annuelles ct bisannuelles. Rev. Gen. de Bot. **11**, 136—151, 1899.

De Vries, Die Mutationstheorie. Leipzig. 2 Bd., 1901—1903.

— Species and Varieties, their Origin by Mutation. Open Court Pub. Co., Chicago, pp. 1—847. 1906.

— The Mutation Theory. Open Court Pub. Co., Chicago, 2 vols, 1909—1910.

East, E. M., The Mendelian Notation as a Description of Physiological Facts. Am. Nat. **46**, 633—655, 1912.

— Inheritance of Flower Size in Crosses between Species of *Nicotiana*. Bot. Gaz. **55**, 177—188, Pl. VI—X, 1913.

East, E. M. and Hayes, H. K., Inheritance in Maize. Conn. Agr. Exp. Sta. Bull. No. 167 and Contrib. Lab. of Genetics, B. I. H. U. No. 9, pp. 1—142, Pl. 1—25, 1911.

Emerson, R. A., Genetic Correlation and Spurious Allelomorphism in Maize. Ann. Rpt. Nebr. Agr. Exp. Sta. **24**, 58—90, 1911.

— Inheritance of Certain "Abnormalities" in Maize. Rpt. Am. Breed. Assoc. **8**, 385—399, 1912 a.

— Getting Rid of „Abnormalities" in Corn. Ibid. **8**, 400—404, 1912 b.

Engler, A., Syllabus der Pflanzenfamilien. Berlin, pp. I—XXII + 256, 1909.

Gerarde, J., The Herball of Generall Historie of Plantes, London, 1597, 1st ed., see pp. 323—325. See also pp. 1220 (Fig. 3) —1221, ed. of 1633.

Godron, A., Melanges de Tératologie Végétale. Soc. Nat. des Sci. Naturelles Cherb. Mem. **16**, 81—127, 1871—72.

Goebel, K., Organography of Plants. Clarendon Press, Oxford, 2 vols, 1900—1905.

Gregory, R. P., The abortive development of the pollen in certain sweet-peas *(Lathyrus odoratus)*. Proc. Cambridge Phil. Soc. **13**, 148—157, Pl. 1—2, 1905.

Hasselbring, H., Types of Cuban Tobacco. Bot. Gaz. **53**, 113—126, Pl. IV—X, 1912.

Hus, H., Fasciation in *Oxalis crenata* and Experimental Production of Fasciation. Rpt. Mo. Bot. Gard. **17**, 147—152, Pl. 17—19, 1906.

— Fasciations of Known Causation. Am. Nat. **42**, 81—97, 1908.

Hus, H. and Murdock, A. W., Inheritance of Fasciation in *Zea mays* L. Plant World **14**, 88—96, 1911.

Johannsen, W., Elemente der exakten Erblichkeitslehre. G. Fischer, Jena, pp. I—VI. 515, 1909.

— The Genotype Conception of Heredity. Am. Nat. **45**, 129—159, 1911.

Kajanus, B., Über einige vegetative Anomalien bei *Trifolium pratense* L. Zeitschr. f. Abst. u. Vererb. **9**, 111—133, 1913.

Kerner, A. and Oliver, F. W., The Natural History of Plants. London, 2 vols, 1902.

Kidd, H. W., On fasciation. Science Gossip **19**, 196—198, 1883.

Klebs, G., Über künstliche Metamorphosen. Abh. naturf. Gesell. Halle, **25**, 134, 1903—1906.

— The Influence of Environment on the Forms of Plants. Darwin and Modern Science, Cambridge Univ. Press, pp. 223—246, 1909.

Knight, T. A., On cultivation of Cockscomb. Trans. Hort. Soc. of London, **4**, 321, 1822.

Knox, A. A., Fasciations in *Drosera*, Ibervillea and Cecropia, Torreya. **7**, 102—103, 1907.

— Induction, Development and Heritability of Fasciations. Carneg. Inst. Pub. No. 98, 20 pp., 1 Textfig., 5 pl., 1908.

Kraemer, H., Some notes on the modifications of color in plants. Science, n. ser. **29**, 828, 1909.

Lamarlière, L. G. de, Sur la production expérimentale de tiges et d'inflorescences fasciées. Comptes Rend. **128**, 1601, 1899.

Lock, R. H., Present State of Knowledge of Heredity in *Pisum*. Ann. Roy. Bot. Gardens, Peradeniya, Ceylon **4**, 92—111, 1908.

Lynch, I., The Evolution of Plants. Journ. Roy. Hort. Soc. **25**, 34—37, 1900.

Makousky, A., Verh. Naturf. Ver. in Brünn, **3**, 19, 1864.

Masters, M. T., Vegetable Teratology. London, pp. I—XXXVIII + 534, 1869.

Maiden, J. H., Personal letter. 1913.

Mendel, G. J., Versuche über Pflanzen-Hybriden. Verh. Naturf. Ver. in Brünn, Bd. 10, Abh. p. 1, 1865.

Molliard, M., Hypertrophie pathologique des cellules végétales. Rev. Gén. de Bot. **9**, 33, 1897.

— Cas de virescence et de fasciation d'origine parasitaire. Rev. Gen. de Bot. **12**, 323—327, 1900.

— Comptes Rend. Acad. Sci. (Paris) **139**, 930—932, 1904.

Moquin-Tandon, A., Éléments de Tératologie Végétale. Paris, pp. I—XII + 403, 1841.

Nestler, A., Untersuchungen über Fasciationen. Öster. Bot. Zeitschr. **44**, 343, 1894.

Osborn, H. F., The Continuous Origin of Certain Unit Characters as Observed by a Paleontologist. Am. Nat. **46**, 185—206, 249—278, 1912.

Owen, Fasciated medlars. Gardener's Chronicle **23**, 112—113, Fig. 21, 1885.

Penzig, O., Pflanzen-Teratologie. Genua, 2 Bd., 1890—94.

Petch, T., The physiology and diseases of *Hevea brasiliensis*. London, p. 240, 1911.

Pulney-Andy, S., Branching Palms. Trans. Linn. Soc. **26**, 661, 1869.

Reed, T., On Morphology and Physiology of Fasciated Seedlings. Ann. Bot. **26**. 388—402, 1912.

Sachs, J., Physiologische Versuche über die Keimung der Schminkbohne. Sitzungsb. d. k. k. Akad. d. Wiss. in Wien, **37**, 57, 1859.

Setchell, W. A., Studies in *Nicotiana* I. Univ. Calif. Publications in Bot. **5**, 1—86, Pls. 1—28, 1912.

Shull, G. H., A New Mendelian Ratio and Several Types of Latency. Am. Nat. **42**, 433—51, 1908.

Sorauer, P., Handbuch der Pflanzenkrankheiten. **1**, 334, 1906.

Starr, F., (See Trans. Acad. Sc., St. Louis **9**, XX), 1899.

Vasey, G., Fasciation in *Sophora secundiflora* Lag. Bot. Gaz. **12**, 160, Pl. X, 1887.

Worsdell, W. C., Fasciation; Its Meaning and Origin. New Phyt. **4**, 55—74, 1905.

White, O. E., The Bearing of Teratological Development in *Nicotiana* on Theories of Heredity. Am. Nat. **47**, 206—228, 1913.

— Studies of teratological phenomena in their relation to evolution and the problems of heredity. I. A study of certain floral abnormalities in *Nicotiana* and their bearing on theories of dominance. Am. Journ. of Botany, **1**, 23—36, Figs. 1—4, 1914.

— A new cytological staining method. Science, n. ser. **39**, 394—396, 1914.

Tables 1—26.

Explanatory note. In the majority of these tables, the various races are cited by pedigree number rather than by name. The number and name are both given in the body of the paper under "materials and methods". Tables 21, 22 and 25, representing the character of certain F_2 populations, were tabulated from selected plants and not taken from plant after plant as they stood in the row. These selected plants, however, represent practically all the various types that appeared. In all other tables of the same type, the plant numbers represent the plant populations as they stood in the row in the field-plots.

These tables are so constructed that a definite unprejudiced conception of the variableness of the expression of the fasciation factor may be easily gained. Take, for example, the character of plant number 1 in Table 6. 25 flowers were examined; 15 had 5 sepals, 9 had 6 sepals and one had 7; 8 had 5 petals, 11 had 6 petals and 6 had 7 petals; 10 had 5 stamens, 10 had 6 stamens, and 5 had 7 stamens; 12 flowers had 2 ovary-locules while the remaining 13 had 3. This plant was 19·0 dcm. high at maturity and had 27 leaves. The figures within circles (⑭) are floral leaf class range numbers placed thus to avoid lengthening the table. In tabulating the inheritance of calycanthemy, 0·0 represents absolute absence of this condition, 0·5, its presence on a portion of 1 sepal, 1·0, 2·0, 3·0, its presence on 1, 2 and 3 sepals.

Table I. Materials.

Designation		No. of Individuals	Year	Grown at
Original Mutant (300)		1	1907	Alquiza, Cuba.
Dewey's Nos. 1—99 (E. 300—309)		99	1908	No. Bloomfield, Ct.
East's Nos. 300—309		148	1909	" " "
307 × 13—29 (402)	F_1	23	1909—10	Greenhouse, B. I. H. U.
304 × „ „	F_1	23	1909—10	" "
Pure strain (×) Fasciated, No. lost		22	1909—10	" "
301—1 (Normal selection)		32	1910	B. I. H. U. Exper. Plots.
303—1 (Abnormal „)		36	1910	" " "
324 × 301	F_1	14	1910	" " "
304 × 402	F_1	39	1910	" " "
(304 × 402)—1	F_2	66	1910	" " "
(301 × 332)	F_1	2	1910	" " "
(331 × 301)	F_1	1	1910	" " "
402		15	1910	" " "
332		18	1910	" " "
373		15	1910	" " "
353		18	1910	" " "
301—1		16	1911	" " "
303—1		16	1911	" " "
301—1—2 (Selection exper.)		66	1911	" " "
301—1—29 „ „		69	1911	" " "
303—1—12 „ „		65	1911	" " "
303—1—14 „ „		39	1911	" " "
402		124	1911	No. Bloomfield, Ct.
(304 × 402)—1	F_2	31	1911	B. I. H. U. Exper. Plots.
„ „ —1—6 Het.	F_3	42	1911	" " "
(„ „)—1—7 Norm.	F_3	42	1911	" " "
(„ „)—1—8 Abn.	F_3	41	1911	" " "
(„ „)—1—10 Norm.	F_3	40	1911	" " "
(„ „)—1—12 Abn.	F_3	40	1911	" " "
(„ „)—1—14 Norm.	F_3	108	1911	" " "
(„ „)—1—28 Norm.	F_3	109	1911	" " "
(„ „)—1—31 Norm.	F_2	104	1911	" " "
(„ „)—1—34 Het.	F_2	108	1911	" " "
301—1—1 × 353—3	F_1	38	1911	" " "
353—3 × 301—1	F_1	42	1911	" " "
301—1—5 × 373	F_1	36	1911	" " "
303—1—24 × 332	F_1	40	1911	" " "
303—1—13 × 327	F_1	9	1911	" " "
402		—	1911	" " "
Transport		1797		

Table I. Materials, continued.

Designation	No. of Individuals	Year	Grown at
Transport	1797		
353	—	1911	B. I. H. U. Exper. Plots.
373	—	1911	„ „ „
Greenhouse starvation cultures 7 pots-survivors	98	1912	B. I. H. U. Greenhouse.
300 (Seed of original mutant)	33	1912	B. I. H. U. Exper. Plots (Poor soil).
301—1	5	1912	„ „ „
303—1	24	1912	„ „ „
304—1	23	1912	„ „ „
402—1	7	1912	„ „ „
373—1	6	1912	„ „ „
353—1	15	1912	„ „ „
(402—1 × 303—1—35) F_1	76	1912	„ „ „
(304 × 402)—1—6—2 Het. F_4	67	1912	„ „ „
(„ „)—1—7—10 Norm. F_4	41	1912	„ „ „
(„ „)—1—10—30 Novm. F_4	80	1912	„ „ „
(„ „)—1—12—38 Abn. F_4	64	1912	„ „ „
*(304 × 402)—1—28—32 Het. F_4	78	1912	„ „ „
301—1—1 × 353—3 F_1	25	1912	„ „ „
(353—3 × 301—1)—12 F_2	227	1912	„ „ „
(301—1—1 × 353—3)—7 F_2	75	1912	„ „ „
301—1—5 × 373 F_1	33	1912	„ „ „
(301—1—5 × 373)—17 & —5 F_2	269	1912	„ „ „
Total	3043		
Fasciation × calycanthemy			
396	18	1910	B. I. H. U. Exper. Plots.
396 × 402 F_1	20	1910	„ „ „
396	3	1911	„ „ „
(396 × 402)—1 F_2	53	1911	„ „ „
396—1	25	1912	„ „ „
301—1—2—5 × 396—1 F_1	52	1911—12	B. I. H. U. Greenhouse & Exper. Plots.
301—1—3 × 396 F_1	11	1911—12	„ „ „ „
301—1—1 × 396 F_1	12	1911—12	„ „ „ „
396 × 301—1 F_1	10	1911—12	„ „ „ „
396—1 × 303—1—200 F_1	43	1912	„ „ „ „
(396 × 301—1)—10 F_2	135	1912	„ „ „ „
(301—1—2—5 × 396—1)—11 F_2	233	1912	„ „ „ „
(301—1—1 × 396)—12 F_2	109	1912	„ „ „ „
Total	724		

Table 2. Frequency distribution

Designation	Year Grown	Grown at	No. Plants	26	27	28	29	30	31	32	33	34	35
Original Mutant (300)	1907	Alquiza, Partidos, Cuba	1										
Dewey's Nos. 1—99	1908	(Shaded) Bloomsfield, Conn.	99					1			1		
East's Nos. 301—309	1909	„ „ „	148										
East's Plant × Progeny	1909—10	B. I. H. U. Greenhouse, Mass.	22	1	3	2	1	3	3	1		2	2
301—1	1910	Experimental Plots, B. I. H. U.	32			1	1	4	2	7	1	2	2
303—1	1910	„ „ „	36						1	1	1		1
301—1—2—5	1911	„ „ „	4										
303—1—12—1911	1911	„ „ „											
303—1—200	1911	„ „ „											
(304 × 402)—1—12	1911	„ „ „	39										
(304 × 402)—1—8	1911	„ „ „	20										
(304 × 402)—1—12—38	1912	„ „ „	26										
304—1	1912	„ „ „	1										
301—1	1912	„ „ „	5			1		1					1

Table 2. Frequency distribution

Designation	Year Grown	Grown at	No. Plants	69	70	71	72	73	74	75	76	77	78
Original Mutant (300)	1907	Alquiza, Partidos, Cuba	1										
Dewey's Nos. 1—99	1908	(Shaded) Bloomsfield, Conn.	99	4	3	1	2	1	5	1	2		2
East's Nos. 301—309	1909	„ „ „	148										
East's Plant × Progeny	1909—10	B. I. H. U. Greenhouse. Mass.	22										
301—1	1910	Experimental Plots, B. I. H. U.	32										
303—1	1910	„ „ „	36	2									
301—1—2—5	1911	„ „ „	4										
303—1—12—1911	1911	„ „ „											
303—1—200	1911	„ „ „											
(304 × 402)—1—12	1911	„ „ „	39		1			1	1	1			1
(304 × 402)—1—8	1911	„ „ „	20	2	1		1	2		1		3	
(304 × 402)—1—12—38	1912	„ „ „	26		2					1			
304—1	1912	„ „ „	1										
301—1	1912	„ „ „	5										

of number of leaves per plant.

36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
											1				2		3	1	3	2	7	2	4	6	2	1	6	5	4	3	1	
	1		1	1					1																							
	5	2	3	1		1																										
3	3	3	1	2	3		3	1	1		1				1	1	1	1											1			
																			1													
1									1			1	1	2		2	1	2	3	1		1	2	2		2	1	1	1	1		3
																					1										1	1
		1		1		1			1	1	1				1		1	1				2		1	1	1	1	1		1		
1																																

of number of leaves per plant (continued 1).

79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
2	4	1		1	1	2				1		1		1	1			1						1		1	2		1
									1																	1			
														2															1
1					1												1									1			1
1	1					2	1				1						1												
	2									1																			

Table 2. Frequency distribution

Designation	Year Grown	Grown at	No. Plants	109	110	111	112	113	114
Original Mutant (300)	1907	Alquiza, Partidos, Cuba	1						
Dewey's Nos. 1—99	1908	(Shaded) Bloomsfield, Conn.	99						
East's Nos. 301—309	1909	„ „ „	148						
East's Plant × Progeny	1909—10	B. I. H. U. Greenhouse, Mass.	22						
301—1	1910	Experimental Plots, B. I. H. U.	32						
303—1	1910	„ „ „	36						
301—1—2—5	1911	„ „ „	4						
303—1—12—1911	1911	„ „ „							
303—1—200	1911	„ „ „							
(304 × 402)—1—12	1911	„ „ „	39						
(304 × 402)—1—8	1911	„ „ „	20						
(304 × 402)—1—12—38	1912	„ „ „	26		1				
304—1	1912	„ „ „	1						
301—1	1912	„ „ „	5						

Table 2. Frequency distribution

Designation	Year Grown	Grown at	No. Plants	139	140	141	142	143	144
Original Mutant (300)	1907	Alquiza, Partidos, Cuba	1						
Dewey's Nos. 1—99	1908	(Shaded) Bloomsfield, Conn.	99						
East's Nos. 301—309	1909	„ „ „	148						
East's Plant × Progeny	1909—10	B. I. H. U. Greenhouse, Mass.	22						
301—1	1910	Experimental Plots, B. I. H. U.	32						
303—1	1910	„ „ „	36						
301—1—2—5	1911	„ „ „	4						
303—1—12—1911	1911	„ „ „							
303—1—200	1911	„ „ „							
(304 × 402)—1—12	1911	„ „ „	39						
(304 × 402)—1—8	1911	„ „ „	20						
(304 × 402)—1—12—38	1912	„ „ „	26						
304—1	1912	„ „ „	1						
301—1	1912	„ „ „	5						

of number of leaves per plant (continued 2).

115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138
																	1	1					
															1								

of number of leaves per plant (continued 3).

145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167
							1															
																				1		

Table 3.

Frequency distribution of floral leaves per flower in *Nicotiana* 301—1 × 303—1.

Designation	Kind of Organ	Floral leaf classes																										Total Number	No. Flowers	No. Plants	Mode	Average
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26					
301—1	Sepals				3	29	295	371	113	8	3		3															5566	825	33	7	6·75
	Petals					5	63	396	236	74	22	9	9	3	3	2	2	1										6316			7	7·66
	Stamens					5	89	439	155	42	27	25	21	11	5	3	2				1							6357			7	7·71
	Ovary-locules		27	306	306	125	34	13	8	2	1	1	1	1														3244			3	3·93
303—1	Sepals					33	199	374	214	21	3	4	2															5976	850	34	7	7·03
	Petals					4	47	295	228	145	55	28	23	11	4	2	2	1	2	2			1					7004			7	8·24
	Stamens					4	57	296	217	81	52	48	61	12	10		2	4	2	1						2	1	7206			7	8·48
	Ovary-locules		7	169	261	218	77	47	33	15	6	6	2	3	3		1			1		1						4132			4	4·86

Table 5[1]).

Frequency distribution of floral abnormalities per flower per plant in two generations of *Nicotiana t. calyciflora.*

Plant No.			396—1	396—2	Progeny of 396—1					
					1	2	3	4	5	6
Sepals	Floral leaf class ranges	5	25	10	25	13	22	10	25	20
		6								
Petals		5	24	9	25	12	21	10	25	20
		6	1			1	1			
		7		1						
Stamens		5	18	2	20	13	19	5	23	15
		6	7	8	5		3	6	2	5
		7								
Ovary-locules		2	25	10	25	13	22	10	25	20
		3								
Calycanthemy		0·0								
		1·0								
		2·0			1					
		3·0	8	6	6	12	13	4	19	5
		4·0	17	4	18	1	9	6	6	15

---

[1]) Table 4 next page.

Table 4. Range of variability in number of leaves, height, and number of floral parts per flower per plant in *Nicotiana t. fasciata* (301—1) (303—1).

301—1

	Plant No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	31	22	23	24	25	26	27	28	29	30	31	32	33
Sepals	4												1												2									
	5	2		1			1	1		1	1	1			1			1		5		1	2	1	1		2	3	1				1	2
	6	5	15	17	9	13	10	4	2	7	15	14	12	15	8	4	5	12	6	11	9	13	7	6	15	10	14	6	9	2	5	6	6	5
	7	15	7	6	14	11	11	3	8	12	6	9	11	10	12	12	15	11	14	6	13	11	13	10	9	13	9	13	13	13	10	15	13	15
	8	3	3	1	1	1	1	6	15	5	2		1		4	8	5		5	3	3		2	9		1		2	2	10	10	4	5	3
	9	2			1											1							1	1		1		1						
	10										1	1						1																
	11																																	
	12						2	1																										
Petals	4																																	
	5		1			2						1										1												
	6		1	5	3	1	1	1		1	4	8	8	5	1	2	1		1		2	5	1		4	1	1	2					3	1
	7	15	13	8	12	12	14	10	8	11	12	12	9	11	13	9	12	7	4	19	12	10	10	13	19	10	18	12	20	10	8	18	12	13
	8	8	9	6	6	5	5	7	12	8	4	1	6	6	5	8	9	11	15	4	8	6	7	11	2	9	4	3	5	11	13	7	6	9
	9	2	1	3	2	1	2	3	4	1	1	1	2	3	3	5	1	2	4	1	2	2	6	1		4	1	3		4	4		3	2
	10			2		2		1	1	3	1				2	1	1	1	1			1				1	1	2					1	
	11				1	2					2	1						2										1						
	12									4	1	1			1		1	1		1	1							1						
	13			1			1	1																										
	14				1		1																1											
	15						1											1																
	16							2																										
	17																											1						
Stamens	4																																	
class ranges	5		1			2						1										1												
	6		5	7	3	3	3	1		2	3	9	9	7	3	2	1	1		1	3	4	1	2	9	1	1	3					2	3
	7	22	15	8	13	14	14	11	11	14	10	11	11	12	13	6	16	11	10	20	13	13	10	12	15	9	17	13	20	11	14	17	17	16
	8	3	2	3	5	1	4	8	9	5	3	1	2	3	5	9	5	1	7	1	6	3	8	10	1	9	5	3	4	7	7	8	2	5
	9		1		1	1		1	3	1	1			1	1	5	1		5	1	2		3	1		2	2	1		4	1		2	1

Stamens	Floral leaf	10		1	2		2			2				1			3		3	3	1		1	2			1				2	2		1	
		11			1	2	1				2	4	3		1	2			4				1				1				1	1		1	
		12			2			2				1		2	1	1		2	2		1	1	1	1			1		3						
		13			1		1	1	1		1	1							2				1						1	1					
		14			1				1			1							1								1								
		15				1						1																	1						
		16							2																										
		17																																	
		18																																	
		19																																	
		20						1																											
		21																																	
		22																																	
		23																																	
		24																																	
Ovary-locules		2			3	1	1	1				3	9	6				2			1														
		3	16	17	14	16	9	11	1	1	13	11	12	15	13	13	4	4	11	5	13	5	15	5	3	19	5	12	12	10		3	10	1	7
		4	8	6	1	5	10	9	12	15	8	5	1	4	9	8	12	16	3	12	8	11	6	12	14	6	5	9	6	12	11	15	13	19	15
		5	1	1	2	2	1	1	7	9	1	3			1	2	9	1	3	8	2	7	2	6	8		12	3	3	2	13	6	2	4	3
		6		1	4		2	1	1		2	1	1		1	2		2	5			1	2				2	1	1	1	1	1		1	
		7			1	1	2		1				2		1				2		1	1					1		1						
		8							2		1	1							1					2											
		9						1				1																							
		10						1																											
		11																											1						
		12							1																										
		13																											1						
		14																																	
		15																																	
		16																																	
		17																																	
		18																																	
		19																																	
		20																																	
Leaf Count			32	33	38	35	32	39	31	36	32	40	42	—	38	36	30	36	32	37	35	29	34	30	32	30	28	36	39	32	34	31	39	32	30
Height (dcm.)			18·3	17·5	19·8	19·8	19·8	19·8	—	19·8	21·4	19·8	21·4	—	19·8	19·0	17·5	20·6	20·6	22·1	22·9	21·4	18·3	21·4	20 6	—	22·1	21·4	19·0	20·6	19·0	21·4	20·6	19·0	19·0

Table 4 (continued). Range of variability in number of leaves, height, and number of floral parts per flower per plant in *Nicotiana t. fasciata* (301—1) (303—1).

303—1

		Plant No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Sepals		4																																					
		5		2	4	1	2	1		2			1			2		1	2				4	2	2			3					3		1	1	1		
		6	3	11	4	2	6	6	6	6	8	12	3	9	3	10	2	2	7	4	5		13	6	5	4	4	9	7	8	7	6	5	4	2	6	6	1	9
		7	7	6	11	12	12	13	16	9	9	7	15	11	14	11	7	11	13	12	14	Dead	6	13	8	8	15	8	14	13	9	10	8	8	14	8	16	13	10
		8	12	6	4	9	5	3	3	8	8	6	6	4	7	2	15	11	3	6	6		2	4	1	6	6	4	4	2	1	9	9	12	7	9	1	9	6
		9	3		2	1		1						1	1		1			2						4				1				1	1	1		1	
		10																								1		1									1		
		11																		1						2												1	
		12						1																						1									
Petals		4																																					
		5			1					1						1										1													
		6	1	2	2		1		3		1			1		1			4				5	4		2		5	1	2	1	1	2	1	1	2	1	1	3
		7	3	13	12	6	5	10	14	9	7	9	13	4	2	7	4	8	10	9	13		6	9	8	2	12	6	15	5	5	9	9	6	12	11	13	8	14
		8	8	3	8	11	10	4	3	11	10	3	9	3	2	11	10	5	6	6	6		4	7	6	4	7	3	7	9	6	10	11	5	7	9	4	8	4
		9	10	3	2	4	7	5	2	2	4	5	3	3	2	3	6	11	4	4	3		5	2	1	4	5	4	2	6	2	2	3	11	2	3	5	5	3
		10	2	2		3	1	4	1	1	1	5		3	10	1	3	1	1	4			2	1		2	1	2		1	1	1		1	1				
		11		2		1	1		2	1	1	1		6	3	1							1	2	1					1					2		2		1
		12	1								1	1		3	5		1				3		1			5		2			2								
		13						1						1	1								1			1		2				2		1					
		14						1				1																1										1	
		15																		1						1												1	
		16												1												(18) 1													
		17															1			(19) 1						1 (19) 1				(18) 1								(22) 1	
Stamens	class ranges	4																							1														
		5			2					1						1																							
		6	1	2	1	1	1	1		2			1	1		1			5	2	1		5	3		4		5	5	4	1	1		1	1	3	2		3
		7	4	11	12	9	8	10	15	8	6	7	12	4	2	11	3	5	12	8	11		3	10	8	2	13	3	11	6	7	9	13	4	10	11	14	13	16
		8	9	5	8	10	8	5	4	7	6	4	7	3	1	3	12	8	5	6	6		5	2	4	3	9	2	9	10	3	10	7	11	10	9	1	7	5
		9	7	1	1	1	2	2		4	3	3	3	2	2	5	7	9	2				2	4	1	2	1	2		2		2	5	5		1	1		

	Floral leaf																			
Stamens	10		4	1	1	2		2	1	6	4	2		3	1	1			1	1
	11	2			2	1	2	2	2	1	5		6	4	2		1	1	1	2
	12	1	2		1	1	4	2		2	2		6	8		1	2		4	3
	13	1				1				1			1	4	1				1	1
	14					1							1	1						
	15																			
	16						1													
	17												1			1			1	
	18																			
	19																			
	20																			
	21																			
	22																			
	23																			
	24																		(25) 1	
Ovary-locules	2																		1	
	3		11	5	2		8	9	6	4	3	4	3		11			7	13	7
	4	10	6	14	11	10	4	6	8	9	6	6	3	3	7	7	4	6	2	8
	5	10	2	6	7	12	7	5	7	4	4	11	3	2	2	14	18	11		1
	6	3	3		4	1	3	5	2	4	2	2	6	8	3				5	4
	7	1	2		1		1		1	3	5	1	2	7	2		1	1	1	4
	8	1				1	1		1	1	2		4	2			2		1	1
	9		1								2	1	2	1						
	10													1						
	11					1	1													
	12										1			1						
	13												1						1	
	14												1							
	15																			
	16																		1	
	17																			
	18																			
	19																			
	20																			
Leaf Count		31	39	37	37	36	35	38	43	35	43	31	69	41	40	33	38	36	53	51
Height (dcm.)		19·0	21·4	19·8	20·6	20·6	21·4	20·6	20·6	22·1	16·8	20·6	19·0	22·1	22·1	19·8	20·6	19·8	21·4	19·8

	Floral leaf																		
Stamens	10		5		1	2	1	4			1			1	1	1	5	2	
	11		1	3		4	1	1			1	1		1			2		1
	12		4	3	1	2		4		2	3	1		1	3			1	
	13					1													
	14					2		3			1	1						1	
	15																		
	16					1													
	17									1									
	18							1						1					
	19					1													
	20																		
	21																		
	22																		
	23																		
	24					(25) 1												(25) 1	
Ovary-locules	2			1		2		3											
	3		7	9	2	3	1	6	8	5	2	2	5	1	4	4	4	9	8
	4		5	5	6	4	13	1	9	6	6	14	11	10	12	12	9	8	12
	5		1	2	6	2	9	2	8	12	3	6	9	12	5	9	4	5	4
	6		4	4		3	1	5			3	1		1			2		1
	7		3		1	3		2			1	1			2		3		
	8		2	3	1	1		4			1	1			2		2	1	
	9		1			5	1	1		2				1					
	10			1		1											1		
	11		2			1		1			1								
	12																		
	13					1													
	14					1												1	
	15																		
	16																		
	17																		
	18																		
	19																	1	
	20					(21) 1													
Leaf Count		30	52	65	47	69	32	—	41	40	44	43	54	38	40	45	105	88	37
Height (dcm.)		—	21·4	15·3	16·8	16·8	19·8	19·0	17·5	22·1	21·4	19·8	22·1	19·0	19·8	17·5	16·0	17·5	16·8

Table 6. Range of variability in height, number of floral leaves
F_1 generation of (304 × 402) and

Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Sepals	Floral leaf class ranges	5	15	4	2	4	8	3	7	19		18	8	10	11	10	15	9	16	10	9
		6	9	10	8	16	10	7	9	6	11	6	9	12	10	9	9	13	8	8	9
		7	1	9	13	5	7	15	9		12	1	7	1	4	6	1	3	1	6	7
		8		2	2						2		1	2						1	
		9																			
		10																			
		11																			
Petals		5	8	1		1	2		1	13		6	2	5	2	2	7	2	5	1	2
		6	11	8	4	11	10	2	13	11	6	12	8	15	14	9	11	14	13	12	11
		7	6	14	20	13	12	22	11	1	19	6	14	5	9	14	7	9	7	11	11
		8		2	1		1	1				1	1								
		9																		1	
		10																			
		11																			
Stamens		5	10			1	2		4	14	1	7	2	5	3	2	6	3	3	1	3
		6	10	8	5	12	9	2	9	10	7	13	9	10	14	11	12	13	16	13	11
		7	5	15	20	12	14	22	12	1	17	5	10	7	8	11	7	6	6	10	12
		8		1				1					4	3		1					
		9																		1	
		10		1																	
		11																			
		12																			
Ovary-locules		2	12	1	1	3	6	4	2	12	3	8	6	9	6	5	10	4	5	9	3
		3	13	23	23	21	19	18	23	13	21	17	17	15	19	20	15	21	20	16	22
		4		1	1	1		3			1		2	1							
		5																			
		6																			
Leaf Count			27	25	26	26	26	27	26	27	26	25	25	26	25	25	26	26	28	26	24
Height (dcm.)			19·0	19·0	19·0	19·0	19·8	20·6	20·6	19·0	19·0	19·8	20·6	19·8	21·4	21·4	20·6	20·6	19·8	19·0	19·8

per flower per plant, number of foliage leaves per plant in an reciprocal (402—1 × 303—1—35). .

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	1[1]	2[1]
17	16	14	12	10	13	10	7	15	13	7	15	10	13	9	11	20	15	12		6	8
8	7	10	9	10	11	14	16	9	11	13	8	15	11	12	12	5	9	9	1	17	15
	2	1	4	4	1	1	2	1	1	5	2		1	3	2		1	4	12	1	2
				1															10	1	
																			1		
														1					1		
6	9	8	4		4	5	3	6	7	4	6	1	2	4	2	16	8	4		2	7
11	10	12	13	12	11	14	15	10	12	12	16	12	19	10	19	7	13	9		15	11
12	6	5	8	12	10	6	7	9	6	9	3	12	4	10	4	2	4	12	10	8	7
				1															6		
																			8		
																			1		
														⑫ 1							
5	9	11	3		6	7	4	8	8	4	6	2	6	6	5	15	9	3		6	7
15	10	9	14	13	13	13	13	9	11	13	15	10	14	8	17	10	11	11		12	10
5	6	5	8	11	6	5	7	8	6	8	4	13	5	10	3		5	11	8	7	8
				1			1												6		
																			8		
																			2		
														⑭ 1					⑭ 1		
4	11	10	8	6	3	5	6	11	8	8	5	17	7	5	4	20	8	7		7	9
21	14	15	17	19	22	19	19	14	16	17	20	8	17	19	21	5	17	17	1	18	15
						1			1				1					1	13		1
														1					6		
																			4		
																			⑪ 1		
25	25	26	26	21	25	26	25	26	25	26	27	24	24	25	25	24	26	25	30	27	32
19·8	19·8	21·4	19·8	21·4	20·6	21.4	21·4	22·1	21·4	22·1	21·4	21·4	22·9	18·3	22·1	19·0	22·1	21·4	19·8	18·3	21·4

---

[1] Reciprocal.

Table 7. Range of variability in height, number of floral leaves per flower per plant, and number of foliage leaves per plant in an F₁ generation of (301—1—5 × 373).

Plant No.	Floral leaf range classes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Sepals	5	24	18	17	20	19	21	16	23	17	20	21	21	20	20	12	21	22	22	23	20	17	18	16	23	21	21	20	20	19	21	23	21	17	13	22	23
	6	1	6	7	5	5	4	8	2	8	4	2	3	5	5	12	3	3	3	2	5	8	5	8	1	3	3	5	5	6	4	2	4	7	11	3	1
	7		1	1				1			1	2	1			1	1						2	1	1	1	1							1			1
	8					1																													1		
Petals	5	22	17	19	16	20	21	16	23	16	20	21	21	19	22	4	16	24	19	23	22	17	4	19	16	23	23	19		20	15	24	21	12	9	21	23
	6	2	8	6	8	4	4	8	2	8	4	3	3	2	3	19	8	1	6	2	3	8	16	5	6	1	2	6	24	5	10	1	3	12	14	4	1
	7	1			1	1				1	1	1	1			2	1						4	1	3	1			1				1	1	2		1
	8							1															1														
Stamens																					④ 1																
	5	23	18	23	19	22	20	19	24	19	21	21	20	19	23	6	17	23	19	24	21	21	5	18	17	23	23	21	24	23	15	23	22	19	11	22	23
	6	1	7	2	6	3	5	6	1	5	4	4	2	2	2	17	8	2	6	1	3	4	16	7	6	2	2	4	1	2	10	2	3	4	12	3	1
	7	1								1			3			2							4		2									2	2		1
	8																																				
Ovary-locules	2	25	24	25	25	25	25	25	25	23	25	25	24	24	25	21	24	22	25	25	25	25	22	25	24	24	25	23	25	25	22	25	25	25	18	25	25
	3		1							2			1	1		4	1	3					3		1	1		2			3				6		
Leaf Count		28	28	28	30	30	29	32	26	30	31	(Taken 1911)																									
Height (dcm.)		19·8	22·1	21·4	22·9	22·9	—	21·4	22·1	19·8	22·1	24·4	24·4	24·4	22·9	22·9	24·4	—	22·1	22·1	22·9	21·4	24·4	24·4	22·9	24·4	24·4	20·6	22·9	22·9	19·8	22·1	21·4	22·9	19·0	19·0	—
[1]) Leaf Count		23	27	26	22	24	22	24	26	23	23	24	24	21	20	23	25	25	24	25	22	27	27	25	27	27	23	23	23	22	22	24	25	21	(Taken 1912)		
[1]) Height (dcm.)		19·8	19·8	19·8	19·0	20·6	21·4	20·6	21·4	20·6	16·8	20·6	17·5	19·0	19·8	18·3	21·4	20·6	19·8	21·4	20·6	19·8	19·8	20·6	19·8	20·6	19·0	19·8	20·6	22·9	19·8	19·0	17·5	17·5	(1912).		

---

[1]) Taken from a different population of the same F_1 family.

Table 8a. Range of variability in number of floral leaves per flower per plant in an F_1 generation of (301—1—1 × 353—3).

Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Sepals	Floral leaf class ranges	4																							1	1		1									1			
		5	18	22	19	21	16	18	17	10	6	18	12	17	7	15	10	20	16	20	19	20	21	15	19	15	21	16	6	14	10	13	20	20	12	17	15	20	12	13
		6	7	3	6	4	8	7	6	10	18	6	9	6	15	9	9	5	8	4	6	5	4	10	5	8	4	6	1	10	14	12	5	4	12	8	9	5	12	9
		7					1		2	5	1	1	4	2	3	1	6			1						1		2		1	1			1	1				1	3
		8																	1																					
Petals		4																																						
		5	21	23	23	24	19	17	17	6	8	21	6	21	4	14	5	19	14	20	19	19	21	15	18	18	19	15	6	10	8	11	20	23	12	17	13	19	10	15
		6	4	2	2	1	5	8	5	13	15	3	16	2	7	8	3	6	10	5	6	6	4	10	7	5	6	8	1	11	13	11	4	2	9	8	11	6	13	9
		7					1		3	6	2	1	3	2	2	3	1		1							2		2		4	4	3	1		4		1		2	1
		8																																						
Stamens		4																																						1
		5	22	23	24	23	18	19	18	7	10	21	10	21	3	16	5	20	17	20	22	22	23	15	22	20	19	19	7	9	8	18	22	24	14	18	16	19	12	17
		6	3	2	1	2	6	6	5	13	15	3	12	3	8	8	4	5	7	5	3	3	2	10	3	5	6	4		14	15	6	3	1	7	7	8	6	13	6
		7					1		2	5		1	3	1	1	1												2		1	2	1			4		1			1
		8																	1											1										
Ovary-locules		2	25	25	25	24	25	25	22	24	25	25	24	25	22	25	23	25	25	25	24	24	25	25	25	25	24	24	7	25	22	25	25	25	25	24	25	25	24	23
		3				1			3	1			1		3		2				1	1					1	1			3					1			1	2

Table 8b. Reciprocal of the F_1

Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sepals	Floral leaf class ranges	4								1												
		5	21	18	18	14	21	15	18	21	11	8	16	19	14	17	14	18	19	12	20	18
		6	4	7	7	8	3	8	5	3	14	13	8	6	10	8	11	7	6	11	5	7
		7				3	1	2	2			3	1		1					2		
		8										1										
Petals		4								1												
		5	21	21	15	16	23	14	19	22	10	7	13	22	14	19	18	20	20	2	19	20
		6	4	4	9	7		10	5	2	15	13	11	3	10	6	7	5	5	9	5	5
		7			1	2	2	1	1			4	1		1					1	1	
		8										1										
Stamens		4														1						
		5	21	23	18	16	21	17	16	24	13	9	15	22	12	19	20	21	21	2	21	20
		6	4	2	7	7	3	6	8	1	12	12	10	3	11	5	5	4	4	10	4	5
		7				2	1	2	1			4			1							
		8													1							
Ovary-locules		2	25	25	25	24	25	25	24	25	25	24	22	25	22	24	24	24	24	25	25	25
		3				1			1			1	3		3	1	1	1	1			

Table 8c. Range of variability in height and number of

Plant No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Leaf Count	18	23	16	18	17	17	16	20	25	17	18	18	16	17
Height (dcm.)	12·2	14·5	13·0	14·5	15·3	15·3	14·5	15·3	16·8	16·8	16·8	17·5	15·3	14·5

cross tabulated in Table 8a.

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
												1									
15	20	15	16	18	20	17	20	18	20	15	15	13	20	14	17	22	16	18	13	18	20
9	4	10	8	7	5	7	4	7	5	10	10	10	5	11	8	2	9	6	12	6	5
1	1		1			1	1					1				1		1		1	
												1									
19	21	19	18	20	21	20	20	21	22	15	14	14	23	14	16	22	16	20	14	17	20
6	4	6	6	5	4	5	5	4	3	9	10	10	2	11	9	3	8	4	9	8	5
			1							1	1						1	1	2		
					1							1				1					
21	23	19	19	21	23	22	22	22	24	17	19	14	23	15	20	21	14	21	13	21	22
4	2	6	6	4	1	2	3	3	1	8	6	10	2	10	5	3	11	4	12	4	3
						1															
25	25	25	24	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	24	24	25
			1																1	1	

leaves per plant in an F_1 generation of (301—1—1 × 353—3).

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
15	16	18	18	19	17	17	18	17	18	22	16	23	20	16	17	19	20	19
16·8	16·8	16·8	14·5	17·5	16·8	16·0	16·8	17·5	17·5	17·5	17·5	19·0	16·8	17·5	16·0	16·8	16·8	16·0

Table 9. Range of variability in height, number of floral
plant in an F_1 generation

Plant No.	Floral leaf class ranges	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sepals	5		4	1	7	5	8	2	1	1	4	9	5	3	3	3	10	2	2	14	12
	6	9	13	13	8	15	11	18	11	13	8	8	13	13	12	9	8	14	8	8	8
	7	15	6	11	8	4	6	3	13	10	12	8	4	7	9	13	5	9	13	3	5
	8	1	2		2	1		2		1	1		3	2	1		2				
	9																				
	10																		1		
Petals	5					1	3	1		1		3		1	1	3				5	6
	6	5	6	3	4	16	11	10	4	7	5	4	12	7	5	14	8	7	5	12	10
	7	16	14	21	16	8	10	11	19	16	19	18	10	14	17	8	15	18	17	8	9
	8	4	5	1	5		1	3	2	1	1		3	3	2		2		3		
Stamens	5			1	1	2	3	1		1	1	4	4		1	6	2	1	1	6	6
	6	5	5	5	8	14	11	11	6	8	4	7	10	9	8	10	9	9	3	12	11
	7	17	14	19	14	9	10	10	17	15	19	13	9	12	15	9	12	15	19	7	8
	8	3	6		1		1	3	2	1	1	1	2	4	1		2		2		
	9																				
Ovary-locules	2	11	9	10	13	11	14	11	13	13	12	12	16	8	12	19	11	17	15	15	21
	3	13	15	14	11	13	11	14	12	12	12	13	7	15	13	6	14	7	10	10	4
	4	1	1	1	1						1		2	2				1			
Leaf Count		34	37	34	35	36	35	37	35	36	35										
Height (dcm.)		30·0	28·2	28·2	27·5	27·5	25·9	27·5	27·5	27·5	27·5	27·5	23·6	25·2	26·7	27·5	26·7	25·9	27·5	25·9	26·7

---

1) Poor soil. — Nos. 19—40. Plants tabulated later in the season. — Nos. 41—42. From

leaves per flower per plant and number of foliage leaves per of (303—1—24 × 332).

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
																				④1	
3	14	2	24	2	19	5	4	10	4	9	11	1	6	4	5	13	6	18	16	7	9
12	8	14		7	5	11	11	10	10	10	13	8	14	14	15	7	7	7	6	10	11
9	3	8		13	1	9	10	3	8	6	1	15	5	6	4	5	12		2	7	5
1		1	1	2				2	3			1		1	1				1		
				1																	
																				④1	③1
	9	5	18		7		1	1	1	3	3		2		1	6	4	13	11	7	9
3	9	18	6	3	13	8	3	9	3	9	13	8	11	6	9	8	8	11	11	13	14
19	7		1	20	5	17	21	12	19	13	9	14	12	19	14	11	13	1	3	4	1
3		2		2				3	2			3			1						
																④1					④1
	9		19		7	2		1	1	3	6	5	4		3	9	4	12	9	8	10
6	11	3	6	3	7	8	10	7	5	10	10	4	10	8	7	7	10	13	10	10	9
16	5	19		19	11	15	15	14	18	11	9	14	11	17	15	8	11		5	6	5
3		2		3				3	1	1		2							1	1	
		1																			
9	21	10	20	5	16	21	14	11	12	15	20	10	20	11	17	21	10	23	18	22	17
16	4	15	5	19	9	4	11	13	13	10	5	14	5	13	8	4	15	2	7	3	8
				1				1				1		1							
																				28	27
26·7	26.7	27·5	25·2	27·5	24·4	28·2	25·9	25·9	25·9	28·2	27·5	28·2	28·2	27·5	28·2	27·5	22·9 1)	19·8 1)	22·9 1)	28·2	27·5

a different cross of these same species, grown in 1911.

Table 10. Range of variability in calycanthemy and number of families of (396 × 301—1)

Plant No.			1	2	3	4	5	6	7	8	9	10	11¹)	12²)	13	14	15	16	17	18	19	20
Sepals	Floral leaf class ranges	5	5	4	5	5	2	1	3		2	3	27	12		6	3	2	1	5	4	3
		6	1	3		1	3	3	3	5	3	2	13	13	6		2	3	5	2	2	3
		7						1		1			1	1			1	1		1		
		8															1	1				
Petals		5	5	4	3	5	2	1	5	1	3	3	31	11			5	4	1	5	4	2
		6	1	2			2	4	1	3	2	1	10	13	6	6	2	3	5	2	2	4
		7		1		1	1			2				2						1		
Stamens		5	6	7	3	6	5	5	6	3	4	4	38	22	6	6	7	5	6	8	5	6
		6								3	1		3	4				1			1	
		7																⑫1				
Ovary-locules		2	5	7	5	5	5	3	6	3	5	5	38	19	6	6	4	4	5	5	4	4
		3	1			1		2		3			3	7			3	2	1	3	2	2
		4																				
		5																1				
Calycanthemy		0·0	2			2	3						20	20	2	5	1			1	3	1
		0·5	2	5		1	1						8	3	3		2			2	3	1
		1·0	2	1	5	2	1	1	4	2	3	4	12	3	1	1	3	3	2	4		3
		2·0		1		1		4	2	4	2	1	1				1	2	4	1		1
		3·0																1				
		4·0																1				

---

¹) 1 flower selected at random from each of 41 field-grown plants.

²) Field-grown plants.

floral leaves per flower per plant in 5 different F_1 generation and reciprocal (301—1 × 396).

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41[2])	42[2])	43[2])
5	5	3	4	5	5	1	3	7	6	6	4	5	6	3	1	6	3	2	3	24	22	25
2	2	3	2	1	1	5	2	1			2	1		2	5		2	2		1	3	
														1								
6	3	4	5	4	6	2	4	6	6	6	5	5	6	2	2	2	2	3	3	24	24	25
1	3	2	1	2		4	1	2			1	1		2	4		2	1		1	1	
														2								
7	7	6	6	6	6	6	5	8	6	6	6	6	6	3	5	6	5	4	3	25	24	25
														2	1						1	
														⑧1								
6	7	6	6	5	6	6	4	6	6	6	6	6	6	3	4	6	5	4	2	25	25	24
1				1			1	2						3	2				1			1
5	3		2	3	4	1		2	3	2	1	3	3	2	1	1	4	1	1	24	16	8
1	1	1	4	1	2		2	2		3	5	1			2				1		6	3
1	3	5		2		1	1	3	3	1		2	3	3	3	5	1	2	1	1	3	9
						4	2	1						1				1				4
																						1

Table 11. Range of variability in number of floral leaves per flower per plant in an F_1 generation of (303—1—13 × 327).

Plant No.	Floral leaf class ranges	1	2	3	4	5	6	7	8	9
Sepals	5	11	4	2	6	13	8	2	1	
	6	5	10	5	6	2	9	10	2	1
	7	1			1	1		3		
	8	1								
Petals	5	6	5		1	2	2	1		
	6	9	9	4	6	5	10	7	1	
	7	3		3	6	9	5	7	2	1
	8									
Stamens	5	8	9			5	3	2		
	6	6	4	5	7	2	9	5	1	1
	7	4	1	2	6	9	5	8	2	
	8									
Ovary-locules	2	14	14	5	6	12	11	10	1	1
	3	4		2	7	4	6	5	2	

Table 12. Range of variability in number of floral leaves per flower per plant in an F_1 generation of (324 × 301).

Plant No.	Floral leaf class ranges	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Sepals	5				1								1		
	6	8	7	4	3	2	6	8	5	5	3	5	10	4	3
	7	17	17	18	19	20	19	17	20	19	17	8	14	18	19
	8		1	3	2	2				1	5	1		3	3
	9					1									
Petals	5														
	6	4	2	1	5		3	4	3	1		6	8	4	1
	7	21	22	23	20	23	22	20	22	23	22	8	17	20	20
	8		1	1		2		1		1	3			1	4
Stamens	5	2											1		
	6	5	3		5		3	3	3	2		6	10	3	1
	7	18	18	18	19	23	19	21	20	21	20	8	14	22	18
	8		4	6	1	2	3	1	2	2	4				5
	9			1							1				1
Ovary-locules	2	4		2	1		2		2					3	
	3	18	13	15	17	11	6	2	16	11	4	1	6	9	15
	4	3	11	8	7	12	11	17		13	21	8	18	9	9
	5		1			2	6	4	1	1		5	1	3	1
	6							2						1	
	7								1						

Table 13. Frequency distribution of number of floral leaves per flower in F_1 crosses involving the factor A.

Pedigree No.	Kind of Structure	Floral leaf classes 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total of flower parts	No. of flowers	No. of plants	Mode	Ave.
324 × 301	Sepals					2	68	234	20	1						2225	325		7	6·85
	Petals						36	275	14							2253			7	6·93
	Stamens					3	38	251	30	3						2267			7	6·97
	Ovary-loc.		14	143	139	25	3	1								1163		13	3	3·58
304 × 402	Sepals					431	411	158	22	1		1				5934	1025		5	5·79
	Petals					168	458	374	14	9		1	1			6422			6	6·26
	Stamens					196	445	352	18	9	3				2	6397			6	6·24
	Ovary-loc.		268	717	28	7	4					1				2869		41	3	2·80
303—1—24 × 332	Sepals			1	1	286	428	276	32		1					6203	1025		6	6·05
	Petals				1	121	325	526	52							6657			7	6·49
	Stamens				2	151	336	488	44	4						6628			7	6·47
	Ovary-loc.		592	419	14											2497		41	2	2·44
303—1—13 × 327	Sepals					47	50	6	1							585	104		6	5·62
	Petals					17	51	36								643			6	6·18
	Stamens					27	40	37								634			6	6·09
	Ovary-loc.		74	30												238		9	2	2·29
301 × 396	Sepals					197	91	7	2							1596	297		5	5·37
	Petals					204	82	11								1589			5	5·35
	Stamens					281	14		1				1			1509			5	5·08
	Ovary-loc.		257	39		1										636		77	2	2·14
301—1—1 × 353—3	Sepals				4	561	256	29								4560	850		5	5·36
	Petals					561	244	45								4584			5	5·39
	Stamens				1	611	211	26	1							4515			5	5·31
	Ovary-loc.		833	17												1717		34	2	2·02
353—3 × 301—1	Sepals				2	700	300	22	1							5470	1025		5	5·34
	Petals				2	739	262	21	1							5430			5	5·30
	Stamens				4	785	223	12	1							5371			5	5·24
	Ovary-loc.		1009	16												2066		41	2	2·02
301—1—5 × 373	Sepals					707	173	18	2							4715	900		5	5·24
	Petals					635	234	29	2							4798			5	5·33
	Stamens				1	699	179	21								4720			5	5·24
	Ovary-loc.		868	32												1832		36	2	2·04

Total No. floral leaves 108,723 from 5551 flowers from 292 plants.

Table 14. Classification of progeny of F_1, F_2 and F_3 heterozygotes of the cross (304 × 402).

Designation	Gen.	A A	A a	a a	Total	Theoretical
(304 × 402)—1	F_2	12	33	21	66	16·50 : 33·00 : 16·50
(304 × 402)—1	F_2	5	19	7	31	7·75 : 15·50 : 7·75
(304 × 402)—1—6	F_3	11	19	12	42	10·50 : 21·00 : 10·50
(304 × 402)—1—34	F_3	27	54	28	109	27·25 : 54·50 : 27·25
(304 × 402)—1—6—2	F_4	22	26	19	67	16·75 : 33·50 : 16·75
(304 × 402)—1—28—32	F_4	21	41	16	78	19·50 : 39·00 : 19·50
	Totals	98	192	103	393	98·25 : 196·50 : 98·25

Table 15. Range of variability in height, number of floral leaves per flower per plant and number of foliage leaves per plant in an F_2 generation from (304 × 402)—1.

Plant No.	class ranges	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Sepals	4							1													1													
	5	15	24	11		5	11	24		10	25	17		25	25	24		12	18		23	13	11	25	25	21	16	21	23		19	22	24	14
	6	10	1	13	1	16	13		3	15		7	2			1		11	6	3	1	11	11			4	9	4	2	5	4	3	1	9
	7			1	8	4	1		4			1	9				9	2	1	11			2							12	2			2
	8				11				17				8				10			6		1	1							7				
	9				5				1				1				3			4										1				
	10												3				1			1														
	11																																	
	12												2				1																	
	13																																	
	14																1																	
	15																																	
	16																																	
	17																																	
Petals	4																																	
	5	5	25	10		1	4	25		3	25	11		25	25	25		5	10		25	3	4	24	25	12	15	17	22		13	23	24	12
	6	13		12		15	12			18		8						19	13			19	17	1		10	10	8	3		8	2	1	10
	7	7		3	5	9	9		9	4		6					7	1	2	3		3	4			3				6	4			3
	8				4				10				7				9			10										5				
	9				8				5				2				4			9										8				
	10				6								2							2										3				
	11																1			1														
	12				2								6																	1				
	13								1																									
	14																1																	
	15												4				1													1				
	16																1																	
	17																																	
	18												1																					
	19																																	
	20												1				1																	
	21												1																					
												㉔	1																					

	Floral leaf																																	
Stamens	4																																	
	5	6	25	11		1	4	25		6	25	13		25	25	25		7	11		25	7	4	24	25	14	16	20	23		14	23	24	14
	6	13		12		17	16		2	16		9	1					17	14			16	16	1		11	9	5	2	1	9	2	1	8
	7	6		2	6	7	5		11	3		3	6				8	1		3		2	4							7	2			3
	8				6				8				6				11			11			1							6				
	9				10				3				1				2			9										6				
	10				1								2							1										2				
	11																			1										1				
	12				1								2				1													2				
	13																																	
	14				1				1								1																	
	15												2				1																	
	16												2																					
	17																																	
	18												2				1																	
	19																																	
	20																																	
	21																																	
													(24) 1																					
Ovary-locules	2	8	25	8		8	4	25		5	25	12		25	25	25		18	15		25	10	4	25	25	12	15	21	25		20	25	25	12
	3	16		17		17	20		8	20		13	3				9	7	10			15	20			13	10	4		1	5			13
	4	1			7		1		11				5				12			5			1							8				
	5				4				4				4							14										8				
	6				3								1							5										3				
	7				9				1				5				1			1										1				
	8				1								1																	2				
	9				1				1																					1				
	10												1				1													1				
	11																1																	
	12																1																	
	13												1																					
	14												1																					
	15												1																					
	16												1																					
													(21) 1																					
Leaf Count		32	21	32	84	35	32	22	72	34	24	33	80	23	21	21	82	35	33	68	23	32	36	21	23	34	42	30	21	66	32	23	22	33
Height (dcm.)		16·0	16·0	17·5	16·0	17·5	19·0	19·0	17·5	20·6	19·0	17·5	19·0	17·5	17·5	17·5	17·5	19·0	18·3	18·3	19·0	21·4	18·3	16·8	19·8	19·8	22·9	19·0	18·3	18·3	20·6	19·0	16·8	20·6
Class		Aa	aa	Aa	AA	Aa	Aa	aa	AA	Aa	aa	Aa	AA	aa	aa	aa	AA	Aa	Aa	AA	aa	Aa	Aa	aa	aa	Aa	Aa	Aa	aa	AA	Aa	aa	aa	Aa

Table 15 (continued). Range of variability in height, number of floral leaves per flower per plant and number of foliage leaves per plant in an F_2 generation from (304 × 402)—1.

Plant No.		34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Sepals	4			1				1			1	1					2														1			
	5			16		7	1	12	14	4	11	14	11	25	10	14	23	6	25	14	13	16	25	25	10	11	25	Abnormal (AA)	13	24	23	25	10	18
	6	3	8	7	7	17	9	9	10	9	9	10	12		13	8		12		11	12	8			14	13			9	1	1		12	6
	7	8	12	1	11	1	6	3	1	5	1		2		2	3		7				1			1	1			3				3	
	8	9	5		4		7			4																								1
	9	2			2		1			2																								
	10				1		1																											
	11	1																																
	12	2																																
	13																																	
	14																																	
	15																																	
	16																																	
	17									1																								
Petals	4																1														1			
	5			5		4		6	9		10	3	8	25	6	11	23	1	25	6	6	5	25	25	2	5	24		5	25	23	25	4	8
	6		2	18	6	20		12	12	8	13	17	12		11	8	1	9		18	18	17			17	16	1		16		1		15	15
	7	10	8	2	6	1	9	7	4	4	2	5	5		8	6		14		1	1	3			6	4			4				6	1
	8	7	10		6		6			5								1																1
	9	1	4		2		7			3																								
	10		1		1					1																								
	11	2			1																													
	12	2					1			1																								
	13																																	
	14	1			2																													
	15									2																								
	16	1					2																											
	17																																	
	18	1			1																													
	19																																	
	20																																	
	21																																	
class ranges										(25) 1																								

	Floral leaf																																	
Stamens	4			(3) 1																										1			
	5			7		6		7	10		10	5	9	25	6	11	25	2	25	7	7	7	25	25	5	5	25		5	25	24	25	5	9
	6		4	15	7	19	2	16	14	11	13	15	12		14	8		12		16	18	15			15	16			16				15	15
	7	13	15	2	11		14	2	1	4	1	5	4		5	6		11		2		3			5	4			4				5	
	8	4	4		2		3			1																								1
	9	1	2				3			3	1																							
	10	1			1					1																								
	11	1								1																								
	12	2			3		2			2																								
	13																																	
	14	1																																
	15	1			1					1																								
	16	1																																
	17																																	
	18						1																											
	19																																	
	20																																	
	21																																	
										(24) 1																								
Ovary-locules	2	1		13	1	14		15	7	5	13	11	8	25	6	11	25	2	25	10	11	10	25	25	5	7	25		6	25	25	25	8	11
	3	12	18	12	16	11	13	10	18	10	11	13	17		19	13		22		15	14	15			20	18			19				17	13
	4	6	5		3		6			2		1				1		1																
	5		2				1				1																							1
	6				2		1			3																								
	7	1			1		2			2																								
	8	3			1		1																											
	9																																	
	10				1																													
	11									2																								
	12																																	
	13	1																																
	14	1																																
	15																																	
	16																																	
							(17) 1			(25) 1																								
Leaf Count		63	72	34	63	40	74	33	34	60	33	37	37	25	32	35	25	34	22	35	35	34	22	25	33	35	23		29	22	25	23	31	31
Height (dcm.)		19·0	19·8	20·6	20·6	21·4	19·8	21·4	21·4	21·4	16·8	18·3	16·0	18·3	19·0	16·0	16·0	19·0	11·4 [1]	17·5	16·8	17·5	16·0	16·8	16·8	19·0	17·5		19·0	16·8	16·0	18·3	19·0	18·3
Class		AA	AA	Aa	AA	Aa	AA	Aa	Aa	AA	Aa	Aa	Aa	aa	Aa	Aa	aa	Aa	aa	Aa	Aa	Aa	aa	aa	Aa	Aa	aa	AA	Aa	aa	aa	aa	Aa	Aa

---

[1] Grown in poor soil.

Table 16. Range of variability in number of floral leaves per flower per plant and number of foliage leaves per plant in an F_2 segregate (Aa) and its F_3 progeny (304 × 402)—1—6.

Parent	Plant No.	class ranges	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
—1—6																																												
11	Sepals	5	25	5	1	3	6	2		Abnormal	10	25		25	3	25	25	25		1			24	4	9	2	4	24	2	25	3	7	19		11	6	25	25	1	2		25		1
13		6		13	14	17	10	10	17		13				10				1	8	1	1	1	10	13	10	18	1	9		12	14	3	2	10	11			8	10			1	3
1		7		7	10	5	8	13	8		2		8		11				9	8	6	15		7	3	12	3		13		10	4	2	15	3	7			15	12	6		9	11
		8					1						15		1				14	8	17	9		3		1			1				1	7	1	1			1	1	18		13	10
		9											1						1		1			1										1							1			
		10																																									2	
		11																																										
		12																																										
		13																																										
		14																																										
		15																																										
		16																																										
		17																																										
		18																																										
4	Petals	4								Abnormal																																		
12		5	25	1				1			3	25		25		25	25	25					24	1	1		2	25	1	25		1	10	1?	3		25	25				25		
9		6		10	7	11	12	8	7		14				6								1	8	13	2	15		7		2	9	11	3	14	4			3	2			1	
		7		14	18	14	12	15	18		8		1		18				3	4	1	8		12	11	23	8		16		22	14	4	9	7	21			12	21	5		5	5
		8					1	1					11		1				8	7	14	8		3					1		1	1		3	1				8	2	9		9	12
		9											11						9	5	5	5		1										4					2		7		6	7
		10											2						2	7	5	4																			2		3	
		11																	3	1														4							2			
		12																																									1	
		13																																1										
		14																		1																								
		15																																										
		16																																										
		17																																										1
		18																																										
		19																																										
		20																																										
		21																																										

4	Stamens	Floral leaf	5	25	1		1	1	1		Abnormal	4	25		25		25	25	25					24	1	2		3	25	1	25	22	1	11		5		25	25				25		
16			6		10	7	9	7	5	6		12				6								1	7	13	6	15		9		3	7	11	1	12	5			5	2				1
5			7		14	18	15	16	18	11		9		5		18				3	5	3	7		13	10	18	7		14			16	1	12	7	19			12	22	4		6	7
			8					1	1	8				12		1				11	9	13	12		3		1			1			1	2	3	1	1			4	1	13		14	10
			9											5						4		7	3		1															3		5		4	5
			10																	5	7	2	3												2							1		1	1
			11											1						2	1														1							1			
			12											2							1														1							1			
			13																		2														3					1					
			14																																										
			15																																										
			16																																2										
			17																																										1
			18																																										
			19																																										
			20																																										
4	Ovary-locules		2	25				2	1		Abnormal	3	25		25		25	25	25					25	1	8		2	25	2	25	1	1	10	1	4	2	25	25	1			25		
20			3		24	23	25	22	23	25		21		1		25				2		1	1		21	17	24	22		20		24	23	14	8	21	23			4	25				1
1			4		1	2		1	1			1		4						5	10	2	3		3		1	1		3			1	1	3					11		4		9	11
			5											17						13	7	20	18												3					7		12		15	12
			6											2						4	5	2	3												2					2		4		1	
			7											1						1	1														5							4			
			8																																1										
			9																		1																					1			
			10																																1										1
			11																																1										
			12																																										
			13																		1																								
			14																																										
			15																																										
			16																																										
			17																																										
			18																																										
32	Leaf Count			22	32	31	33	30	33	34	68	34	25	53	24	33	25	24	26	40	75	43	51	24	33	39	34	32	23	30	23	30	30	32	52	31	34	24	24	56	32	43	23	54	45
19·0	Height (dcm.)																																												

Table 17. Range of variability in number of floral leaves, segregate plant (AA) and its F_3 gene-

Parent	Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
—1—12		Floral leaf class ranges																	
	Sepals		5	1	3	1				1									
2			6	4	5	5	1	3	2	2		4	1	1	2	5	2	4	5
9			7	12	7	10	13	10	4	12	6	12	1	9	10	10	6	12	10
8			8	6	10	7	10	7	18	10	19	7	22	12	13	6	14	9	9
1			9	2			1	1	1			2	1	3		3	3		1
3			10			1		2											
			11													1			
2			12			1		1											
			13																
			14																
			15					1											
			16																
			17																
			18																
	Petals		4																
			5		1													1	1
			6	1	2	3	1	1		1		1		2			4	3	2
			7	7	7	6	6	9	5	7	3	7		2	5	6	10	3	2
7			8	10	9	10	8	5	10	12	12	5	17	8	9	3	5	9	10
2			9	2	2	2	4		5	4	5	2	5	5	3	5	2	4	
2			10	2	3	2	3	2	5	1	5	2	2		4	7	1	2	3
			11	1		1	3	3			1	6		2	3	2	1	1	4
6			12	1		1		2					1	2	1			1	2
			13	1	1							2		2		1		1	
			14					1						2					
4			15														1		1
			16														1		
			17																
1			18					1								1			
			19																
1			20																
㉑ 1								㉖ 1											
㉔ 1																			
	Stamens		5											?			2		
1			6		3	1		2		3						1	6	1	2
6			7	12	7	11	7	11	3	6	3	12	2	4	6	6	12	6	6
6			8	6	8	6	7	2	14	14	11	1	17	5	4	2	2	11	4
1			9	1	3	1	2	1	2	1	8		4	2	6	2		1	3
2			10	4	2	1		1	5		1	3	1	2	4	4			
			11			2	1	1	1		2	1		3	3	2	2	1	5
2			12	1		1	4	1				7	1	5	2	4	1		2
			13				3	1						1		2		3	1
			14		2	1	1	1				1				1		2	1
2			15	1															1
2			16					2											
			17																
2			18											1		1			
			19																
			20			1													
								㉒ 1											
㉔ 1								㉚ 1											
	Ovary-locules		2					1											
3			3	3	1	8	9	10		3		8		3	1	7	12	6	4
5			4	13	14	8	4	4	2	9	2	4	7	5	7	4	8	7	8
4			5	2	5	3	3	3	19	11	11	6	14	7	9	2	2	5	5
1			6	3	1	3	4	2	3	1	10	3	3	3	7	5		2	4
5			7	2	2	2	3	1	1		1	3	1	4	1	4	2	1	1
1			8	2			1					1		2		1	1	3	3
			9								1								
1			10		1														
			11					2		1								1	
			12				1								1				
1			13					1								1			
1			14		1														
1			15																
1			16																
			17																
			18			1													
㉑ 1								㉔ 1											
80	Leaf Count			59	56	50	63	105	68	78	73	60	68	66	75	50	48	64	62
19·0	Height (dcm.)			20·6	19·8	21·4	22·9	21·4	19·0	21·4	22·9	19·0	19·0	24·4	25·2	19·8	22·9	24·4	22·9

in height and number of foliage leaves in an F_2 generation
ration progeny (304 × 402)—1—12.

17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
				1	1								1		1		1			4			
2	5	1	4	7	2	4	3	1	1	2	5	1	5		2	5	8	2		8	7	4	
10	14	6	5	11	7	8	15	14	14	11	8	8	12	11	14	9	9	13	10	12	9	12	6
10	6	9	12	5	7	10	6	9	10	11	10	7	7	12	7	9	7	10	15	1	8	9	17
2		6	2		7	3	1	1			2	9		1	1	1					1		2
1		1	1	1						1						1							
		1												1									
			1																				
					1																		
		1																					
																	1						
						1			1				1										
	4			6	1	1	4		3	1		1	2		2	1		1		4	2		
7	4		6	11	3	5	13	4	4	7	7	7	9	3	7	2	8	8	5	12	10	6	10
10	12	3	5	5	6	7	5	16	3	10	7	8	6	12	5	9	11	12	12	7	2	15	9
2	2		7	2	1	2	2	4	6	4	6	1	6	8	6	8	4	3	4	1	5	3	5
1	2		1		2	1		1	1		2	2		1	2	3	1	1	3	1	3	1	1
1	1	1	1	1	2	2			3	2	2	2			1								
2			4		6		1		3		1	3	1			2					2		
1					1	1						1			1				1		1		
			1			3				1					1								
					1	1																	
					1	1			1														
1		1																					
					㉔ 1									㉔ 1									
						1			?											1			
1	2			7			6		4	1	1	2	1		1	1		1		6	1	1	
7	9	2	12	12	5	5	12	5	3	6	6	10	12	6	8	7	13	12	11	14	11	14	8
8	10	1	5	3	6	7	2	17	3	13	6	3	6	13	6	9	10	8	8	3	3	7	12
2			1	1		2	1	2	3	2	3	2	5	5	2	5	2	3	3			3	4
	1		1	1		1					3	3	1		1	2		1	1		2		1
2	2		1		3	1	1		2		1	3				1				1	3		
2	1		2	1	4	2	2	1	3	1	2	1			3				1				
2			1		3	2	1		3	1		1			2						1		
					1				2		3				1				1		4		
					1	1																	
			1		1	1				1													
						2																	
			1																				
		1													1								
㉒ 1					㉔ 1									㉒ 1									
									?														
				1		1	1		1							1				1			
10	10	4	15	18	5	2	10		4		1	7	2	1	3	1		1	1	6	2	1	
7	10	7	3	3	8	10	9	18	7	12	5	9	12	9	10	11	14	16	9	15	10	8	11
3	2	2	1	1		3	1	6	2	7	11	3	9	10	3	9	10	8	11	2	6	13	14
3	2	1	1	2	2	2	1	1	4	4	4	6	2	4	5	3	1		2		1	3	
2	1	2	1		2	1	3		5		1				3				1	1	3		
		2	2		4					1	2								1				
			1								1												
			1		3																2		
		2				1			1														
		1				2				1					1						1		
		2				3																	
		2												1									
					㉜ 1																		
59	45	74	55	59	108	96	65	36	54	84	79	52	52	55	58	60	68	53	49	54	70	55	?
22·9	21·4	20·6	24·4	24·4	22·9	19·0	?	19·0	19·0	19·8	24·4	21·4	24·4	19·0	19·0	21·4	22·9	21·4	21·4	22·9	21·4	21·4	?

Table 18. Range of variability in height, number of floral per plant in an F_3 homozygous

Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Sepals	Floral leaf class ranges	5	25	25	24	24	24	25	22	24	24	25	22	25	25	24	25	23	23	25
		6			1	1	1		3	1	1		3			1		2	2	
Petals		5	25	25	25	24	25	25	25	25	24	25	23	25	25	25	25	25	25	25
		6				1					1		2							
Stamens		5	25	25	25	24	25	25	25	25	24	25	23	25	25	25	25	25	25	25
		6				1					1		2							
Ovary-locules		2	All 2-loculed																	
		3																		
Leaf Count			25	22	24	23	20	21	21	23	24	23	22	22	23	23	23	23	22	23
Height (dcm.)			17·5	16·8	17·5	19·0	19·8	18·3	19·8	19·8	19·8	19·8	19·8	20·6	19·8	19·8	19·8	19·0	19·8	19·8

Table 19. Similar to Table 18, but representing the parent (aa)

Plant No.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Sepals	Floral leaf class ranges	4													1				
		5	25	24	25	25	25	24	25	25	24	24	25	23	23	24	22	25	25
		6		1				1			1	1		2	1	1	3		
		7																	
Petals		5	25	24	25	25	25	25	25	25	24	25	25	24	25	25	23	25	25
		6		1							1			1			2		
Stamens		4														1			
		5	25	24	25	25	25	25	25	25	24	25	25	24	25	24	23	25	25
		6		1							1			1			2		
Ovary-locules		2	All 2-loculed unless																
		3																	
Leaf Count			24	20	26	23	21	25	22	22	23	21	22	20	23	24	22	22	23
Height (dcm.)			17·5	16·8	19·0	18·3	16·8	18·3	16·8	19·0	18·3	18.3	19·0	18·3	18·3	20·6	19·8	19·0	19·8

Table 20a. Ratio of abnormal to normal segregates in F_2 generations from two distinct normal varieties crossed with the fasciated race.

Designation	Gen.	Classes			Total	Theoretical Expectancy
		AA	Aa	aa		
(301—1—5 × 373)—17 + —15	F_2	194		75	269	201·75 : 67·25
(353—3 × 301—1)—12	F_2	44	110	73	227	56·75 : 112·5 : 56·75
(301—4—1 × 353—3)—7	F_2	11	47	17	75	18·75 : 37·5 : 18·75
		212		90	302	226·5 : 75·5

leaves per flower per plant and number of foliage leaves population (aa) [(304 × 402)—1—7].

19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
24 1	25	24 1	25	24 1	24	23 2	25	25	23 2	24 1	25	24 1	23 2	25	22 3	23 2	25	24 1	25	25	24 1
25	25	25	25	25	25	25	25	25	24 1	24 1	25	25	25	25	24 1	25	25	25	25	25	24 1
25	25	25	25	25	25	25	25	25	24 1	24 1	25	25	25	25	24 1	25	25	25	25	25	24 1
All 2-loculed																					
23	24	26	25	23	23	23	22	23	23	25	23	23	24	21	24	23	24	21	—	21	23
19·8	19·8	19·8	19·8	19·8	19·8	19·8	19·8	20·6	19·8	19·0	19·8	19·8	19·8	19·8	19·8	19·8	19·0	19·8	—	19·8	20·6

character of the progeny of a different F_2 homozygote [(304 × 402)—1—10).

18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
25	25	25	25	25	24 1	24 1	24 1	25	25	25	24 1	23 1 1	25	25	25	25	35	25	25	24 1
25	25	25	25	25	25	24 1	25	25	25	25	25	25	25	25	24 1	25	25	25	25	25
25	25	25	25	25	25	24 1	25	25	25	25	25	25	25	25	25	1 24	35	25	25	25
otherwise noted															24 1					
23	23	23	24	21	21	25	21	22	22	22	23	23	23	22	24	24	24	22	23	25
19·8	19·8	20·6	20·6	19·8	19·8	19·8	19 8	19·8	19·8	19·8	19·8	19·8	19·8	19·8	19·0	19·8	19·8	19·8	19·8	20·6

Table 20b. Ratio of fasciate-stemmed plants to normal-stemmed plants in the population noted in Table 20a.

Designation	Gen.	Classes		Total
		Fasciate-stem	Normal-stem	
(301—1—5 × 373)—17 + —5	F_2	45	224	269
(353—3 × 301—1)—12	F_2	26	201	227
(301—1—1 × 353—3)—7	F_2	6	69	75

Table 21. Range of variability in height, number of floral
per plant in an F_2 generation

Parents		Plant No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1–5	1–17		Floral leaf class ranges																			
19	22	Sepals	5	17		14	3	12	9	24			20	22	17	20	25	12	14	25	24	24
5	3		6	8	5	11	13	12	13	1	2	4	5	3	8	5		11	11		1	1
			7		16		8	1	3		19	17						1				
1			8		4		1				4	4						1				
			9																			
			10																			
20	24	Petals	5	16		5		3		25			18	24	11	18	25	7	12	23	25	24
4	1		6	9		18	2	5	7		1		6	1	11	7		14	12	2		1
1			7		10	2	20	6	14		7	22	1		3			3	1			
			8		13		3	6	3		13	3						1				
			9		1			2			3											
			10					1	1		1											
			11					2														
			12																			
			13		1																	
22	23	Stamens	5	19		12		3		25			18	24	14	22	25	10	15	23	25	25
3	2		6	6		11	5	6	11			1	7	1	9	3		12	8	2		
			7		13	2	13	6	6		6	20			2			1	2			
			8		7		3	2	6		13	4										
			9		3		3	4	1		3											
			10		1		1	4			1							1				
			11						1		1							1				
			12								1											
			13	⑮	1																	
25	22	Ovary-locules	2	25		22	3	7	3	25		2	23	25	22	21	25	15	17	24	25	25
	3		3		7	3	10	10	17			14	2		3	4		7	8	1		
			4		12		9	2	4		3	9						1				
			5		4													1				
			6				1	4			2											
			7				1	2			2											
			8		2		1		1		1							1				
			9																			
			10																			
			11																			
			12																			
30	—	Leaf Count		43	46	26	43	46	19	16	22	38	27	25	24	30	16	46	22	18	18	20
22·9	—	Height (dcm.)		20·6	24·4	19·8	19·0	22·9	19·8	19·8	16·8	20·6	19·8	19·0	19·8	21·4	19·0	19·8	21·4	19·8	19·8	19·8

leaves per flower per plant and number of foliage leaves [(301—1—5 × 373)—17 and —5].

20	21	22	23	24	25	25·5	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	41·5
5	18	25	7	15	18	25	24	15	24	18	17	18		2	1	4	22	13	17	3	22		2
12	5		11	10	4		1	8	1	6	6	6		13	10	13	3	10	8	13	3	3	11
5	2		7		3			1		1	2	1		7	14	7		2		9		14	11
3								1						2		1						8	1
														1									
													⑭ 1										
	12	25		9	7	25	21	8	24	17	9	13		2			19	3	13		24		
3	12		7	16	12		4	13	1	7	24	11		4	1	6	6	8	10		1		9
8	1		17		6			3		1	2	1		7	12	16		14	2	16		8	16
14			1					1						10	10	3				9		12	
														1	2							5	
														1									
													⑲ 1										
	12	25		9	6	25	22	5	25	16	11	18		2			23	2	14		24		
4	12		6	16	13		3	16		8	13	7		2		7	2	9	9	4	1		11
7	1		19		5			4		1	1			9	13	11		13	2	13		9	14
11					1									8	10	4		1		8		12	
1															1	1						4	
2														1	1	2							
														2									
													⑭ 1	⑰ 1									
2	21	25	5	22	15	25	23	20	25	19	23	22		2		1	25	3	20	3	25		12
13	4		20	3	10		2	5		6	2	3		17	16	21		22	5	22		10	13
7														2	7							14	
2															1	1							
1														2		1						1	
														2		1							
															1								
													1										
56	27	22	26	22	21	24	24	21	28	29	27	31	36	65	28	24	20	32	33	40	28	25	33
22·9	24·4	22·9	22·1	19·8	17·5	20·6	21·4	18·3	20·6	22 1	20·6	17·5	10·7	20·6	19·0	20·6	19·0	18·3	25·9	20·6	23·6	22·9	23·6

Table 21 (continued). Range of variability in height, number of
per plant in an F_2 generation

Parents		Plant No.			42	43	44	45	45·7	46	47	48	49	50	51	52	53	54	55	56	57	58
1–5	1–17																				?	
19	22	Sepals	Floral leaf class ranges	5	22	9		25	24	20	3	6	4	1	9	11	22	24	9	6	14	1
5	3			6	2	14	10			5		18	13	9	13	11	2	1	13	16	9	4
				7	1	2	14		1		16	1	8	12	3	1	1		3	3	1	9
1				8			1				6			3								7·
				9																		
				10																		
20	24	Petals		5	14	10		24	25	12	2	6	5		1	? 3	22	25	1	5	9	
4	1			6	9	10	5	1		10	2	16	13	4	12	17	2		11	13	15	1
1				7	2	5	16			3	12	3	7	16	12	2	1		13	7	1	9
				8			4				8			4								8
				9							1			1								1
				10																		
				11																		1
				12																		
				13																		1
22	23	Stamens		5	16	14		25	25	12	2	7	4	1	2	4	23	25	2	5	14	
3	2			6	7	9	10			12	3	16	15	5	8	19	1		19	12	11	3
				7	2	2	14			1	12	2	6	11	15		1		4	8		12
				8			1				7			4								3
				9							1											
				10																		
				11										3								2
				12																		
				13										1							⑭	1
25	22	Ovary-locules		2	19	25	3	25	25	22	6	19	19	9	2	13	25	24	23	21	20	6
	3			3	6		18			3	17	6	6	11	23	10		1	2	4	5	13
				4			4				2			2								4
				5										1								
				6										2								1
				7																		
				8																		1
				9																		
				10																		
				11																		
				12																		
30	—	Leaf Count			22	25	27	23	18	25	22	27	21	32	21	24	24	23	26	23	30	30
22·9	—	Height (dcm.)			21·4	21·4	21·4	19·8	22·9	24·4	20·6	20.6	18·3	22·1	19·8	22·1	22·1	20·6	24·4	21.4	25·9	19·8

floral leaves per flower per plant and number of foliage leaves [(301—1—5 × 373)—17 and —5].

59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
25	11	9	13	14	25		25	5	15	25	10	23	18	17	17	1							
		6	10	10		1		16	9		2	2	7	8	3	10							
		8	2	1		8		3	1						5	9							
		2				16		1															
25	11	3	2	6	25		25	1	15	25	2	23	21	19		2							
		8	16	12		2		6	10		3	2	4	6		6							
		10	7	7		3		17			5				18	9							
		3				18		1			2				6	1							
						2									1								
		1														1							
																1							
25	11	2	3	12	25		25	2	19	25	1	24	21	22		2							
		8	14	11				10	6		7	1	4	3		7							
		12	8	2		8		13			2				16	8							
		2				15					2				4	1							
						1									4								
															1								
																1							
		1				1																	
															(15)	1							
25	11	7	11	24	25		25	16	24	25		25	23	25		1							
		11	14	1		8		9	1		11		2		21	13							
		5				16									2	5							
		1				1									2								
		1									1												
																1							
24	16	31	26	29	18	38	23	19	25	16	33	27	28	26	24	70	25	121	87	70	70	111	40
18·3	15·3	21·4	23·6	20·6	18·3	18·3	19·8	18·3	18·3	19·8	19·8	21·4	20·6	19·8	21·4	18·3	26·7	22·9	16·0	21·4	23·6	20·6	22·9

Table 22. Range of variability in height, number of floral per plant in an F_2 generation

Plant No.	Floral leaf class ranges	1	2	3	5	6	7	8	10	11	13	14	15	16	17	18	19	20	21	22	24	25	25·5
Sepals	5	24	8	6	24			12		11			17	9	1	3	9	19	23	2	3	11	
	6	1	13	10	1	3	3	10		12	3	1	6	15	2	9	12	6	2	12	10	9	2
	7		4	9		17	22	3	3	2	12	15	1	1	20	12	4			11	12	5	21
	8					5			22		10	9			2	1							1
	9																						1
	10												1										
Petals	5	23	7	6	24			8		11			11	9		4	5	17	24	1	2	14	
	6	2	14	10	1	2		13		12	4	1	12	12	2	10	14	8	1	9	8	8	2
	7		4	9		20	23	4	2	2	9	12	1	4	19	11	2			15	15	3	19
	8					2	2		16		8	8			3		1						1
	9					1			5		4	3	1		1								1
	10								1			1											1
	11																						1
	12																						
	13								1														
	14																						
Stamens	5	24	6	9	24			9		20	1		12	14		4	14	19	25	2	1	16	
	6	1	13	15	1	5		12	1	5		1	11	9	6	12	8	6		9	9	9	2
	7		6	1		13	21	4	4		12	16	1	2	16	8	3			13	14		18
	8					6	4		6		6	5			3	1				1	1		
	9								10		5		1										2
	10								3		1	2											1
	11								1			1											2
	12																						
	13					1																	
	14																						
Ovary-locules	2	25	14	18	25	2		23		24	1		23	24	10	10	18	25	25	12	11	19	
	3		11	7		17	13	2		1	12	8	1	1	14	15	5			13	14	6	19
	4					5	10		7		12	13			1		1						1
	5					1	1		14			3	1				1						1
	6						1		3			1											2
	7								1														
	8																						2
Leaf Count		13	22	38	16	20	23	16	46	23	28	21	24	17	35	18	34	13	28	19	21	32	42
Height (dcm.)		16·8	16·0	10·7	17·5	17·5	16·0	18·3	21·4	22·1	19·0	16·0	20·6	16·0	21·4	18·3	19·8	15·3	22·9	15·3	18·3	19·8	23·6

leaves per flower per plant and number of foliage leaves from (353 × 301) and reciprocal.

26	27	28	30	31	32	33	34	35	35·5	36	38	39	40	41	42	43	44	45	46	48	49	50	51
3	21	25	17	5	11	12		7		11	25	6		24	2	2		1	24	16	1		
6	2		8	17	5	11	3	15	1	12		17	1	1	9	13	5	8	1	7	8	9	4
15	2			3	8	1	20	2	11	2		2	12		10	10	16	12		2	13	13	13
1					1	1	2	1	13				12		3		4	4			3	2	3
																						1	
6	20	25	18	6	11	18		9		18	25			24	1				24	16	1		
7	3		6	15	10	6	4	10		6		1		1	2	13			1	8	2	2	2
11	2		1	4	4	1	21	6	19	1		20	10		11	6	19	3		1	15	13	13
1									6			4	14		6	6	5	17			7	8	4
													1				1	3				1	1
																		2				1	
7	23	25	18	7	18	23	3	7	22	20	25			25	2	9		1	25	20	1		
11	2		6	13	6	2	4	13	3	5					11	12	1	3		4	2	3	6
7			1	4	1		17	5				22	13		11	4	20	8		1	16	8	11
				1			1					3	11		1		3	5			5	13	3
													1				1	6					
																		1			1		
																						1	
																		1					
22	23	25	20	21	20	25	6	24		23	25			25	2	25	10	4	25	25	6	4	
3	2		5	3	5		18	1	15	2		18	10		16		14	9			18	17	6
							1		9			6	13		7		1	2			1	3	11
				1					1			1	1					4					3
													1					5				1	
																		1					
17	27	18	14	19	17	20	41	15	42	28	17	27	27	20	61	16	22	38	15	32	33	16	24
17·5	21·4	19·0	15·3	16·0	13·7	15·3	20·6	10·7	21·4	20·6	21·4	18·3	20·6	21·4	24·4	16·8	20·6	22·9	16·0	22·1	19·0	16·0	19·0

Table 22 (continued). Range of variability in height, number of
per plant in an F_2 generation

Plant No.			52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
Floral leaf class ranges	Sepals	5	15	25	25	25		6		5	7			25		25		24	17		25		4	19
		6	9				3	5	3	10	11	1	1		3		3	1	8	1		1	11	5
		7	1				15	4	22	10	7	8	19		18		12			5		8	10	1
		8					6					16	5		4		9			19		15		
		9					1										1							
		10																				1		
	Petals	5	16	25	25	24	1	2		5	6			25		25		25	18		25	1	4	21
		6	8			1	1	7		7	12		2		4		4		7			5	11	3
		7	1				14	6	22	13	7	8	21		17		17			2		10	10	1
		8					8		3			13	2		4		2			22		7		
		9					1					3								1		1		
		10										1												
		11															2							
		12																						
		13																				1		
		14																						
	Stamens	5	17	25	25	24		4		6	9			25		25	1	25	20		25	3	5	21
		6	7			1	4	5	1	7	15		5		3		2		5			8	12	3
		7	1				11	6	21	12	1	6	18		16		9			10		10	8	
		8					4		1			10			6		6			13		3		1
		9					6		1			3	1				4			2				
		10							1			3	1				1							
		11										1					1							
		12										1												
		13										1					1							
		14																			⑯	1		
	Ovary-locules	2	24	25	25	25	1	4		14	23		9	25		25		25	25		25	10	21	24
		3	1				10	11	15	11	2	8	13		13		3			11		12	4	1
		4					12		10			12	2		11		15			13		2		
		5					2					4	1		1		4			1				
		6										1					2					1		
		7															1							
		8																						
Leaf Count			29	22	20	14	21	12	42	16	24	19	37	15	24	15	64	21	23	22	27	43	37	17
Height (dcm.)			19·8	21·4	20·6	18·3	14·5	14·5	16·0	13·7	19·0	16·8	22·1	16·8	13·7	18·2	22·1	22·9	16·0	18·3	20·6	16·0	22·9	168.

floral leaves per flower per plant and number of foliage leaves from (353 × 301) and reciprocal.

75	76	77	78	79	80	81	82	83	84	85	86	87	89	90	91	92	93	94	96	97	98	99	101
5				25			25	20	25	24			25	21	25	22	15	7	25	25	12	24	
11	4		17		2	4		5		1		6		4		2	8	16			11	1	4
7	14	10	8		10	13					12	14				1	2	2			2		16
2	7	15			12	8					13	5											5
					1																		
1			12	25			25	13	25	25			25	21	25	18	15	3	25	25	13	25	
4	2		8		1	4		10			1	2		4		6	10	17			11		2
17	17	13	5		11	14		2			12	15				1		5			1		16
2	6	8			12	4					12	7											5
1		2				3																	2
		2			1																		
												1											
1			13	25			25	12	25	25			25	21	25	21	16	1	24	25	14	25	
6	3		6		1	5		11			2	3		4		4	7	22	1		11		3
16	19	8	6		12	15		2			19	11					2	2					13
2	3	11			11	5					3	6											5
		4									1	1											4
		1										2											
		1			1							1											
												⑰ 1											
8	1		24	25		1	25	25	25	25		2	25	25	25	22	21	20	25	25	21	25	
17	12	1	1		10	14					18	15				3	4	5			4		17
	12	16			15	8					3	6											5
		5				2					4	1											3
		2																					
		1																					
												1											
15	20	71	19	19	18	26	14	19	16	17	26	23	20	18	14	15	15	19	24	18	83	17	24
13·0	13·0	22·9	17·5	18·3	13·7	14·5	15·3	20·6	16·0	16·8	13·0	22·9	19·8	17·5	15·3	11·4	15·3	13·7	18·3	16·0	24·4	17·5	17·5

Table 23. Frequency distribution of segregate classes in an F_2 generation from (301 × 396) and reciprocal.

Designation	Count	AABB	AABb	AaBB	AaBb	AAbb	Aabb	aaBB	aaBb	aabb	Total	Total No. of Plants
(301—1—1 × 396)—12	1	1	5	9	21	1	12	6	14	18	87	109
	2	2	12	11	19	1	18	9	20	16	108	
	3	3	11	6	18	8	11	8	19	23	107	
(301—1—2—5 × 396—1)—11	1	3	13	29	79	3	21	12	33	18	211	233
	2	7	24	24	68	5	25	13	43	21	230	
	3	8	28	11	51	5	35	20	48	29	235	
(396 × 301—1)—10	1	3	6	18	37	2	9	7	27	12	121	135
	2	5	14	16	37	3	15	8	19	14	131	
	3	5	14	14	39	3	13	6	22	15	131	
Total	2	14	50	51	124	9	58	30	82	51	469	477
	3	16	53	31	108	16	59	34	89	67	473	
Theoretical		29·56	59·12	59·12	118·24	29·56	59·12	29·56	59·12	29·56	473	
Theoretical Ratio		1	2	2	4	1	2	1	2	1	16	

		Abnormal	Normal	Total	Theoretical Ratio
Calycanthemy × Normal (B × b)	2	351 B	118 b	469	351·75 B : 117·25 b
	3	331 B	142 b	473	357·75 B : 119·25 b
Fasciation (A) × Normal (a)	2	306 A	163 a	469	As above
	3	283 A	190 a	473	

Table 24. Fasciate- to normal-stemmed plants in an F_2 population from (396 × 301) and reciprocal.

	Designation	Fasciated	Normal	Total
1 st count	(301—1—1 × 396)—12	12	97	109
	(301—1—2—5 × 396—1)—11	26	207	233
	(396 × 301—1)—10	8	127	135
	Total 1 st count	46	431	477
	Total 2 nd count	50	427	477
	Total 3 rd count	50	427	477
	Total Count by alterations in normal phyllotaxy	55	422	477

Table 25. Character of an F_2 population [(396 × 301)—12], [(301—1—2—5 × 396—1)—11], [(396 × 301—1)—10], as regards variability in height, number of floral leaves per flower per plant, number of foliage leaves per plant and the presence or absence of calycanthemy.

	Class	AABB									AABb																	
	Plant No.	9	25	32	41	46	49	52	61	65	5	14	19	20	26	30	31	35	38	39	44	54	59	66	70	71	72	74
Sepals	5	1	5	3	1	1	1	16	6	1	2	1		2	8	2	1	1			3	3		3	2			12
	6	4	7	10	22	5	2	8	8	17	10	4	1	5	10	5	17	5			4	10	2	4	9	1	5	11
	7	13	12	5	2	6		1	7	6	9	17	10	15	6	10	6	17	5	15	13	12	16	13	13	8	19	1
	8	3	1	7		8	1		4	1	3	3	7	3	1	8	1	7	17	9	4		7	5	5	10	1	
	9					3	1												2		1					3		
	10	1																								2		
	11						2													1						1		
	12	2																										
	13	1					(14) 1				1																	
Petals	3				1																							
	4				2																							
	5	5	18	.9	18	5	3	8	8	9	9	2		2	11	7	1	2			2	1		3	2		2	14
	6	9	6	4	4	4	1	15	5	9	12	6		5	10	7	15	8		3	7	8	2	4	10	1	6	10
	7	6		6		6	1	2	4	3	2	12	12	14	4	7	8	11	4	15	3	7	15	10	9	11	12	
	8	3	1	4		1	1		3	3		3	6	3		3	1	2	9	5	5	5	7	6	1	5	4	
	9			2		5			5	1	1	2		1				1	4	1	6	4	1	1	2			
	10					1	1				1					1		1	3		2			1	1	2		
	11					1													3							1	1	
	12						1																			2		
	13																		1							1		
	14																			1						1		
	15	1																										
	16																									1		
	17	1																										
Stamens	4																		1									
class ranges	5				1			3	4	5	1	4		1	8		1	1			1	2		2	4		2	13
	6	9	4		6	6		13	5	15	7	7		4	9	6	4	7		3	2	5		2	6	1	9	9
	7	4	9	1	8	2	4	8	3	5	6	6	8	8	7	8	8	8	5	17	5	8	12	4	4	12	9	1
	8	5	8	8	5	5		1	5		4	2	6	5		5	4	4	5	1	3	6	7	2	6	4		1
	9	1	3	6	5	4			5		1	2	3	3	1	2	3	1	1	1	3	1	5	3	1	1		
	10	1	1	5					3		2	2		2		2	4	3	2	1	3	2		2	2		1	

Stamens	Floral leaf	11						1				2		1	1			1		3		4		1	4	1		3	
		12	1		3			3				2			1		2		1	2	1	2			4		2		
		13						1					1							3		1	1		1	1	1	1	
		14	2		1			1	1											1							2		
		15			1																	1							
		16											1								1				1		1		
		17																									1		
		18							3																				
		19																											
			(20)2																	(20)1									
Ovary-locules		2	3		1	1		1	5	1	4	2	2	1	2	5	1	5	3			1	5	3	4	10		2	21
		3	7	12	2	13	5	3	16	8	20	13	16	10	17	17	15	13	17	9	8	9	14	19	4	10	5	18	3
		4	8	7	9	4	11		3	9	1		3	7	2	2	4	2	1	2	13	1	1	2	4		12	2	
		5	1	2	2	2	1						2		1	1	1	5	2	2	2	4	2	1	4		1		
		6	2		2	4				1		6	1		1		1		1	6	1	6	3		4		4	1	
		7		2	2	1	4			3		2	1		1		1		1	2		2			2	3	1		
		8	1	1	5		2			1		1					2			1		1					1	1	
		9		1	1			1		2		1			1					1		1				2			
		10						1	1																2		1		
		11			1															1									
		12	1					1																				1	
		13	1																										
		14																							1				
		15	(20)1					1																					
Calycanthemy		0·0								1				25	17			21	11		11	4		19	4	18	23	24	4
		0·5								2					5				7		4	1	1	5	4	1	1		1
		1·0	1				1		1	5	1	3	1		1	6	2	3	6		4	13	6	1	11	2		1	9
		2·0	5	1		1	2		2	5	4	11	12	H	2	13	10	1	1	H	3	5	11		5	4	1		11
		3·0	9	6	8	3	4		10	6	9	8	8			4	10				3	2	6		1				
		4·0	6	9	7	17	7	1	10	4	10	3	3			2	3						1						
		5·0	2	7	6	3	6	3	2	2																			
		6·0	1	2	4	1	3	2			1		1																
		7·0																											
		8·0	1																										
		9·0						2																					
		10·0																											
Leaf Count			41	26	34	34	15	76	28	14	38	34	17	33	18	32	20	16	42	20	31	51	22	29	29	43	85	50	31
Height (dcm.)			13·7	15·3	16·8	13·7	13·7	21·4	11·4	15·3	21·4	18·3	17·5	17·5	18·3	20·6	15.3	14·5	20·6	14·5	19·8	24·4	18·9	16·0	18·3	16·0	16·8	19·8	17·5

Table 25 (continued 1). Character of an F_2 population [(396 × 301)—12], [(301—1—2—5 × 396—1)—11], [(396 × 301—1)—10], as regards variability in height, number of floral leaves per flower per plant, number of foliage leaves per plant and the presence or absence of calycanthemy.

Class		AaBB				AaBb											AAbb			Aabb						
Plant No.		16	22	27	36	3	4	6	7	10	21	28	42	53	58	73	40	47	51	12	13	33	43	48	56	69
Sepals	5	23	14	15	25	7	13	1	18	16	4	6	1	1	11			3	5	8	1	9	14	12	12	8
	6	2	11	9		12	11	4	6	7	9	13	2	4	13	2	3	2	8	14	17	13	6	13	11	15
	7			1		6	1	12	1	2	8	4	18	16	1	17	9	3	12	3	7	3			2	2
	8							7			4	2	4	4		6	11	13								
	9							1									1	4								
	10																									
	11																1									
	12																									
	13																									
Petals	3																									
	4				2																					
	5	24	24	21	22	7	14	1	22	23	1	14	4	3	13			4	4	13		12	18	18	16	21
	6	1	1	4	1	15	9	1	3	1	6	8	15	11	10	5	5	2	5	10	18	9	2	6	7	3
	7					3	2	13		1	10	2	5	8	2	16	10	2	13	2	7	4		1	1	1
	8							5			5	1		3		4	7	5	2						1	
	9							4			1							2								
	10							1			1		1				2		1							
	11										1							3								
	12																	6								
	13																	1								
	14																									
	15																1									
	16																									
	17																									
Stamens	class ranges 4																									
	5	4		20	1	2	16		23	23		17	4	6	13			5	4	16	2	18	25	24	16	22
	6	19	2	3	22	8	9	2	2	1	6	7	8	14	11	7	10		7	8	17	6		1	7	3
	7	2	13	2	2	7		7		1	8	1	8	4	1	16	6	5	11	1	6	1			2	
	8		10			6		8			3		3	1		1	3	4								
	9							3			5		1					1	1							
	10					1		3			1							2								

Stamens	Floral leaf	11					1		2									1	2	1							
		12										1		1						1							
		13															1	4	3								
		14																1	2								
		15										1							1								
		16																									
		17																									
		18																									
		19																									
Ovary-locules		2	16	2	23	18		24	3	25	22	1	11		7	25	4		5	9	17	17	19	25	25	14	25
		3	9	21	2	7	22	1	16		3	17	13	20	15		19	15		14	8	8	6			11	
		4		2					4			1	1	3	3		1	4	9								
		5					1					4		1			1	2	1	1							
		6										1						3	2	1							
		7					1		1			1							3								
		8							1					1					3								
		9																	1								
		10					1												1								
		11																									
		12																									
		13																1									
		14																									
		15																									
Calycanthemy		0·0			7			25	15	8	21	21	6		1	25	20	25	21	25	25	25	24	23	25	25	25
		0·5			5		4		7	9	2	3	5		3		1		4				1	1			
		1·0			7		9			2			6	4	10		2							1			
		2·0	3		4	9	7	H	3	2	2	1	8	21	9	H	2							H			
		3·0	19	13	2	15	4			3					2												
		4·0	2	11		1	1			1																	
		5·0	1	1																							
		6·0																									
		7·0																									
		8·0																									
		9·0																									
		10·0																									
Leaf Count			10	16	22	24	13	33	20	17	19	17	17	19	33	19	15	19	57	35	17	32	12	21	24	13	20
Height (dcm.)			10·7	13·7	19·0	23·6	16·0	22·1	16·0	19·0	17·5	17·5	13·7	14·5	20·6	18·3	17·5	17·5	24·4	24·4	19·0	15·3	13·7	16·0	24·4	13·0	17·5

Table 25 (continued 2). Character of an F_2 population [(396 × 301)—12], [(301—1—2—5 × 396—1)—11], [(396 × 301—1)—10], as regards variability in height, number of floral leaves per flower per plant, number of foliage leaves per plant and the presence or absence of calycanthemy.

Class		aaBB				aaBb					aabb								
Plant No.	class ranges	8	15	17	63	18	23	24	45	57	1	2	11	29	34	37	55	60	62	75
Sepals	5	20	24	22	20	25	23	23	23	25	24	25	25	23	25	23	25	25	25	25
	6	5	1	3	5		1	2	2		1			2						
	7						1													
	8																			
	9																			
	10																			
	11																			
	12																			
	13																			
Petals	3	1																		
	4				1															
	5	22	25	24	10	25	23	25	25	25	24	25	25	24	25	23	25	25	25	25
	6	2		1	13		2				1									
	7				1									1						
	8																			
	9																			
	10																			
	11																			
	12																			
	13																			
	14																			
	15																			
	16																			
	17																			
Stamens	4	10	11	1	3	25	25	25	25	25	25	25	25	25	25	23	25	25	25	25
	5	14	13	23	18															
	6	1	1	1	4															
	7																			
	8																			
	9																			
	10																			

Stamens	Floral leaf	11																			
		12																			
		13																			
		14																			
		15																			
		16																			
		17																			
		18																			
		19																			
Ovary-locules		2	3	24	23	21	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
		3	22	1	2	4															
		4																			
		5																			
		6																			
		7																			
		8																			
		9																			
		10																			
		11																			
		12																			
		13																			
		14																			
		15																			
Calycanthemy		0·0					25	19	22	23	25	24	24	25	25	25	23	25	25	25	25
		0·5						3	1	1			1				2				
		1·0				1		3	2	1		1									
		2·0	7	1	10	1	H				H										
		3·0	12	23	12	18															
		4·0	5	1	2	5															
		5·0	1		1																
		6·0																			
		7·0																			
		8·0																			
		9·0																			
		10·0																			
Leaf Count			14	17	12	17	14	15	10	17	12	15	16	12	13	12	10	14	13	16	10
Height (dcm.)			16·0	18·3	14·5	14·5	19·8	20·6	16·0	16·8	16·0	13·0	16·0	16·8	15·3	16·0	13·7	16·0	16·8	19·8	12·2

wohl die älteste Arbeit, welche uns von einer zweifellosen Klonumbildung bei Bakterien berichtet, die auch von den extremsten Anhängern der Lehre von den Bakterienmutationen bis vor kurzem als „Mutation“ aufgefaßt werden mußte. Die Sachlage ist die folgende.

Gruber hatte in einer 307 Tage alten Kultur des Vibrio Finkler-Prior auf Gelatineplatten neben zahlreichen typischen Kolonien anscheinend als Verunreinigung in geringer Zahl Kolonien einer weniger rasch verflüssigenden Bakterienart gefunden. Dieselben erregten seine Aufmerksamkeit dadurch, daß sie bei oberflächlicher Betrachtung eine gewisse Ähnlichkeit mit den Kolonien des Choleravibrio zeigten. Auf Grund dieser Beobachtung stellte dann Firtsch seine Untersuchungen an.

Die von Gruber gefundene, anfangs als Verunreinigung angesprochene Form des Finkler-Priorschen Vibrio unterschied sich vom Typus vor allem durch das Verhalten auf Nährgelatine; der Verflüssigungstrichter im Gelatinestich bildete sich viel langsamer und nahm andere Form an als beim Typus; zudem war die Beweglichkeit des neuen Vibrio geringer, das Bild der Oberflächenkolonie abweichend usw. Bei längerem Suchen wurde dann auf weiteren älteren Kulturen wiederholt dieselbe abweichende Form gefunden, außerdem aber kamen noch zwei andere abweichende Formen zur Beobachtung. Dabei stellte es sich heraus, daß der am wenigsten abweichende Typ in 33—54 Tage alten Gelatinestichkulturen (Vibrio I), der zuerst gefundene, mittlere Typ (Vibrio II) in 48 Tagen bis $^1/_2$ Jahr alten Kulturen auftrat, während der letzte Typ (Vibrio III) in über einem Jahr alten Gelatinekulturen vorherrschte. Während nun Vibrio I seine Eigenschaften nicht dauernd behielt, sondern relativ leicht, wenigstens teilweise, in den ursprünglichen Typus rückführbar war, gelang diese Rückwandlung bei Vibrio II und III bei regelmäßigem Verimpfen innerhalb einer über vier Monate sich erstreckenden Arbeitszeit nicht. Bemerkenswert ist weiter, daß außer den drei besonders hervortretenden Typen noch relativ konstante Zwischentypen gefunden wurden.

Als wichtigstes Ergebnis führen wir die folgenden Worte Firtschs an: Aus ein und derselben Bakterienart wurden vier Formen gezogen, die in ihrer Kolonienform (teilweise auch in der mikroskopischen Wuchsform) durchgreifende Verschiedenheiten zeigen und von denen wenigstens drei (der typische Proteus Vibrio II und III) diese unterscheidenden Merkmale mit solcher Zähigkeit bewahren, daß sie einzeln für sich untersucht — nach dem bisher geübten Modus der Artbestimmung — zweifellos als besondere Arten aufgefaßt werden müßten.

M. a. W.: Firtsch hat in seinem Vibrio II und III eine „Bakterienmutation“ im Sinne zahlreicher neuerer Bakteriologen im Jahre 1886 festgestellt; er hat aber gleichzeitig in seinem Vibrio I eine Dauermodifikation im Sinne Jollos usw. (vgl. Lehmann, 1916, S. 297) beschrieben.

Durchaus bemerkenswert und lehrreich für die Bakteriologen, welche jeden in einer älteren Kultur beobachteten etwas abweichenden Stamm als Mutation bezeichnen, ist aber der folgende Satz aus Firtschs Arbeit: So bedeutend die Unterschiede im Aussehen der Kolonien (der verschiedenen Vibrionenformen) auf Nährgelatine sind, so lassen sie sich doch mit großer Wahrscheinlichkeit auf verschiedene Grade von Abschwächung der Wachstumsenergie überhaupt, der Fähigkeit, die Gelatine zu verflüssigen und der Eigenbewegung zurückführen; Abschwächungsvorgänge, die gewiß nicht bedeutsamer sind, als der Verlust der Fähigkeit, Sporen zu bilden, der Gärtätigkeit, der Virulenz.

Wie recht Firtsch hatte, geht aus den Untersuchungen Fürsts hervor.

Als wichtigste Vervollkommnung der Firtschschen Versuche wird von Fürst das Burrische Tuschepunktverfahren zur Isolierung einzelner Bakterien als Ausgangsmaterial der Stämme eingeführt. Wenn allerdings Fürst hierdurch glaubt, mit reinen Linien zu arbeiten, so verfällt er in denselben Fehler, welcher von so vielen neuzeitlichen Bakteriologen, die sich mit „Bakterienmutationen" beschäftigten, gemacht wurde. Es handelt sich bei solchen auf ein Individuum zurückgehenden Bakterienstämmen nicht um reine Linien, sondern um „Klone", wie ja den Lesern dieser Zeitschrift geläufig ist.

Bei vier solchen Klonen des Vibrio Finkler-Prior ließen sich nun die von Firtsch gemachten Angaben hinsichtlich der Zeit des Auftretens der Vibrionenformen und ihrer kulturellen Eigenschaften in völlig übereinstimmender Weise wiedererlangen. Zudem werden die Untersuchungen Firtschs noch in bedeutsamer Weise erweitert.

Einmal untersuchte Fürst, ob durch Auslese von Plus- oder Minusvarianten der in der Größe sehr variablen Individuen des Typus eine Verschiebung des Gipfels der Variationskurve in der Nachkommenschaft möglich sei. Es gelang dies nicht. Ebensowenig hatte eine solche Auslese einen Einfluß auf das hämolytische und peptolysierende oder agglutinative Vermögen der aus ihnen hervorgegangenen Stämme.

Die verschiedenen Typen aber lassen sich, wie Fürst zeigte, noch durch eine Reihe anderer Merkmale, als Firtsch angegeben hatte, differenzieren. So konnte festgestellt werden, daß bei den extremsten Typen mit dem Verlust der Beweglichkeit der Verlust des Geißelapparates Hand in Hand ging. Parallel damit ging weiterhin der Verlust der spezifischen — also der Gelatineagglutinabilität. Hingegen blieb das Säurebildungsvermögen bei allen Typen das gleiche.

Für die Frage der „Bakterienmutationen" weitaus am wichtigsten ist indessen die Feststellung Fürsts, daß wohl bei regelmäßiger Weiterimpfung von Gelatine- zu Gelatinekultur die extremen Stämme sich konstant erhalten, daß aber bei längerem Stehen der Kultur auch Vibrio II und III Firtschs stets von 2—2$^1/_2$ Monaten an nach und nach wieder in den Normaltypus zurückschlagen.

Damit aber ist, wie Fürst zu Ende seiner Arbeit mit Recht sagte, bewiesen, daß es sich wenigstens bei den von Firtsch beobachteten, mehr oder weniger lang vererbbaren Variationen nicht um echte Mutationsvorgänge, die zur Entstehung neuer Arten Anlaß geben, handeln kann.

In einem Nachwort hebt dies Gruber noch weiter hervor, indem er die beobachteten Abweichungen von der Norm nicht als genotypischer, sondern phänotypischer Natur aufgefaßt haben will: „Das lang dauernde Bestehenbleiben der neu aufgetretenen Eigentümlichkeiten bei den Nachkommen auch unter veränderter Lebenslage (z. B. bei Umzüchtung auf Agar) ist nicht echte Vererbung, sondern „falsche", auf „Nachwirkung" (Woltereck) beruhende".

So sind also die ursprünglich nur als „Mutationen" deutbaren Firtschschen neuen Vibrionenformen durch Fürst als Dauermodifikationen erwiesen.

Es ist das eine wertvolle Lehre für die Zukunft. Findet man abweichende, über kürzere oder längere Zeit konstante Bakterienstämme, so bezeichne man sie nicht sogleich als Mutationen, sondern als Klonumbildungen, bis ihre Natur als Dauermodifikation durch Rückbildung erwiesen ist, oder aber es später einmal möglich wird, die eine oder andere als auf genotypischer Grundlage zustandekommend zu erweisen. E. Lehmann.

Kießling, L. Erbanalytische Untersuchungen über die Spelzenfarbe des Weizens. Ein Beitrag zur angewandten Vererbungslehre. Landwirtschaftliches Jahrbuch für Bayern 1914. Nr. 2.

Vor 10 Jahren wurde vom Verfasser mit der Beobachtung der Folgen spontan bei Weizen *(Triticum vulgare)* eingetretener Bastardierungen begonnen. Eine erste Mitteilung über dieselben erfolgte 1908 in „Fühlings landwirtschaftlicher Zeitung“, S. 737. Einige Nachkommenschaften zeigten bezüglich des in erster Linie beobachteten Merkmals, Spelzenfarbe ein Verhalten, das der Annahme des *Pisum*-Schemas entspricht: braune Spelzenfarbe : Br × weiße Spelzenfarbe : br in F_1 : Brbr mit Dominanz von Braun, in F_2 : BrBr; Brbr; brBr; brbr oder aber ein Verhalten, das mit der Annahme des *Zea*-Schemas in Einklang zu bringen ist. Bei anderen ergaben sich aber andere Spaltungsverhältnisse, insbesondere erschienen weniger weißspelzige Pflanzen aus braunspelzigen und es gaben auch extrahierte weißspelzige Pflanzen, die rein vererben sollten, einzelne braunspelzige Pflanzen. Die Erklärung, die Nilsson-Ehle für Fälle seiner Hafer- und Weizenbastardierungen anwandte und die mehrere gleichsinnig wirkende Anlagen für eine sichtbare Eigenschaft annimmt, wurde dann zur Erklärung der selbst beobachteten abweichenden Fälle benützt. Sind zwei Anlagen für braun vorhanden, von welchen die eine: Br_1 gewöhnliches Braun, die andere: Br_2 helleres Braun und beide zusammen: $Br_1 Br_2$ dunkleres Braun bewirken, so würde sich in F_2 ergeben:

$Br_1 Br_1 Br_2 Br_2$ dunkelbraun, rein vererbend,
$Br_1 Br_1 br_2 br_2$ braun, rein vererbend,
$br_1 br_1 Br_2 Br_2$ hellbraun, rein vererbend,
$br_1 br_1 br_2 br_2$ weiß, rein vererbend,
$Br_1 Br_1 Br_2 br_2$ dunkelbraun, nach 1 : 2 : 1 spaltend,
$Br_1 br_1 Br_2 Br_2$ dunkelbraun, nach 1 : 2 : 1 spaltend,
$Br_1 br_1 Br_2 br_2$ braun, nach 1 : 2 : 2 : 4 : 1 : 2 : 1 : 2 : 1 spaltend,
$Br_1 br_1 br_2 br_2$ hellbraun, nach 1 : 2 : 1 spaltend,
$br_1 br_1 Br_2 br_2$ sehr hellbraun, fast weiß, nach 1 : 2 : 1 spaltend.

Die Spaltungsverhältnisse aufgefundener Individuen von Winter- und Sommerweizen wurden nun weiter verfolgt und ihr Ergebnis durch die erwähnte Erklärung zu deuten versucht. Die Individualauslesen, innerhalb welcher jährlich einige Individuen ausgelesen wurden, standen dabei ohne künstlichen Schutz gegen Fremdbestäubung nebeneinander. Es ergaben sich verschiedene Abweichungen: wiederholte Abspaltung von braunspelzigen Individuen in der Nachkommenschaft von weißspelzigen, Spaltungszahlen, die sich nicht in das Schema einfügen, unregelmäßig erscheinen, oder die Annahme von mehr als zwei Anlagen für braune Spelzenfarbe nahelegen, Auftauchen von Abstufungen der Braunfärbung und abweichende Spaltung nach solchen Individuen, Auftreten von Fleckung der Spelzen und dergleichen. Weiterhin ergab eine genauere Durchmusterung des Versuchsmateriales und einer Reihe von Formenkreisen von Sommer- und Winterweizen, daß es rein weiße Spelzen nicht gibt, und eine Untersuchung der Farbe der Weizenspelzen legt die Annahme nahe, daß die verschiedene Färbung der Spelzen durch Abbau oder Umwandlung des Chlorophylls bewirkt wird. Beide Feststellungen führten zu dem Schluß, daß es sich bei Braun und Weiß nicht um die Wirkung einer Anlage und ihres Fehlens handeln könne, sondern daß auch weißspelzige Individuen irgend welche Anlage für Braunspelzigkeit besitzen. Der Verfasser nimmt im weiteren Verlauf zur Erklärung der Verhältnisse eine Anzahl von Anlagen an, die alle Braunfärbung bedingen, aber verschiedene Wirkungsintensitäten aufweisen. Br ist dabei die Gesamtanlage für Braunfärbung; $Br_1\,Br_2\,Br_3$ usw. sind Einzelanlagen, die alle eine bedeutendere Intensität bewirken und z. B. die untereinander nur wenig verschiedenen Werte 4,001, 4,002, 4,003 besitzen, während $Br_0^m\ Br_0^n\ Br_0^o$ Einzelanlagen sind, die eine geringere Intensität bewirken und z. B. die untereinander wenig verschiedenen Werte 0,999, 1,000, 1,001 aufweisen; br_1, br_2, br_0^m, br_0^n deutet dann das Fehlen der betreffenden Anlage an. Die bei der Berechnung der Gesamtintensität sich ergebenden Intensitäten 4, 3,99, 3,97 und die nächsten Stufen würden braun entsprechen, die um 1 gelegenen Stufen weiß und die zwischen 1,5—2,5 liegenden hellbraun, Eine monohybride Spaltung würde demnach in der zweiten Generation geben: 1mal $Br_1\,Br_1\,Br_0\,Br_0$; 2mal $Br_1\,br_1\,Br_0\,Br_0$; 1mal $br_1\,br_1\,Br_0\,B_0$ und die Berechnung der Gesamtintensität dann Intensität: $\frac{4+4+1+1}{4} = 2{,}5$; $\frac{4+0+1+1}{3} = 2$; $\frac{0+0+1+1}{2} = 1$. Die dihybride Spaltung, mit Br_0 bei beiden Eltern, würde sich dann wie folgt darstellen:

Strukturformeln:	Intensitätsrechnung:	Farbe:
a) $1 \cdot Br_1 Br_1 Br_2 Br_2 Br_0 Br_0$	$4+4+4+4+1+1 = 18:6 = 6$	= braun,
b) $2 \cdot Br_1 Br_1 Br_2\, br_2 Br_0 Br_0$	$4+4+4+0+1+1 = 14:5 = 2{,}8$	= braun,
c) $2 \cdot Br_1\, br_1 Br_2 Br_2 Br_0 Br_0$	$4+0+4+4+1+1 = 14:5 = 2{,}8$	= braun,
d) $1 \cdot Br_1 Br_1\, br_2\, br_2 Br_0 Br_0$	$4+4+0+0+1+1 = 10:4 = 2{,}5$	= hellbraun[1]),
e) $4 \cdot Br_1\, br_1 Br_2\, br_2 Br_0 Br_0$	$4+0+4+0+1+1 = 10:4 = 2{,}5$	= hellbraun[1]),
f) $1 \cdot br_1\, br_1 Br_2 Br_2 Br_0 Br_0$	$0+0+4+4+1+1 = 10:4 = 2{,}5$	= hellbraun[1]),
g) $2 \cdot Br_1\, br_1\, br_2\, br_2 Br_0 Br_0$	$4+0+0+0+1+1 = 6:3 = 2{,}0$	= hellbraun,
h) $2 \cdot br_1\, br_1 Br_2\, br_2 Br_0 Br_0$	$0+0+4+0+1+1 = 6:3 = 2{,}0$	= hellbraun,
i) $1 \cdot br_1\, br_1\, br_2\, br_2 Br_0 Br_0$	$0+0+0+0+1+1 = 2:2 = 1{,}0$	= weiß.

Auch wenn Br_0 nur von einem Elter kommt, wobei F_1 dann z. B. $Br_1\,br_1\,Br_0\,br_0$ ist, läßt sich die dihybride Spaltung und die Intensitätsrechnung in analoger Weise darstellen.

Zur Erklärung der beobachteten Fleckung: auf fast weißen Spelzen dunklere Zeichnung entlang den Rändern und Nerven, wird ein Fleckungsfaktor angenommen, der nur wirkt, wenn Farbfaktoren vorhanden sind. (FBr gefleckt, Fbr nicht.) Heterozygoten für Br sowohl wie für F (Brbr und Ff) würden kleinere oder seltenere Flecke aufweisen. Eine weitere Möglichkeit bei der Erklärung der Fleckung ist gegeben, wenn eine zweite Anlage für Braunfärbung angenommen wird, die von F nicht beeinflußt wird. Es läßt sich aber auch ohne Annahme einer besonderen Anlage für Fleckung auskommen nur mit Annahme von bestimmten Braunanlagen, welche neben Braunfärbung auch die Fleckung veranlassen.

Die vom Verfasser aufgestellte Intensitätshypothese arbeitet mit einer größeren Zahl von Anlagen, die sich voneinander nur durch verschieden abgestufte Wirkung unterscheiden. Die in der Arbeit verwendeten bestimmten Zahlen für diese Wirkung sind nur beispielsweise. Die Verteilung der Anlagen bei der Geschlechtszellenbildung und die Zusammentritte der verschieden veranlagten Geschlechtszellen erfolgt entsprechend Mendel, Vorhandensein und Fehlen je einer Anlage wird dazu angenommen. Die Begriffe Dominanz, Rezessivität, Prävalenz, Epistasie und Hypostasie sind

---

[1]) An der Grenze von braun.

durch einen Zahlenwert, die Intensitätszahl, ersetzt, welche die gegenseitige Beeinflussung der einzelnen Anlagen scharf ausdrückt.

In Beziehung auf die Züchtung läßt die Arbeit auch wieder den Wert der Fortsetzung der Auslese, auch bei Selbstbefruchtern, erkennen, da sie nachweist, daß viele Spaltungen sich der Wahrnehmung entziehen und daß erkennbare Folgen von, nicht als solche erkannter, Heterozygotie nach weiterer Spaltung früher oder später auftauchen können. Fruwirth.

Stark, Peter. Untersuchungen über die Variabilität des Laubblattquirls bei Paris quadrifolia. Zeitschr. f. Bot. 1915, 7, S. 673—766.

Die statistische Untersuchung findet immer mehr Eingang in die botanische Wissenschaft. Für die Abstammungs- und Vererbungslehre ist das, wie längst erkannt, von besonderer Bedeutung. Denn die auf statistischer Grundlage gewonnenen Ergebnisse bilden eine sichere Grundlage, auf welcher Abstammungs- und Vererbungslehre weiterbauen können.

Der Verf. der vorliegenden Arbeit hat es nun unternommen, die Variabilität des Laubblattquirls bei *Paris quadrifolia* auf statistischer Grundlage nach den verschiedensten Richtungen zu untersuchen und ist dabei auf sehr interessante Tatsachen und zu weitgehender Klärung der untersuchten Variabilitätsverhältnisse gekommen. Betrachten wir die Hauptergebnisse:

Die Blattzahl der Einbeere schwankt in dem untersuchten Gebiet zwischen 1 und 7; die Variabilitätskurve zeigt einen sehr steilen Gipfel über 4. Die Gesamtkurve aller Standorte zeigt infolge der stärkeren Ausbildung des linken Schenkels eine unverkennbare Asymmetrie. Der Mittelwert liegt dementsprechend etwas unter 4,0. Umfangreiche Messungen führten dann zu dem Ergebnis, daß gleichzeitig mit der Gliederzahl auch Stengellänge und Blattlänge ansteigen.

Das Gesamtmaterial läßt sich in blühende und nichtblühende Stengel einteilen; bei den letzteren überwiegen die Minus-, bei den ersteren die Plusvarianten. Bei den blühenden Sprossen ist also der rechte, bei den nichtblühenden der linke Gipfel besonders stark ausgeprägt.

Junge Pflanzen haben eine geringe Gliederzahl, ältere steigen unter unregelmäßigen Oszillationen bis zum normalen Viererstadium, bei günstigen Verhältnissen aber bis zu höheren Quirlzahlen empor. Bei Betrachtung größerer Genossenschaften auf statistischer Basis findet man im Verlauf der Generationen bestimmte Gesetzmäßigkeiten in diesen Oszillationen, welche in einem steten Hinfluten zum Mittelwert gipfeln.

Zwischen Haupt- und Seitensproß bestehen enge Beziehungen im Variationsverhalten. Die Seitensprosse wiederholen die Erscheinungen der Hauptsprosse im allgemeinen. Durch Verfaulung von Rhizomstücken kommt es zu Einzelindividuen, niederzähligen Zwergexemplaren, die sich auch durch künstliche Zerstückelung erzielen lassen.

Von besonderem Interesse sind weiter die Resultate, welche für die Abhängigkeit der Variabilität von äußeren Bedingungen vorliegen. Verf. hat in bezug auf Unterlage, Pflanzengenossenschaft usw. verschiedene Standorte getrennt untersucht. Er findet eine enge Beziehung zur Unterlage. Kalkböden begünstigen Plus-, Kieselböden Minusvarianten. Auch wirkt Bodenfeuchtigkeit, Belichtung usw. erhöhend. Sehr interessant ist es, die Angaben über die Variabilität in Beziehung zu den Beständen im einzelnen zu verfolgen. Mykorrhizenbildung scheint Plusvarianten zu begünstigen.

Sodann glaubt Verf., daß sich eine gewisse Erblichkeit der Gliederzahlverhältnisse darin kund tut, daß die Nachkommen hochzähliger Sprosse denen niederzähliger in mancher Hinsicht überlegen sind. Sie keimen rascher, wahrscheinlich auch in größerer Anzahl und steigen in ihrer Entwicklung schneller zu höheren Gliederzahlen empor. Das durch Aussaatversuche gewonnene Material ist zwar nicht sehr umfangreich, die soeben ausgeführte Überlegenheit der Abkommen von Plusvarianten ist aber nicht zu bezweifeln. Indessen läßt sich hier wohl sicher nicht von Vererbung, sondern nur von einem ernährungs-modifikatorischen Einfluß der Eltergeneration sprechen, etwa wie bei der sogenannten kongenitalen Vererbung, zieht sich ja doch durch die gesamten hier erörterten Variationsverhältnisse der Einfluß der Ernährung auf die Variabilität der Gliederzahl. Eine exakte Vererbungsuntersuchung von *Paris* stößt aber auf ganz erhebliche technische Schwierigkeiten, welche hauptsächlich in der langen Dauer bis zum Eintritt der Blühreife begründet sind.

Die Schwankungen der Gliederzahl bei *Paris quadrifolia* werden dann auch unter phylogenetischen Gesichtspunkten erörtert. Verf. schließt auf eine ständige Zunahme und gleichzeitig damit eine entsprechende Vermehrung der Quirlzahlen in der *Trillium-Paris*-Gruppe.

Es ist hervorzuheben, daß sämtliche Zahlenwerte auf exakt kritischen Werten beruhen.

Die Untersuchungen sollen noch weiter auf die Blütenglieder ausgedehnt werden. Ref. würde als besonders wünschenswert erachten, wenn dabei auch der Korrelationsverhältnisse der Zahlen in den aufeinanderfolgenden Wirteln eingehend gedacht würde.

Alles in allem bietet die Arbeit eine Fülle interessanter Tatsachen und es wäre nur zu wünschen, daß bald ähnlich vielseitige Variationsuntersuchungen an anderen Pflanzen angestellt würden. E. Lehmann.

Zeitschrift für induktive Abstammungs- und Vererbungslehre

Inhaltsverzeichnis von Bd. XVI Heft 1/2

Abhandlungen

Referate

[Reprinted from PSYCHE, Vol. XXI, No. 1]

OBSERVATIONS ON THE RELATION BETWEEN FLOWER COLOR AND INSECTS.

BY E. M. EAST and R. W. GLASER.
Bussey Institution, Harvard University.

In 1909 a cross was made between the small red flowered *Nicotiana forgetiana* Hort (Sand) and *Nicotiana alata* Lk. and Otto var. *grandiflora* Comes, the large white N. affinis of horticulture, for the purpose of studying certain problems of heredity. About fourteen thousand plants of the second, third and fourth hybrid generation have been grown, and it has been established beyond a reasonable doubt that each plant is completely self-sterile though it crosses easily with any of its neighbors. Several hundred carefully controlled self-pollinations have not yielded a single seed, while histological studies have shown self-fertilization to be practically impossible. On the other hand, hundreds of artificial cross pollinations have yielded capsules full of seed in almost every instance, showing with what ease cross-fertilization takes place, for artificial pollination is usually not as successful as natural pollination. The fact that every capsule formed naturally on these plants must have resulted from a cross-pollination produced by an insect, serves to excuse our adding to the already huge literature on the relations between insects and plants. The sixteen different color forms that have segregated from the original cross permit observations on the percentage of flowers cross-fertilized and the selective value, if any, of distinct color varieties.

Our knowledge of the behavior of insects relative to flowers has been greatly extended during the past few years by the work of Plateau, Forel, Lovell, Grænicher and others, but it has resulted in that obscurity which precedes aggregation and precipitation by disclosing the marvelous complexity of the relation. The adjustment between certain insect forms and certain types of flowers is just as obvious now as when pointed out by Sprengel, but few entomologists or botanists will admit its adequate interpretation by the simple natural selection idea as believed by Hermann Müller and his followers who did not see the obstacles to this view as plainly as did Darwin.

The attitude of botanists has been affected chiefly by genetic investigation. Mendelian research and hypotheses regarding mutational evolution have at least gained a serious reconsideration of the origin, inheritance, and cause of survival of flower forms. Investigations on cross- and self-fertilization, by giving a clear and reasonable interpretation of the vigor of first generation hybrids and the converse—the apparent deterioration through inbreeding hybrids—have caused us to view mechanisms for cross-pollination at a new angle. Self-pollination gives inherently stranger races (vigor not masked by heterozygosis) and insures reproduction, but practically precludes the trial of variations not of decisive value or of various recombinations of new variations with old characters. On the other hand, cross pollination, while permitting the survival of weak types through the vigor of heterozygosis, and while rendering reproduction more dubious, does assure a trial of all new variations in all the combinations possible in a mendelian sense.

The appreciation of the intricacy of the behavior of insects toward flowers is due primarily to the knowledge of insect sense organs, to the ingenuity of the experiments of animal psychologists, and to the passing of the tendency to interpret all the actions of the lower animals as tropisms.

For these reasons the question as to whether particular flower colors have a survival value due to the preference of certain insects for them, upon which we have gathered a few data, would probably be answered somewhat as follows by the majority of biologists. Excluding any question of olfactory sense, it may be assumed that insects perceive color differences from short distances but seldom if ever exercise a choice. Night flyers, of course, perceive white much more easily than colors. These conclusions are supported by the data in the following table:

Flower color.	Total number of flowers on 10 average plants.	Total number of flowers fertilized.	Per cent. of flowers fertilized.
White	18,035	7,052	39.10
Yellow	26,686	4,836	18.12
Red	14,165	2,154	15.21
Purple	9,721	1,628	16.74

Ten average plants of each of the four colors—white, yellow, red and purple—were selected at random. The total number of flowers produced on each color type during the flowering season (July 15 to October 15) was determined by counting the places on the racemes where flowers had been. The number of capsules present was assumed to be the number of flowers fertilized, although this count is not as accurate as the first by reason of the accidental loss of capsules. Long experience with Nicotianas, however, leads us to believe that this error is small.

The first point to be noted is the comparatively small percentage of cross-pollination by insects. Numerous experiments on artificial cross-pollination have shown that a very small amount of pollen causes normal development of the capsules, yet the yellow, red and purple types had only about 17 per cent. of their blossoms crossed. According to the table, the percentage of white flowers fertilized was more than twice as high as any of the colored types. The reason for this is obvious. From the beginning of the flowering period, about July 15, to the end period of summer heat, about September 15, the flowers opened at about 4 p. m. and remained open until about 7.30 a.m. During the last month of flowering, the weather was so cool that the flowers also were open throughout the day. Nearly two thirds of the fertilizations occurred during the last month as could be determined by the positions of the flowers on the racemes. Furthermore the percentage of fertilizations on the white type during the last month was about the same as on the colored types. Roughly, one might say then that about 6 per cent. of the pollinations of the colored types were made by night-flyers (Sphingidæ, etc.), while during the same period these insects pollinated from 20 per cent. to 25 per cent. of the white type. In other words, there was a high rate of selection of white flowers during the period when the flowers were pollinated at night, but there was no selection of colors when daylight pollinations were made by the Hymenoptera and Diptera that frequented the plants.

Reprinted from the BOTANICAL GAZETTE, 57: No. 3, March 1914

CURRENT LITERATURE

BOOK REVIEWS

Genetics

Some one once said, perhaps more epigrammatically than truthfully, "the progress of a science is in direct proportion to the mathematics used in its development." Whether generally true or not, the constant and rapid progress of genetics since the introduction of Mendel's mathematical notation is a great argument in favor of the statement. At the same time, the chaos that can result from the unwarranted use of mathematics without other premise or analysis is only too familiar to biologists. It has seemed as if those best trained in mathematics were the first to forget that their science is merely a shorthand method of stating the facts, that no more can come out than goes into the mill, though it should come out in a shape more conducive to thorough mental digestion. The slogan of certain biometricians, "there are no premises, all is treatment," has brought many biologists to that state of mind in which they could take seriously POE's sly dig in the "Purloined Letter." In speaking of the necessity of putting oneself in the mental attitude of the thief if the hiding place of the stolen letter were to be discovered, he says: "As poet *and* mathematician, he (the thief) would reason well; as mere mathematician he could not have reasoned at all."

It remained for JOHANNSEN to prove that he is poet, biologist, and mathematician, by showing some four years ago the true relation of KARL PEARSON'S beautiful developments of mathematical methods to genetic research. The motto through the whole 25 chapters of his 500-page book was: "Wir müssen die Erblichkeitslehre mit Mathematik, nicht aber als Mathematik treiben!" JOHANNSEN'S work on the comparative permanence of homozygous types published under the title *Ueber Erblichkeit in Populationen und in reinen Linien* (1903) had already been enthusiastically received by many investigators, partly by reason of the author's mastery of a persuasive style and partly because the conclusions fitted data with which his readers were personally familiar. For these reasons, this elaboration of his ideas met with a cordial reception that is not the fate of many textbooks. But one unfavorable criticism of any importance could be made. The author did not treat adequately the numerous genetic researches in which the problems of heredity had been attacked by methods unlike his own. There is no hesitancy, therefore, in saying that th new edition,[1] with its 30 chapters and 722 pages, to which this criticism may not

---

[1] JOHANNSEN, W., Elemente der exakten Erblichkeitslehre. Zweite Auflage. 8vo. pp. xi+723. *figs. 33.* Jena: Gustav Fischer. 1913.

be applied with justice (if one excepts cytological research), will be a welcome addition to genetic literature.

In its present form, the work might very easily be divided into two books with separate titles that could be used independently. The one is a thorough introduction to statistical methods as they should be used in the service of biology; the other is a well balanced discussion of the present status of genetic conceptions.

As might be expected, it has been the general discussion of heredity that has received the bulk of the revision; the chapters on biometry were admirably done in the first edition, and the static nature of their substance was such that little change has been necessary. Scarcely a word has been altered in the first five chapters, though CHARLIER'S short method for determining the standard deviation has been added. In chapter 6 the discussion of mean error has been revised and a demonstration from the domain of plant physiology has been added. From this point to chapter 22, only chapters 12 and 13 are new, but the remainder of the book is entirely as written.

In chapter 12 the more recent investigations concerning the possible effect of selection on pure lines are described, while in the next chapter the "misunderstandings" of certain authors who have opposed the theory of permanence of homozygous types are taken up and disposed of with very clear logic, though the style of the rejoinder is sometimes a little caustic.

The last seven chapters of the book are so crowded with information that only a hint as to their contents can be given. They must be read by all who are interested in genetics. Sixty pages are given up to the influence of the factors of environment on variation and 160 pages to Mendelism in its various phases, including heterozygosis, inbreeding, sterility, coupling, and sex determination. Mutations are considered rather concisely in the next to the last chapter, the author being rather of the opinion that the peculiar behavior of *Oenothera Lamarckiana* will ultimately be shown to be the result of segregation and recombination, as has been suggested recently by HERIBERT-NILSSON. The final chapter is a résumé, with observations on eugenics, race hygiene, and evolution.

With reference to the position taken in his earlier work concerning the action of selection, the author remains as firm as a rock. He adds further data of his own to support his position and shows very clearly that the seemingly opposing conclusions of various investigators either are due to fallacious reasoning or are based upon material that is not easily divested of complications that confuse the main issue. To critics who deal only with generalities he makes the following reply that may well be taken to heart by those who deal with evolution from an easy chair:

> Man hat mich kurzsichtig genannt, in Bezug auf die Selektion. Ich konstatiere dies mit Vergnügen; die Prämissen einer oft maszlosen spekulativen Fernsichtigkeit waren ja gerade zu untersuchen und würden wertlos gefunden.

It will doubtless surprise many that JOHANNSEN maintains a firm Lamarckian attitude throughout his book, dealing particularly sympathetically with the work of SEMON. He says: "Man hat mich ferner 'reiner Weismannianer' genannt. Jeder solche 'man' hat mein Buch nicht gelesen oder nicht verstanden." The reviewer must admit, therefore, that he has not understood the author, for after reading the volume he is still firmly convinced that in its essentials it is more nearly Weismannian than Lamarckian. Of course he would not accuse the author of maintaining the morphological hypotheses of WEISMANN with the biophores, determinants, and ids all built into a beautiful structure, but the germ-to-germ inheritance, the dependence of transmissible qualities upon germinal constitution, the invalidity of any particular assumption as to breeding power from the appearance of the soma, and the comparative freedom of the germinal substance from the influence of ordinary environmental changes, as maintained throughout the work, will be classed by most biologists as belonging rightly within the scope of WEISMANN'S conception of heredity.

Very few new terms are introduced by JOHANNSEN in this edition of his book, but two have appeared that seem justified in spite of the abuse that has been showered on the roots used. Individuals that belong to the same phenotype are "isophenous"; individuals that belong to the same genotype are "isogenous." In addition he has adopted WEBBER'S term "clone" for a bud individual.

Taken all in all, one must be very critical to have anything but praise for the new *Erblichkeitslehre*, and it is confidently predicted that it will long remain a classic.—E. M. EAST.

Reprinted from the Proceedings of the National Academy of Sciences
Vol. I, p. 95, 1915

AN INTERPRETATION OF SELF-STERILITY

By E. M. East
BUSSEY INSTITUTION, HARVARD UNIVERSITY

Presented to the Academy, December 28, 1914

In certain hermaphroditic animals and plants, self-fertilization is often impossible. This gametic incompatibility has been called self-sterility. In the vegetable kingdom it is known to be comparatively widespread; in the animal kingdom, though it may be found later to be characteristic of many species, as yet only the Ascidian *Ciona intestinalis* has furnished material for study of the problem. (See Morgan,[1] Adkins, in Morgan,[2] and Fuchs.[3])

Ciona is not perfectly self-sterile. Individuals appear to vary in degree of self-sterility, though no case has yet been found where self-fertility is equal to cross-fertility. Morgan believes that there is a great difference in the compatibility of ova to sperm from other individuals, though Fuchs maintains that 100% of segmenting eggs can be obtained in every cross with normal ova if a sufficiently concentrated sperm suspension is used.

Fuchs has shown a chemical basis for the phenomenon by the difference in ease of cross-fertilization after contact of ova with sperm from the same animal and by the variation in ease of self-fertilization after certain artificial changes in the chemical equilibrium of the medium surrounding the ova, and by this work has brought the matter of self-sterility in Ciona in line with that in Angiosperms as worked out by Jost.[4]

Jost has shown that in the plants with which he worked only short tubes were formed after pollination with pollen from the same plant, though the necessary length of pollen-tube was easily developed after cross-fertilization. He saw as cause of these phenomena a chemotropism due to the presence of 'individueller Stoffe.' Pollen was indifferent to 'Individualstoff' from the same plant, but was stimulated by that from other plants.

To Correns[5] such an explanation of self-sterility seemed too general. He believed that a simple interpretation would account for the results he had obtained from *Cardamine pratensis*. Two plants B and G were crossed reciprocally and sixty of the offspring tested by pollinating from the parents, on the parents and from sisters. The back crosses of (B × G) or (G × B) with B and with G seemed to him to indicate four equal-sized classes with reference to gametic compatibility: (1) plants fertile with both B and G; (2) plants fertile with B but not with G; (3) plants fertile with G but not with B; (4) plants fertile with neither B nor G.

These facts were interpreted by assuming the existence of two independently inherited factors that inhibit the growth of pollen-tubes. Representing these factors by the letters B and G, the original plants must be supposed to have had the formulae Bb and Gg respectively, since it is clear that type BB and GG could never be formed. When Bb is crossed with Gg the four types BG, Bg, bG and bg should result, of which the first three should be self-sterile. Plants BG should be fertile with plants bg, plants Bg should be fertile with bG and bg, plants bG should be fertile with Bg and bg, while plants bg should be self-fertile as well as cross-fertile with the other three classes. Attractive as this theory is, it is not clearly in accord with the facts. Plants of the type bg—inherently self-fertile—were not found, and the other classes showed many discrepancies.

Morgan[2] has offered another hypothesis that fits the data from both plants and animals. If I have not misunderstood the meaning of his rather general statement of the proposition, my own theory is only an extension of it, laid down perhaps a little more specifically. He says:

> The failure to self-fertilize, which is the main problem, would seem to be due to the similarity in the hereditary factors carried by the eggs and sperm; but in the sperm, at least, reduction division has taken place prior to fertilization, and therefore unless each animal was homozygous (which from the nature of the case cannot be assumed possible) the failure to fertilize cannot be due to homozygosity. But both sperm and eggs have developed under the influence of the total or duplex number of hereditary factors: hence they are alike; i.e., their protoplasmic substance has been under the same influence. In this sense, the case is like that of stock that has long been inbred, and has come to have nearly the same hereditary complex. If this similarity decreases the chances of combination between sperm and eggs we can interpret the results.

My own work has been done with the descendants of a cross between *Nicotiana forgetiana* (Hort) Sand., a small red-flowered species, and *Nicotiana alata* Lk. and Otto. var. *grandiflora* Comes, the large white-flowered sort commonly known as *Nicotiana affinis*. Both parents were undoubtedly self-sterile as over 500 plants of the F_1, F_2, F_3, and F_4 generations have been found to be self-sterile by careful tests.

Several experiments were made in which selfing, crossing *inter se*, and back crossing were done on a large scale, using plants of the F_2,F_3 and F_4 generations which had segregated markedly in size and were of at least eight different shades of color. In the F_2 generation, twenty plants coming from two crosses between F_1 plants were selected for experiment. Each was selfed many times and in addition 131 inter-crosses were attempted, from four to twelve flowers being used in each trial. All attempts at selfing failed, while only two attempts at crossing were unsuccessful. Of the 129 successful inter-crosses, all but 4 produced full capsules, and it is probable that even this variability in ease of cross-fertilization was caused by attending conditions. One hundred and twenty other inter-crosses were made in the F_2 generation, with three failures.

In the F_3 generation, about one hundred inter-crosses were made between twelve plants which were the progeny of two sister F_2 plants. Six of these attempts failed.

In the F_4 generation, fifty-eight inter-crosses were made between ten plants that were the daughters of two F_3 plants. Fifty-three of these cross-fertilizations were successful.

Back crosses also were made in considerable numbers, though not to the extent one might desire. Plants A, B, C and D were combined in four different ways and among the plants resulting from these combinations eighty-five back crosses were attempted, of which five failed.

These facts will not fit any simple Mendelian formula similar to that proposed by Correns; furthermore, data from an experiment of a different kind appear to support Jost's idea of 'Individualstoffe' rather than Correns' idea of inhibitors. Pairs of plants were provided to furnish series of selfed and crossed flowers. The pistils of these flowers were fixed at regular periods after pollination, stained, sectioned and the pollen-tubes examined. Since the flowers on each plant had about the same length of pistils, curves of pollen-tube development for both crossing and selfing could be constructed. The pollen grains germinated perfectly on stigmas from the same plant, from 1200 to 2000 tubes having been counted in sections of single pistils. The difference between the development of the tubes in the selfed and the crossed styles was wholly one of rate of growth. The tubes in the selfed pistils developed steadily at a rate of about 3 mm. per twenty-four hours, with even a slight acceleration of this rate as the tubes progressed. If the flowers were sufficiently long-lived, one could hardly doubt but that the tubes would ultimately reach the ovules, though this would not necessarily mean that fertilization must occur. Since the maximum life of the flower is about 11 days, however, the tubes never traverse over one-half of the distance to the ovary. On the other hand, the tubes in the crossed pistils, though starting to grow at the same rate as the others, pass down the style faster and faster, until they reach the ovary in four days or less.

From these facts it seems reasonable to conclude that the secretions in the style stimulate the pollen-tubes from other plants instead of inhibiting the tubes from the same plant.

The whole question, therefore, becomes a mathematical one, that of satisfying conditions whereby no stimulus is offered to pollen-tubes from the same plant, but a positive stimulus is offered to tubes from *nearly* every other plant.

The nearly constant rate of growth of pollen-tubes in the pistils of selfed flowers, compared with the regular acceleration of growth of the tubes from the pollen of other plants, undoubtedly shows the presence of stimulants of great specificity akin to the 'Individualstoffe' of Jost, though I believe their action to be indirect. Experiments by several botanists, which I have been able partially to corroborate, point to a single sugar, probably of the hexose group, as the direct stimulant. The specific 'Individualstoffe' I believe to reside in the pollen grains and to be in the nature of enzymes of slightly different character, all of which except the one produced by the plant itself for the use of its own pollen, or by another individual of the same genotype, can call forth secretion of the sugar that gives the direct stimulus. At least this idea links together logically the fact of the single direct stimulus and the need of 'Individualstoffe' to account for the results of the crossing and selfing experiments But whether or not this be the correct physiological inference, the crossing and selfing experiments call for an hypothesis that will account for no stimulation being offered the tubes from the plant's own pollen while at the same time great stimulation will be given the tubes from the pollen of *nearly* every other plant. This is a straight mathematical problem, and it is hardly necessary to say that it is insoluble by a strict Mendelian notation such as Correns sought to give. This is obvious to anyone familiar with the basic mathematics of Mendelism. On the other hand a near Mendelian interpretation satisfies every fact.

Let us assume that different hereditary complexes stimulate pollen-tube growth and in all likelihood promote fertilization, and that like hereditary complexes are without such effect. One may then imagine any degree of heterozygosis in a mother plant and therefore any degree of dissimilarity between the gametes it produces, without there being the possibility of a single gamete having anything in its constitution not possessed by the somatic tissues of the mother plant. From the chromosome standpoint of heredity the cells of the mother plant are duplex in their organization: they contain N pairs. The cells of the gametes contain N chromosomes, one coming from each pair of the mother cell; but they are all parts of the mother cell and contain nothing that that cell did not contain. These gametic cells cannot reach the ovaries of flowers on the same plant because they cannot provoke the secretion of the direct stimulant from the somatic cells of that plant.

All gametes having in their hereditary constitution something different from that of the cells of a mother plant, however, can provoke the proper secretion to stimulate pollen-tube growth, reach the ovary before the flower wilts, and produce seeds. Such differences would be very numerous in a self-sterile species where cross-fertilization must take place; nevertheless like hereditary complexes in different plants should be found, and this should account for the small percentage of cross-sterility actually obtained. It must be granted that this hypothesis satisfies the facts, but that is not all. It is admittedly a perfectly formal interpretation, but from a mathematical standpoint—granting the generality of Mendelian inheritance—it is the only hypothesis possible that can satisfy the facts.

In conclusion it should be mentioned that the cross-pollinated pistils show a considerable variation in the rate of growth of individual pollen-tubes, though our curves of growth have been made by taking the average rate of elongation. Is this variation a result of chance altogether or must one assume a differential rate of growth increasing directly with the constitutional differences existing between the somatic cells and the various gametes? If it is assumed that any constitutional difference between the two calls forth the secretion of the direct stimulus to growth, chance fertilization by gametes of every type different from that of the mother plant will ensue; if there is a differential rate, selective fertilization will occur. This question cannot be decided definitely at present, but two different lines of evidence point toward chance fertilization:

1. Flowers from a single plant pollinated by different males show no decided difference in rate of fertilization.
2. Color differences are transmitted to expected ratios.

Further, it will be recalled that beginning with the F_2 generation sister plants crossed together have given us our F_3 and F_4 populations, and that these F_3 and F_4 populations apparently have given a constantly increasing percentage of cross-sterility. This is what should be expected under the theory that a small difference in germ plasm constitution is as active as a great difference in causing the active stimulation to pollen tube growth. Breeding sister plants together in succeeding generations causes an automatic increase of homozygosity as is well known. This being a fact, cross-sterility should increase. Such an increase in cross-sterility has been observed in the F_3 and the F_4 generations, but it would not be wise to maintain dogmatically that it is significant.

[1] Morgan, T. H., Some further experiments on self-fertilization in Ciona. *Biol. Bull.*, 8, 313–330 (1905).

[2] Morgan, T. H., *Heredity and Sex*. New York. Columbia University Press, ix + 1–282 (1913). (page cited 217).

[3] Fuchs, H. M., On the conditions of self-fertilization in Ciona. *Archiv. f. Entwickl. d. Org.*, 40, 157–204 (1914); The action of egg-secretions on the fertilizing power of sperm. *Archiv. f. Entwickl. d. Org.*, 40, 205–252 (1914).

[4] Jost, L., Zur Physiologie des Pollens. *Ber. d. deut. Bot. Ztg., Heft V and VI* (1907).

[5] Correns, C., Selbststerilität und Individualstoffe. *Festschr. d. med. nat. Gesell. zur* 84. *Versamml. deutsch. Naturforscher u. Arzte. Münster i. W.*, pp. 1–32 (1912).

THE PHENOMENON OF SELF-STERILITY

PROFESSOR E. M. EAST

NEW YORK
1915

[Reprinted without change of paging, from the AMERICAN NATURALIST, 1915.]

[Reprinted from THE AMERICAN NATURALIST, Vol. XLIX., Feb., 1915.]

THE PHENOMENON OF SELF-STERILITY[1]

PROFESSOR E. M. EAST
BUSSEY INSTITUTION, HARVARD UNIVERSITY

IN both animals and plants in which the two sexes have been combined in the same individual, cases have been found where self-fertilization is practically impossible. This gametic incompatibility has been called self-sterility, although the term is hardly proper as applied to normal functional gametes that may fuse with their complements in the regular manner, provided each member of a pair has been matured in a separate individual.

In plants the phenomenon has been known since the middle of the nineteenth century, in animals a corresponding discovery was made in 1896 by Castle, the species being one of the Ascidians, *Ciona intestinalis*. During the eighteen years that have passed since Castle's discovery, *Ciona* has been studied on a large scale by Morgan (1905), Adkins (Morgan, 1913), and Fuchs (1914). The botanists, however, have lagged somewhat behind; for, in spite of having been acquainted with self-sterility in plants for over half a century, and having found over thirty species where a greater or less degree of self-sterility occurs from which to select material, very few thorough investigations into the physiology of the subject have appeared.

The main facts regarding fertilization in *Ciona intestinalis* are about as follows:

1. Under uniform suitable conditions, individuals vary in degree of self-sterility, it being exceptional to find an animal that is perfectly self-sterile.

2. Self-fertility has never equaled cross-fertility, though the possibility remains that some animals may be self-

---

[1] Read by title at the thirty-second meeting of the American Society of Naturalists, December 31, 1914.

fertilized as easily as they may be crossed with certain particular individuals.

3. The ease with which the ova of any animal "*A*" may be fertilized by the sperm of other individuals may vary.

Morgan (1913) concluded from his own work and that of Adkins that there were wide differences in the compatibility of ova to different sperm. Fuchs (1914) maintained that 100 per cent. of segmenting eggs can be obtained in every cross if the ova are normal and a sufficiently concentrated sperm suspension is used. It is possible that Fuchs is correct and that varying concentrations of sperm suspension were the cause of Morgan's and Adkins's results, yet the possibility of differences in this regard inherent in the individual is not to be overlooked. It will be seen later that I regard the matter as of great importance to the general subject.

4. A chemical basis for self-sterility is shown in Fuch's experiments by (*a*) the decrease in ease of cross-fertilization after contact of ova with sperm from the same animal, and by (*b*) the difference in ease of self-fertilization after various artificial changes in the chemical equilibrium of the medium surrounding the ova.

From the botanical side various studies on the physiology of self-sterility have appeared since such investigations were initiated by Hildebrand in 1866. At this time it is necessary for us to consider only those of Jost (1907), Correns (1912), and Compton (1913).

Jost was able to show that in self-sterile plants tubes formed from their own pollen were so limited in their development that fertilization did not occur, although the necessary length of pollen tube was easily developed after a cross-fertilization. He saw as the cause of these phenomena the presence of "individueller Stoffe." Pollen was indifferent to "Individualstoff" of the same plant, but was stimulated by that of other plants.

Correns (1912), working with one of the bitter cresses, *Cardamine pratensis,* obtained results to which he gave a simpler interpretation. Starting with two plants, *B* and

G, he crossed them reciprocally and tested 60 of the offspring by pollinating from the parents, on the parents, and *inter se.* The back crosses of $(B \times G)$ or $(G \times B)$ with B and with G apparently indicated four classes about equal in size with reference to gametic compatibility: (1) plants fertile with both B and G; (2) plants fertile with B but not with G; (3) plants fertile with G but not with B; (4) plants fertile with neither B nor G.

To these facts Correns gave a Mendelian interpretation by assuming the existence of two factors each of which inhibits the growth of pollen tubes from like gametes. Representing these factors by the letters B and G, it is clear that types BB and GG could never be formed. The original plants were supposed to be of classes Bb and Gg, respectively. When crossed there resulted the four types BG, Bg, bG and bg. Plants of types BG, Bg, and bG should be self-sterile, while plants of the type bg should be self-fertile. Plants BG should be fertile with plants bg, plants Bg should be fertile with bG and bg, and plants bG should be fertile with Bg and bg. As a matter of fact Correns's results were not clearly in accord with the theory. Plants of the type bg were not self-fertile, and the other classes of matings showed many discrepancies. It is only fair to say, however, that the author recognized some of these difficulties, but believed them to be due to other inhibitors.

In a part of Compton's (1913) work, a still simpler interpretation of self-sterility is offered, at least for a particular case, that of *Reseda odorata.* Darwin's original discovery that both self-sterile and self-fertile races of this plant exist was confirmed and the following results obtained in crossing experiments. Self-sterile plants crossed ~~either~~ with self-sterile ~~or with self-fertile~~ plants gave only self-sterile offspring. Certain self-fertile plants, however, gave only self-~~sterile~~ fertile offspring either when self-pollinated or when crossed with self-sterile plants. Other self-fertile plants gave ratios of 3 self-fertile to 1 self-~~fertile~~ sterile offspring when self-pollinated, and ratios of 1:1 when crossed with pollen from self-sterile plants. For these reasons he regards self-fertility as a simple Mendelian dominant to self-sterility in the case studied. I believe Compton would draw no such sharp line about self-sterility in general. In fact, he follows Jost in suggesting the presence of a diffusible substance in the tissues of the style and stigma which retards or promotes pollen tube growth after self-pollination or cross-pollination in some manner analogous to the mechanism that promotes animal immunity or susceptibility after infection.

The only alternative general hypothesis has been proposed by Morgan, and this can be discussed more advantageously after the presentation of my own work, of which only an abstract will be given at this time.

In 1909 I made a cross between a small red-flowered *Nicotiana, Nicotiana forgetiana* (Hort.) Sand. and the large white-flowered *Nicotiana* of the garden *Nicotiana alata* Lk. and Otto. var. *grandiflora* Comes. All of the plants of the F_1 generation appeared to be self-sterile. Tests of *Nicotiana forgetiana*[2] have shown these plants also to be self-sterile, but both self-fertile and self-sterile plants of the other parent have been found. From data gathered later, there seems to be no doubt that a self-sterile plant of *Nicotiana alata grandiflora* was used in the actual cross. This conclusion seems reasonable in view of the fact that of over 500 plants of the F_1, F_2, F_3 and F_4 generations tested, not a single self-fertile plant was found.

The plants of the F_1 generation were all vigorous and healthy, and in spite of the fact that they resulted from a species cross which Jeffrey claims always produces large amounts of abnormal pollen, a large number of examinations of pollen from different individuals showed from 90

---

[2] I thought originally that both of these species (East, 1913) were self-fertile. Seed had been obtained from a carefully bagged inflorescence of each species in 1909. Either the plant of *N. forgetiana* which gave this seed was self-fertile—something that I have never been able to find since that time—or there was an error in manipulation. At any rate, the plants resulting from this seed were all self-sterile.

to 100 per cent. of morphologically perfect pollen grains, a condition about the same as was found in the pure species. To this statement there is one exception. A single plant was found with only about 2 per cent. of good sound pollen.

Several experiments were made in which crossing and selfing was done on a large scale, using plants of the F_2, F_3 and F_4 generations which had segregated markedly in size and were of at least 8 different shades of color. In one of these experiments 20 plants of the F_2 generation coming from 2 crosses of F_1 plants were used. It was planned to make all possible combinations of these plants, 400 in all. This task proved overburdensome, however, and in addition to the self-pollinations but 131 inter-crosses were made with the following results.

1. Each plant was absolutely self-sterile.
2. Leaving out of consideration the plant with shrunken imperfect pollen only two crosses failed. This failure of 1.5 per cent. of the crosses may have been due to improper conditions at the time of the attempts, but as a number of trials were made the possibility remains that there is a small percentage of true cross-sterility.
3. Of the 129 successful inter-crosses, 4 produced capsules with less than 50 per cent. of the ovules fertilized. The remaining crosses produced full capsules. It is barely possible that this result shows a slight variability in ease of cross-fertilization, but I am more inclined to believe that these 4 cases where a low percentage of fertilized ovules were obtained were accidental.

Other crossing experiments of the same kind have corroborated these results. Out of 120 inter-crosses, only 3 failed.

Later, something over 100 inter-crosses were made between 12 plants of an F_3 population resulting from crossing two sister F_2 plants. Six of the attempts at cross-fertilization—3 to 8 trials per plant being made—were failures. These plants as well as others tested were completely self-sterile, and apparently there was cross-sterility in about 6 per cent. of the possible combinations.

In the F_4 generation, 10 plants resulting from crossing two sisters of the F_3 generation were selected for experiment. Unfortunately, I was able to make only 58 intercrosses, 5 of which, almost 10 per cent., failed.

Back crosses have furnished another line of experiment, though they have not been carried on as systematically as were those of Correns. Nearly 85 back-crosses using plants from the progeny of four combinations which included four individuals as parents, have been made. The plants themselves all proved self-sterile, and in addition 5 of the back crosses failed.

When these experiments were begun I expected to find that the facts would accord with a simple dihybrid Mendelian formula similar to that which Correns later proposed as an interpretation of his results, yet only by considerable stretching and a vivid imagination will Correns's data fit such an hypothesis, and my own data do not fit at all. No self-fertile plants have been produced by any combination, and cross-sterility is a possibility in only from 1.5 to 10 per cent. of the combinations. Furthermore, Correns's idea of inhibitors appears unlikely from some other data I have gathered with the help of Mr. J. B. Park. Ten plants were involved in this experiment. Pairs of plants were provided to furnish series of selfed and crossed flowers. The pistils of these flowers were fixed at regular periods after pollination, stained, sectioned, and the pollen tubes examined. Fertilization not later than the fourth day marked the end point of the crossed series, the dropping of the flowers between the eighth and the eleventh day ended the selfed series. As the flowers on each plant had about the same length pistils, curves of pollen tube development for both crossing and selfing could be constructed. The pollen grains germinated perfectly on stigmas from the same plant, from 1,200 to 2,000 tubes having been counted in sections of single pistils. The difference between the development of the tubes in the selfed and the crossed styles is wholly one of rate of growth. The tubes in the selfed pistils develop steadily at a rate of about 3 millimeters per twenty-four hours. There is even a slight acceleration of this rate as the tubes progress. If the flowers were of an everlasting nature one could hardly doubt but that the tubes would ultimately reach the ovules, though this would not necessarily mean that fertilization must occur. Since the maximum life of the flower is about 11 days, however, the tubes never traverse over one half of the distance to the ovary. On the other hand, the tubes in the crossed pistils, though starting to grow at the same rate as the others, pass down the style faster and faster, until they reach the ovary in four days or less.

From these facts it seems reasonable to conclude that the secretions in the style offer a stimulus to pollen tubes from other plants rather than an impediment to the development of tubes from the same plant.

The whole question, therefore, becomes a mathematical one, that of satisfying conditions whereby no stimulus is offered to pollen tubes from the same plant, but a positive stimulus is offered to tubes from nearly every other plant.

Morgan has given an answer to this question in a general way. If I understand his position correctly, my own conclusions are not very different from his, but are somewhat more definite. Morgan (1913) states that the results of Adkins and himself on *Ciona intestinalis* can best be understood by the following hypothesis:

> The failure to self-fertilize, which is the main problem, would seem to be due to the similarity in the hereditary factors carried by the eggs and sperm; but in the sperm, at least, reduction division has taken place prior to fertilization, and therefore unless each animal was homozygous (which from the nature of the case cannot be assumed possible) the failure to fertilize can not be due to homozygosity. But both sperm and eggs have developed under the influence of the total or duplex number of hereditary factors; hence they are alike, *i. e.*, their protoplasmic substance has been under the same influences. In this sense, the case is like that of stock that has long been inbred, and has come to have nearly the same hereditary complex. If this similarity decreases

> the chances of combination between sperm and eggs we can interpret the results.

I make this quotation to show Morgan's viewpoint. It is for him to say whether the following conclusions are extensions of his own or not.

The tolerably constant rate of growth of pollen tubes in the pistils of selfed flowers, compared with the great acceleration of growth of the tubes from the pollen of other plants as they penetrate nearer and nearer to the ovary, undoubtedly shows the presence of stimulants of great specificity akin to the "Individualstoffe" of Jost. We are wholly ignorant of the nature of these stimulants, but I am inclined towards a hypothesis differing somewhat from his. Experiments by several botanists, which I have been able partially to corroborate, point to a single sugar, probably of the hexose group, as the direct stimulant. The specific "Individualstoffe" I believe to reside in the pollen grains and to be in the nature of enzymes of slightly different character, all of which, except the one produced by the plant itself for the use of its own pollen or by other plants of identical germinal constitutions, can call forth secretion of the sugar that gives the direct stimulus. At least this idea links together logically the fact of the single direct stimulus and the need of "Individualstoffe" to account for the results of the crossing and selfing experiments. But whether or not this be the correct physiological inference, the crossing and selfing experiments call for a hypothesis that will account for no stimulation being offered the tubes from the plant's own pollen, while at the same time great stimulation is given the tubes from the pollen of nearly every other plant.

This is a straight mathematical problem, and it is hardly necessary to say that it is insoluble by a strict Mendelian notation such as Correns sought to give. This is obvious to any one familiar with the basic mathematics of Mendelism. On the other hand, a near Mendelian interpretation satisfies every fact.

Let us assume that different hereditary complexes stimulate pollen tube growth and in all likelihood promote fertilization, and that like hereditary complexes are without such effect. One may then imagine any degree of heterozygosis in a mother plant and therefore any degree of dissimilarity between the gametes it produces, without there being the possibility of a single gamete having anything in its constitution not possessed by the somatic tissues of the mother plant. From the chromosome standpoint of heredity the cells of the mother plant are duplex in their organization; they contain N pairs. The cells of the gametes contain N chromosomes, one coming from each pair of the mother cell; but they are all parts of the mother cell and contain nothing that that cell did not contain. These gametic cells can not reach the ovaries of flowers on the same plant because they can not provoke the secretion of the direct stimulant from the somatic cells of that plant.

All gametes having in their hereditary constitution something different from that of the cells of a mother plant, however, can provoke the proper secretion to stimulate pollen tube growth, reach the ovary before the flower wilts and produce seeds. Such differences would be very numerous in a self-sterile species where cross-fertilization must take place; nevertheless like hereditary complexes in different plants should be found, and this should account for the small percentage of cross-sterility actually obtained. It must be granted that this hypothesis satisfies the facts, but that is not all. It is admittedly a perfectly formal interpretation, but from a mathematical standpoint,—granting the generality of Mendelian inheritance,—it is the only hypothesis possible that can satisfy the facts.

Let us now look into a few of the ramifications of the subject. Examinations of the pistils that have been sectioned after cross-pollination show a considerable variation in the rate of growth of individual pollen tubes, though our curves of growth have been made by taking the average rate of elongation. Is this variation a result of chance altogether or must we assume a differential rate of growth increasing directly with the constitutional differences existing between the somatic cells and the various gametes? If we assume that any constitutional difference between the two calls forth the secretion of the direct stimulus to growth, chance fertilization by gametes of every type different from that of the mother plant will ensue; if there is a differential rate, selective fertilization will occur. This question can not be decided definitely at present, but two different lines of evidence point toward chance fertilization.

1. Flowers from a single plant pollinated by different males show no decided difference in rate of fertilization.

2. Color differences are transmitted in expected ratios.

Further, it will be recalled that beginning with the F_2 generation, sister plants crossed together have given us our F_3 and F_4 populations, and that these F_3 and F_4 populations apparently have given a constantly increasing percentage of cross-sterility. This is what should be expected under the theory that a small difference in germ plasm constitution is as active as a great difference in causing the active stimulation to pollen tube growth. Breeding sister plants together in succeeding generations causes an automatic increase of homozygosity as is well known. This being a fact, cross-sterility should increase. Such an increase in cross-sterility has been observed in the F_3 and the F_4 generations, but it would not be wise to maintain dogmatically that it is significant.

There are various questions, including the important one of the origin of self-sterility, that can not be discussed at this time. In conclusion, therefore, let us turn once more to the phenomenon of self-sterility in *Ciona intestinalis*. It seems to me that the hypothesis outlined above has few, if any, drawbacks when applied to self-sterility in plants. The question there, as far as we have gone, is one of pollen tube growth, and the theory that the secretion of the direct stimulant can be called forth only by a gamete that differs in its constitution from the somatic cells between which the pollen tube passes, is logical. If the same theory is to be extended to animals, however, it follows that the external portions of the membranes of the animal egg that have been shown by the wonderful investigations of Loeb and of Lillie to have such important functions, must be functionally zygotic in character. I am aware that this suggestion may be considered pretty radical, but it certainly should be given consideration. I do not like to draw an analogy between the animal egg and a pollen grain, but it may be mentioned that in these structures—surely comparable to the animal egg in the fineness of their membranes and walls—both color and shape are inherited as if they were zygotic in nature.

December 5, 1914.

LITERATURE CITED

Castle, W. E. The Early Embryology of *Ciona intestinalis* Flemming (L.). Bull. Mus. Comp. Zool., Harvard University 27, 201–280. 1896.

Compton, R. H. Phenomena and Problems of Self-sterility. *New Phytologist,* 12, 197–206. 1913.

Correns, C. Selbststerilität und Individalstoffe. Festschr. d. mat.-nat. Gesell. zur 84. Versamml. deutsch. Naturforscher u. Ärzte, 1912. Münster i. W., pp. 1–32.

East, E. M. Inheritance of Flower Size in Crosses between Species of *Nicotiana. Bot. Gaz.,* 55, 177–188. 1913.

Fuchs, H. M. On the Conditions of Self-fertilization in *Ciona. Archiv. f. Entwickl. d. Org.,* 40, 157–204. 1914.

—— The Action of Egg-secretions on the Fertilizing Power of Sperm. *Archiv. f. Entwickl. d. Org.,* 40, 205–252. 1914.

Hildebrand, F. Ueber die Nothwendigkeit der Insektenhilfe bei der Befruchtung von Corydalis cava. *Jahrb. wiss. Bot.,* 5, 359–363. 1866.

Jost, L. Zur Physiologie des Pollens. *Ber. d. deut. bot. Gesell.,* 23, 504–515. 1905.

—— Ueber die Selbststerilität einiger Blüten. *Bot. Ztg.,* Heft V and VI. 1907.

Morgan, T. H. Some Further Experiments on Self-fertilization in *Ciona. Biol. Bull.,* 8, 313–330. 1905.

—— Heredity and Sex. New York. Columbia Univ. Press, pp. ix + 1–282. 1913 (page cited 217).

E. S. Carman

E. M. EAST

Reprinted, without change of paging, from the Journal of Heredity (Organ of the American Genetic Association), Vol. VI, No. 2, Washington, D. C., February, 1915.

E. S. CARMAN

One of the Greatest of American Plant Breeders—His Work Too Little Appreciated—Success With Potatoes Most Noteworthy—His Activity as a Journalist.

E. M. East
Bussey Institution, Forest Hills, Massachusetts.

IT IS a delightful epigram but hardly the actual truth that "If a man preach a better sermon, write a better book, or build a better mouse-trap than his neighbor, though he hide himself in the wilderness, the world will make a beaten path to his door." The world as a whole is likely to give its applause to some very unimportant people. And after all is it not probable that too general a commendation encourages superficial rather than solid work? The anti-socialistic argument that a more even distribution of earthly comforts would oppose progress because it limits ambition is a pure sophism. Few things worth doing have been done with either money, power or fame in view. For this reason there is no need to feel sorry that E. S. Carman, great alike as agricultural journalist, public spirited citizen and creator of new varieties of plants, never received the panegyrics of which some others have been since the recipients. He had the happiness described by Marcus Aurelius: "A man's happiness—to do the things proper to man." Not that Mr. Carman was unknown—perhaps the editor of no rural paper was admired and trusted more—but, even with the temptation of a private medium for exploiting his triumphs, he did no more than describe carefully and impartially success and failures alike with the honesty of a true nature-lover and born investigator.

Mr. Carman would probably have denied that he was a great plant breeder. He originated no new methods and made few contributions to the study of heredity; but he did discover many interesting facts during his hybridization experiments and he added hundreds of millions of dollars to the wealth of the country, keeping nothing for himself. He was a national benefactor, and who will say he was not a great man when he placed public service before private gain? His attitude in the matter is summed up in the final paragraph of an article on the five famous potato varieties placed on the market between 1882 and 1896. "It will now appear that for our 16 years of potato work, we have sold five kinds for precisely $1,000. We dare say that, had we used our columns for advertising the three kinds now offered for sale, retaining the entire control as long as possible, *The Rural New-Yorker* might easily have made a snug little fortune. But, tell us friends, were we to crack up the plants that have originated at the "Rural Grounds" while we sold them to you either directly or indirectly, do you think that you would place as much confidence in the thorough impartiality of our plant reports, as you do now?" Ten years ago the writer made a trip through the great potato regions of Wisconsin and Minnesota. During it one of the most successful and best informed growers stated that in the previous decade 80% of the potatoes of the country were either Mr. Carman's productions or seedlings from them. How much truth there was in this statement it is impossible to say, but discount it as much as one will, can it be said that there is no such thing as altruism?

POTATO CREATIONS.

The famous potatoes from the Rural Grounds were Rural Blush, Rural New-Yorker No. 2, Carman No. 1, Carman No. 3 and Sir Walter Raleigh. They were not raised from hand hybridized seed, though this had been the original intention. Sixty-two varieties were grown as prospective parents, but crossing proved impossible; no functional pollen was formed. A few natural seed berries were found, however, and from them after years of testing these five kinds proved to be the fittest. Even the records of the maternal parents were lost, but the goal set at the beginning was reached. New potatoes better than the old Early Rose and Peachblow were produced. Considering the amount of time and space at command, it was probably the most successful practical plant breeding experiment ever tried.

In all of the other hybridization work, Mr. Carman made careful castrations of the flowers used as female parents, protected the blossoms from foreign pollen and made the crosses by hand. "Guess work in hybridization or crossing," he says, "is altogether abominable, because it is impossible to know whether anything has been effected or not, while the variations sure to appear in the seedling plants, it will be assumed, are evidences of cross-bred parentage."

One of the most interesting pieces of work brought to a successful conclusion, was a cross between the beardless Armstrong wheat and rye made in 1882. Several varieties from this cross were finally introduced, but whether they battled successfully with pure wheats or ryes, I have never heard.[1] The important thing was the variation in a first hybrid generation which was conclusively demonstrated—work which it would be interesting to repeat even now as the constancy or comparative homozygosity of the parents was unknown—and the pioneer work of showing the possibility of making crosses between these two generically different cereals. Mr. Carman saw the salient point very clearly as the following quotation shows: "What do they promise? If the hybrids give us a grain less valuable than rye or wheat, nothing will be gained in this case, except the curious fact that a cross between two different genera of grain is possible. This established, however, the way is opened for further hybridization the pregnant results of wh ch can only be guessed at."

Another interesting specific cross made by Mr. Carman was between the blackberry and the raspberry. It gave nothing of commercial importance, though by repeating it Luther Burbank is said to have produced a valuable berry. Neither Mr. Burbank nor Mr. Carman, however, was the first to make this cross; Mr. Carman, himself, admits obtaining the idea from William Saunders of London, Ontario, who had produced similar hybrids some five years before.

WORK WITH SOLANUMS.

Mr. Carman's taste evidently was partial to the Solanaceæ. He worked for many years on tomatoes, and succeeded in isolating from his various crosses five types that were worthy of introduction to the trade. They were the Longkeeper, Lemon Blush, Terra Cotta, Autocrat and Democrat. Autocrat and Lemon Blush were known for years as the finest of their kind. He also crossed the common tomato with both the Currant Tomato *L. pimpinellifolium* and the nearly related genus Physalis. Whether any valuable types were produced from the first cross or not, I have been unable to find out, but it was demonstrated that the first hybrid generation was intermediate in character and that a few of the individuals of the latter generations combined a fairly large size of fruit with the racemic type of inflorescence. The generic cross was not sufficiently fertile to be propagated, and died out after a couple of generations.

Various other crosses of all kinds kept up the interest of Mr. Carman in his work, in which he was efficiently and enthusiastically aided by Mrs. Carman,

---

[1] W. Van Fleet, who was associated with Mr. Carman in his breeding work, states that none of the real hybrid types survived continued propagation. Segregation occurred to such an extent that the progeny soon became, to all appearances, either rye or wheat. None of the rye types proved of particular value, but several of the wheat types are still in use. Farmers Bulletin No. 616 of the U. S. Department of Agriculture, "Winter Wheat Varieties for the Eastern States," recommends the soft "Rural New Yorker No. 57," one of Carman's creations.—The Editor.

although with one exception the rose hybrids were the only ones that were extremely valuable. This was the Carman Gooseberry. Here was a gooseberry that might have revolutionized gooseberry growing since in a limited test it was mildew proof, but unfortunately the seed firm to which it was sold was unable to propagate it.

The roses were perhaps the real attraction of the "Rural Grounds." The *Rosa rugosa* of Japan was the foundation stock, and upon it were crossed first the Austrian hardy yellow rose known as Harrison's Yellow, then Hybrid Perpetuals and afterwards Hybrid Teas. From these crosses hundreds of plants were raised—most of them, of course, worthless, but some of remarkable beauty. From the first cross mentioned came the Agnes Emily Carman, a fine, hardy, longlived, though thorny variety. In color it was like the Jacqueminot, but many times as profuse in blossoming. From other crosses came procumbent roses, hedge roses, tea roses, etc., etc. They did not attain pre-eminence as did the potato varieties but they helped and still help to brighten many a flower garden.

Elbert S. Carman was born on November 30, 1836, in Hempstead, Long Island. He entered Brown University in 1854, rooming with John Hay. He was obliged to withdraw after two years of work, however, on account of illness. In 1873, he married Agnes E. Brown, by whom he had two children. Immediately after his marriage he moved to River Edge, N. J., where he began to plant and experiment on the place that afterward became so well known as the "Rural Grounds." While here he became so interested in Moore's *Rural New-Yorker* as a contributor, that he purchased the paper and became its editor in 1876. Through an absolutely open and honest policy, he made this journal a power in the agricultural world. For many years it has stood out against all frauds and impostures to the farmer, even though this went against its monetary interests. Mr. Carman died February 28, 1900, regretted by the many friends he had made in his editorial capacity, who wrote of him like the hero of Leigh Hunt's ever popular poem, "as one who loved his fellow men."

AN INTERPRETATION OF STERILITY IN CERTAIN PLANTS.[1]

By E. M. EAST.

(*Read April 23, 1915.*)

It is obvious that it is impossible to investigate the cause of sterility in hybrids by the pedigree culture method when such sterility is complete. Occasionally, however, one finds hybrids which are not wholly sterile. Such is the case in the historic cross, *Nicotiana rustica* L. × *Nicotiana paniculata* L. This hybrid holds an enviable position in experimental botany, since it was the first artificial hybrid to be studied. It was made by Kölreuter in 1760 and was studied by him for several years by means of back crosses with each parent.

This cross I repeated in 1909, using as the *N. rustica* parent a small variety *N. rustica humilis* Comes obtained from Dr. Comes through the kindness of Dr. D. G. Fairchild. It has now been studied through five generations both in the field (general morphology) and in the laboratory (histology and cytology). The essential points noted, as I see them, are as follows:

Two species giving extremely uniform progeny when selfed have, when crossed, given an intermediate F_1 population as uniform as themselves, and an inordinately variable F_2 population.

The germination of F_2 seeds varies in different samples from 20 to 60 per cent.

Practically no two F_2 plants are alike, and the parental forms are recovered once in every 100 to 200 F_2 plants.

In F_1, from 1 to 6 per cent. of the ♀ gametes are functional. It is impossible to determine the percentage of viable ♂ gametes formed from the pollen mother cells, but from 2 to 6 per cent. of the

---

[1] It is impossible to reproduce the photographs shown by means of lantern slides, but an illustrated paper giving the details of the investigation is to be published shortly.

Reprinted from Proceedings American Philosophical Society, Vol. liv , 1915.

pollen found is morphologically perfect. The maturation difficulty in spermatogenesis is largely at the first spermatocyte division.

F_1 plants are as fertile *inter se* as in back crosses with either parent.

Segregation of determiners for fertility occurs in F_1, so that by recombination some perfectly fertile plants are obtained in F_2.

Nearly all fertile F_2 plants selfed give only fertile progeny. Occasionally a fertile F_2 plant selfed may give a slightly non-fertile daughter.

Numerous combinations that should be possible in F_2 are omitted in the population obtained. Combinations approaching *N. rustica* seem to be more frequent than those approaching *N. paniculata.* Many more homozygous combinations occur in F_2 than might be expected.

Perfectly fertile plants giving perfectly fertile progeny, heterozygous for many allelomorphs, do occur in F_2.

No more than a very general formal interpretation of these facts can be made at present, but assuming that the chromosomes carry the hereditary character determiners, and that these react with the cytoplasm under proper environmental conditions to build up the soma, attention is called to the following possibilities of satisfying the conditions imposed by the data.

1. There is selective elimination of F_2 zygotes.

2. There is no evidence of selective fertilization. (I infer this from the fact that F_1 plants are as fertile *inter se* as in backcrosses.)

3. The selective elimination of non-functional gametes that must occur in F_1 and the recombinations of functional gametes that give different grades of fertility in F_2 cannot be interpreted by a Mendelian factorial notation without subsidiary assumptions, but possibly may be the result of one of the two following hypotheses:

(*A*) Through multipolar spindles, mating of non-homologous chromosome pairs at synapsis, or other mitotic aberrations at the reduction division, the 24 chromosomes characterizing each of the two species may be irregularly distributed at gametogenesis. If some of these irregular gametes may function, the majority of the experimental data are satisfied, but there are reasons which there is not time to consider which make this scheme improbable.

(*B*) On the other hand the facts may be interpreted without assuming irregularities of chromosome distribution if (1) there is a group of chromosomes in each parent that cannot be replaced by chromosomes from the other parent; if (2) there is a group of chromosomes from each parent, a percentage of which may be replaced by chromosomes from the other parent, but where functional perfection of the gametes varies as their constitution approaches that of the parental forms; if (3) there are other chromosomes that have no effect on fertility and therefore can promote recombinations of characters in the progeny of fertile F_2 plants; if (4) a naked male nucleus entering the normal cytoplasm of the egg in the immediate cross can cause changes in the cytoplasm that will affect future reduction divisions; if (5) this abnormally formed cytoplasm is not equitably distributed in the dichotomies of gametogenesis in the F_1 generation; if (6) it follows from (4) and (5) that F_2 zygotes may be formed which are less perfect in their gamete forming mechanism than those of the F_1 generation; and if (7) the heterotypic division of gametogenesis does not necessarily form two cells alike in their viability.

Bussey Institution,
Harvard University.

THE CHROMOSOME VIEW OF HEREDITY AND ITS MEANING TO PLANT BREEDERS

E. M. EAST

NEW YORK
1915

[Reprinted without change of paging, from the AMERICAN NATURALIST, 1915.]

[Reprinted from THE AMERICAN NATURALIST, Vol. XLIX, August, 1915.]

THE CHROMOSOME VIEW OF HEREDITY AND ITS MEANING TO PLANT BREEDERS[1]

E. M. EAST

BUSSEY INSTITUTION, HARVARD UNIVERSITY

DEFINITE advice as to practical procedure must be based on a firm foundation of fact if the leaders in the applied science are to retain any confidence in those who lay the first stones in the pure science. At the same time, if it is clearly understood that science only approximates truth, that so-called ''established laws'' are only highly probable and never absolute, it can hardly be said to be unwise if an inventory of fact is taken at any time. The handwriting on the wall is never finished; some words are dim and the erasures and omissions are many, but that is no reason why one should not try to read it and to see what it directs if he has translated aright.

This preliminary justification of the title of this article is made because our present stock of facts regarding heredity points clearly to the chromosomes as vital parts of the mechanism, and I wish to emphasize some important practical deductions in case this position continues to become more firmly established.

A just and complete dissertation upon the rôle of the

---

[1] This paper is based upon two lectures delivered at Harvard University in 1914. I hope that any cytologists who may have their attention called to it will overlook the repetition of some well-known facts in the first few pages, as it is intended to be merely a general statement of a particular point of view with certain deductions that follow if it be accepted. I wish to thank Doctors O. E. White, T. H. Morgan and R. Goldschmidt for their kindness in giving me many suggestions, but in justice to them I should state that they are not responsible for the conclusions drawn.

chromosomes in heredity not only would fill many pages, but would expose numerous gaps in our present knowledge, gaps that leave several important questions in the balance. We shall assume frankly therefore that the chromosomes *are* the bearers of the determiners of practically all of the hereditary characters that have been investigated by pedigree culture methods, acknowledging freely our ignorance on many points, but maintaining that while no facts have been discovered which offer insurmountable arguments against the viewpoint taken, the following logical sequence of truths discovered at various times and by different methods of research make a pretty sound case upon which to base our practical conclusions.

Relative Importance of Nucleus and Cytoplasm

There are several reasons for believing that of the two parts of the cell, the nucleus and the cytoplasm, the former plays the greater rôle in heredity.

In general it is believed that the two parents contribute equally in the production of offspring—that the male and female contribution of potential characters is practically the same. If there were a difference it would be shown by divergent results in reciprocal crosses, but the investigations following Mendel's method make it probable that with the exception of sex and sex-linked characters, the results of reciprocal crosses are generally alike. This being true, it would appear that the principal basis of inheritance must be sought elsewhere than in the cytoplasm, for in most observed cases the sperm is very much smaller than the egg, and this difference is largely a difference in the amount of cytoplasm each carries. Is one not to look for some significance in this disparity in size? Strasburger, as well as other botanists, has even gone so far as to declare the male generative cell in certain angiosperms to be simply a naked nucleus that slips out of its cytoplasmic coat into the embryo sac, leaving the discarded coat behind, and that stimuli proceeding from the nucleus control the assimilation of food in the cell and determine even the character of the cytoplasm itself.

This belief may be too radical. The machine must have all of its parts to do proper work; and it may be, as Conklin suggests, that such characters as polarity, symmetry and localization of organ bases in the egg have their chief seat in the cytoplasm. This is only a possibility and not a fact, however, for one must admit that cytological investigation has not disclosed the presence of a material basis of heredity in the cytoplasm, though he may not be convinced that it is unimportant. Does the same statement hold for the nucleus?

The nuclear cavity contains four substances as they are ordinarily described in connection with morphological investigations. These are nuclear sap, linin, nucleolar material and chromatin.

Nuclear sap probably belongs as much to the cytoplasm as to the nucleus, and we know nothing as to its possible significance and importance within the nucleus.

Linin by some investigators is regarded as very similar to chromatin. Others (Strasburger) consider it to be the framework of the chromosomes, and the only real substance within the nuclear cavity that is continuous from generation to generation. It is a thread-like material staining lighter than chromatin upon which the chromosomes appear to be strung in the early prophases of nuclear division.

Nucleolar substance, though it stains in a different manner from chromatin, is considered by many to be chromatin-like in its nature. It is the substance of which the nucleoli are composed; but as these bodies become vacuolated and finally disappear during nuclear division, one is led to believe with Strasburger that they are temporary storehouses of some necessary food material.

Chromatin, however, as the material of which the chromosomes are composed, plays such a peculiar part in the activities of the cell, that hypotheses as to the meaning of its behavior are certainly more than shrewd guesses, as will be seen.

The chromosomes may be described as morphological elements, of various shapes and sizes that are found within the nucleus; they are especially demonstrable as deeply staining bodies, definite in number for each cell at the period of division. In many cases in both plants and animals they have been found to be made up of small particles, the chromomeres, and various investigators have expressed the belief that these, too, are definite in number and play an important part in the larger collective entity, the chromosome.

Almost from their discovery, the chromosomes have had an especially important part assigned to them in the drama of heredity because of the previous philosophical deductions of Weismann. Weismann reasoned that if there were no reduction of heritable substance in the life cycle of an organism, it would pile up indefinitely because of the nuclear fusion at fertilization. He, therefore, predicted the discovery of some mechanism by which the character conserving substance would be divided. A few years later his prediction was verified in its important details by actual observation of the chromosome reduction in the formation of germ cells in *Ascaris*. From this discovery and from the facts that a specific number was found for the cells of each species, that all the cells of an individual appeared to possess the same number (except when they were halved at gametogenesis), that they were apparently permanent organs, that they were longitudinally halved in division so as to give each daughter cell the same number as well as an exact half of each chromosome possessed by the mother cell, investigators were early tempted to place upon chromosomes the whole burden of inheritance.

Our observations regarding chromosomes and the reduction divisions in plants now rest on a basis of cytological investigation of over 250 species, representing over 150 genera and divided among the four great groups of this kingdom. Montgomery's 1906 list of chromosome numbers in animals represents investigations on 185 species, comprised in about 170 genera, distributed among nearly all the phyla of the animal kingdom. Sex chromosome studies have undoubtedly increased these figures for the animal kingdom to date, by hundreds of species.

Variation in chromosome number among the cells of an individual plant or animal is a recognized fact among cytologists, but this variation is not regarded as of particular significance, as commonly it is held to exist only among old cells, cells highly specialized, or, at any rate, cells which will never have anything in common with reproduction. To quote from Strasburger,

> the number of chromosomes in the nuclei of the somatic cells of both the sexual and the asexual generations have been found to vary. But so far as my experience goes, these observations are always to be observed in the nuclei of cells which are no longer embryonic, like those in an embryo or growing point, but which, on the contrary, are to some extent histologically specialized and are not destined eventually to give rise to reproductive cells. The determinate number is still more frequently departed from in nuclei which are definitely excluded from the sphere of reproduction.

In the reproductive cells, chromosome division is, on the other hand, very exact, and the numbers found, almost invariable, with one exception. This exception is the so-called accessory chromosome or chromosomes, that appear to be coupled with sex differentiation. And the very fact that such accessory chromosomes do exist and by their presence or absence parallel sex distribution, forms one of the most unanswerable arguments in favor of the chromosomes being the chief bearers of character determinants.

Morphological Individuality of the Chromosomes

The next topic to consider is whether there is sufficient evidence to support the idea that these bodies—the chromosomes—are morphological entities persisting from one cell generation to another.

Prochromosomes are deeply staining bodies found in the resting cell nuclei of plants, which probably correspond in number, but not in size, to the chromosomes which are found in the dividing nuclei. These bodies are thought to represent the resting nuclear condition of the chromosomes. Prochromosomes have been found in at least sixty species of plants, and various structures comparable to them in many others. These investigations favor the thought that the chromosomes are persistent morphological entities; nevertheless they are not sufficient to establish the matter if there were no other data at hand.

There is a series of facts, however, which is more convincing. We are told that in addition to each species of animal or plant having in the larger part of its cells a specific number of chromosomes, there is a constant reappearance of the different shapes and sizes of these chromosomes in the same positions relative to one another during cell division after cell division.

Strasburger says: "The observation of such a series of stages of nuclear division as can be obtained by the laying open of embryo sacs in which development of endosperm tissue is commencing, makes it difficult to resist the impression that it is always the same chromosomes which make their appearance over and over again in the repeated divisions. In the prophase, the chromosomes are seen to appear in precisely the same position that they occupied in the preceding anaphase, and if the picture of the anaphase were proportionally enlarged, it would exactly correspond to that of the succeeding prophase."

The facts from which these general conclusions have been drawn can not be denied. Baltzer found odd-shaped chromosomes of similar shape in many maturing eggs of sea urchins. Boveri, Montgomery and later Schaffner pointed out a constant difference in the form and the size relations of the two chromosomes of *Ascaris megalocephala univalens*. Sutton thought he could recognize each individual chromosome in eleven consecutive cell generations of the maturing germ cells of the lubber grasshopper *Brachystola magna*. The so-called sex chromosome which has been found in so many insects and other animals, is a clear case of constancy in appearance. In plants the same phenomenon has been observed. Rosenberg investigated the pollen mother cells of *Crepis virens* and in certain stages in division invariably found two long, two intermediate and two very short chromosomes. Division figures in the somatic cells showed the same differentiation, and in an examination of the nuclei of the pollen grain he found only one chromosome of each kind present. Such other species of this genus as have been investigated also show some variation in chromosome form, although it is not so striking as in *C. virens*. *Hieracium venosum,* exceptionally good material also investigated by Rosenberg, has shown the same thing. Edith Hyde remarks on the fact of the constant reappearance of certain chromosome forms among hundreds of division figures which she observed in *Hyacinthus orientalis.* Sauer mentions a very long chromosome constantly present in pollen mother cell preparations of the lily-of-the-valley, and Strasburger and Lutz found a large chromosome among many small ones in *Lychnis dioica*. In certain species of *Yucca* this chromosome differentiation takes on a dimorphic aspect, ten of the chromosomes being very large and about forty-five very small.

Taking into consideration all of these facts, of which hardly more than a random sample has been given, one is clearly justified in concluding that these cell characters are reproduced generation after generation. Why this constancy if they are not important?

PHYSIOLOGICAL INDIVIDUALITY OF THE CHROMOSOMES

There is also considerable reason for believing that the various chromosomes of a cell may have different functions.

Boveri was the first to endeavor to test this hypothesis by allowing sea-urchin's eggs to be fertilized by two spermatozoa. Three nuclei, each with eighteen chromosomes, were thus present in the same egg, two male and one female. Although cytoplasmic division seemed to proceed normally, the chromosomes were usually distributed irregularly by a three-poled or a four-poled spindle. As a result three or four cells were produced at the first division of the doubly fertilized egg, instead of the two cells that arise after normal fertilization. Various abnormal larvæ were produced later. In such embryos, Boveri found the organism to be divided into definite regions, thirds or fourths, each part traceable to one of the three or four original cells, and the cells of each part differing from the cells of the other parts in their combination of chromosomes and usually in their chromosome number. In rare cases normal embryos were produced, but these were more commonly developed from a doubly fertilized egg which in its first division was three-celled, than from one in which it was four-celled. The thought occurs at once that three cells have a better chance than four cells in securing a full set of chromosomes, both as to number and kind. If the division were normal, each nucleus would receive a full set in the case of the chromosome distribution to three cells, but the division is usually irregular, and because of this irregularity each cell does not usually secure its normal set of chromosomes. Nevertheless it is clear that the embryo parts developed from the three-celled cleavage stand a much greater chance of being normal than those from the four-celled type, although through irregularities in division an eighteen-chromosome-celled region might be formed even where the first division was four-celled.

In some cases, the embryo was completely normal as regards skeleton and pigmentation in one or even two of its thirds, while the remainder was entirely lacking in these characters. Nearly normal embryos occurred which were perfect as to parts and specific characters, but individual variations which normally should have appeared in separate larvæ were present among the thirds. Asymmetrical larvæ also were formed.

More important still are the results Boveri obtained by isolating the three cells of the three-fold type and the four cells of the four-fold type and allowing them to develop into larvæ. When the four cells of a four-celled stage of a normal embryo are separated, each cell produces a normal dwarf embryo alike in every respect, but the three- or four-celled embryos from double fertilized eggs, when treated in the same manner, never produce normal dwarfs even when the chromosome distribution has been numerically equal. Large numbers of larvæ brought into existence through this experiment showed all possible combinations of characters, just as all possible chromosome combinations were found in their nuclei, and from these and other data the conclusion is drawn that "not a certain number, but a certain combination of chromosomes is necessary to normal development, and this clearly points out that chromosomes have different qualities." In other words, the sea urchin has a set of eighteen chromosomes, each chromosome performing at least some different functions from its neighbors, making it necessary for the whole set to be present in order to insure normal development.

In further investigations, Boveri placed sea-urchin eggs which had been normally fertilized and were about to divide under pressure. As a result, division of the nucleus took place, but often no division of the cytoplasm. Such eggs on again dividing often formed more than two poles, resulting in inequalities in chromosome distribution and abnormal larval development. Boveri puts upon these cases an interpretation similar to that of the preceding experiments, as the irregular chromosome distribution seems to be all they have in common.

Morgan comments on Boveri's experiments as follows:

> The evidence makes probable the view that the different chromosomes may have somewhat different functions and that normal development depends on the normal interactions of the materials produced by the entire constellation of chromosomes.

Artificial parthenogenesis and experiments with enucleated eggs have proved that only one set of chromosomes is necessary to normal development of embryos, but it is important, in considering these experiments, to note that two sets of similar chromosomes are present in a normal sexually produced organism.

Pairs of chromosomes of each shape and size (if they differ in shape and size) are *nearly* always found in the somatic cells—the exception being when the so-called accessory chromosomes are present. And since but one of each kind is found in the two gametes that fuse to form the new organism, it is only natural to suppose that one set was contributed by the maternal parent and the other by the paternal parent.

The numerous cases in which this phenomenon has been demonstrated are to many the most convincing evidence of some sort of a morphological individuality of the chromosomes. To them the fact implies pairs of freight boats loaded with the essential materials of life, to others—the minority—it is no more wonderful than the constant recurrence of other plant organs. At any rate, it has been shown that these sets of chromosomes continue an apparently independent existence for some time. Moenkhaus produced hybrids between the two species of fish, *Fundulus heteroclitus* with long straight chromosomes and *Menidia notata* with short curved chromosomes, and the early divisions of the fertilized egg showed clearly complete sets of chromosomes from each parent. Rosenberg obtained similar results in crosses between the two sundews, *Drosera longifolia,* which has forty small chromosomes, and *Drosera rotundifolia,* which has twenty large chromosomes. In some cases similar to the latter, where one parent contributes a greater number of chromosomes, it should be noted that the organism seems to have regulatory powers. The chromosomes unnecessary for a double set are either thrown out or take no part in the activities of cell division. For example, in the supposedly hybrid sundew, *Drosera obovata,* Rosenberg found that its thirty chromosomes behaved in the following peculiar manner. Ten of them paired with another ten, but the other ten remained unpaired and acted in a very abnormal fashion in the reduction divisions. The ten pairs separated normally, one of each pair going to each pole; but the ten unpaired were irregularly distributed, sometimes nearly all of them going to one pole, sometimes most of them becoming lost in the cytoplasm and forming small nuclei. Embryos were produced in a very few cases and these only through back-crossing with pollen of *D. longifolia*. Unfortunately these embryos only developed through a few cell divisions.

These chromosome pairs have been distinguished by the name homologous chromosomes. For a long time it was thought that the paternal and the maternal set of chromosomes separated from each other bodily at the reduction division. Now it is believed to be only a matter of chance which chromosome of a pair passes to a particular daughter cell. There is some cytological evidence for this view, but the main argument in its favor is that this behavior is all that is necessary to fit nearly all the known facts of heredity, with the chromosomes playing the part of the active heredity machinery as will be seen shortly. This statement is true in a broad sense, but the word nearly is used because there is an exception to it. Chance apportionment of either member of a homologous pair of chromosomes to a daughter cell accounts for all facts of alternative (Mendelian) inheritance except where there are breaks in the correlation between characters usually inherited together. Since such breaks in correlation are common, it is clear that there must be a period when chromosome pairs have such an intimate relation that material can be exchanged. Many biologists believe that such a period is found during the maturation of the sex cells. The particular point at which such a conjugation or approximation of chromosome pairs takes place is called synapsis; it occurs as a part of the prophase or first stage of the reduction division. Some investigators have been unable to demonstrate any real chromosome fusion at this time, but all agree that there is an approximation between the two sets, and a chance for some kind of an exchange or interaction to take place.

Evidence of the physiological individuality of the chromosomes may be concluded by referring briefly to the so-called accessory chromosome. This fraction of a chromosome, whole chromosome, or in some cases, group of chromosomes, possesses no true synaptic mate, and therefore at reduction division two types of daughter cells are found. The presence or absence of the "accessory" is so closely associated with sex determination that most biologists now regard it as the morphological expression of a germinal sex determinant. The essential result of researches on this body may be summed up in the following words of Wilson.

> They have established the existence of a visible difference between the sexes in respect to these chromosomes, and have shown that it is traceable to a corresponding difference in the nuclei of the gametes of one sex or the other.

The simplest type of accessory chromosome, where the male possesses an unpaired chromosome which passes to one pole undivided in one of the spermatocyte divisions and hence enters but half the spermatozoa, was discovered by Henking (1891) in *Pyrrhocoris*. This work was confirmed in certain species of Orthoptera in 1902 by McClung, who advanced the hypothesis that the odd chromosome was a sex-determiner. Shortly afterward this was made more probable by Wilson and by Stevens who proved for several species of Hemiptera that the body cells of the males contain one less chromosome than the females. Two accessory or X chromosomes are present in the female, while but one is present in the male.

About the same time, both Wilson and Stevens independently discovered another kind of dimorphism in male germ cells of certain Hemiptera. Here the X chromosome of the male has a smaller synaptic mate Y. The body cells of the female, however, show two of the large X chromosomes. The sexes, therefore, both contain the same number of chromosomes, but have the same type of chromatin difference as was first discovered. The female is XX and the male XY.

Baltzer claimed in 1909 that in the sea urchins *Sphærechinus* and *Echinus* the sex with the dimorphic germ cells is the female instead of the male, but the work of Tennent has shown him to be in error and he has retracted the statement. There is, therefore, no undisputed cytological evidence demonstrating this type of dimorphic eggs; but since breeding results on certain species of birds and of lepidopters can be interpreted only on such an assumption, it is safe to assume that sooner or later they will be found.[2] Whether or not there are animals of this type, however, is of no particular importance in the present discussion. What we desire to emphasize is that a large number of animals, including man, have been shown to have a chromatic difference between the sexes, and that this difference is readily explained by the fact that the eggs are of a single type and the spermatozoa of two types.

In diœcious plants no such morphological differentiation has been found. But this fact does not negate the idea that the visible differences found in animals are really sex-determining differences. We have only to suppose that the dimorphism is primarily qualitative and secondarily quantitative. Indeed Wilson has found that the Y chromosome—the synaptic mate of the X—may vary in different species from a size equal to that of X until it disappears entirely, leaving X without a mate.

There is only one criticism in this whole matter. One may admit these cytological differences between the sexes, but hold that they are early appearances of secondary sexual characters. Morgan, von Baehr and Stevens have answered this impeachment. In the phylloxerans and aphids all the fertilized eggs produce females; males arise only by parthenogenesis, though females may arise in this manner. The cytological facts are as follows: Under favorable external conditions eggs develop without reduction and females are formed. Under unfavorable conditions one or two chromosomes (the sex determiners) are thrown out. If these eggs develop without fertilization

---

[2] Dimorphic eggs in Lepidoptera have recently been demonstrated by both Doncaster and Seiler.

males arise. The somatic condition of the females may therefore be termed XX and that of the males XY. If both reduced normally at any time, ordinary fertilization might be expected to give both males and females. But the spermatocytes without X degenerate, leaving only one type of functional spermatozoa, which produces females. Thus actual causal connection between the X chromosome and sex determination appears to have been demonstrated.

These are the main cytological arguments in favor of the chromosome view of heredity that seem to me to be insuperable. There are minor arguments both pro and con, which, as I said in the beginning, we have not space to consider. Instead it seems more profitable to show how Mendelian results interlock with those from cytology like the parts of a jig-saw puzzle.

Chromosomes and Mendelian Inheritance

The principal phenomena of Mendelian inheritance are: (1) characters that breed true; (2) uniformity of the population of the first hybrid generation in particular traits in which homozygous parents differed; (3) independent segregation of certain character determiners; (4) recombination of certain characters; (5) perfect coupling between certain characters; and (6) partial coupling between certain characters. Let us see how plausibly one can picture the mechanism through which such phenomena may result without imputing to the chromosomes any behavior that is not known to occur. To do this simply let the imagination portray a plant species having four chromosomes, each chromosome having three character determinants that can be followed through the breeding results that are obtained.

Our figures represent the immature germ cells of the plant just previous to the reduction division. Fig. 1 shows the germ mother cell with a duplicate set of hereditary determinants. The mature germ cells are exactly alike, therefore the plant breeds true to the characters concerned.

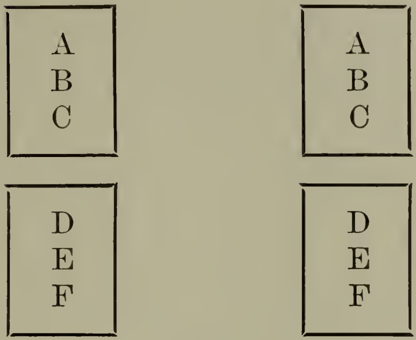


FIG. 1

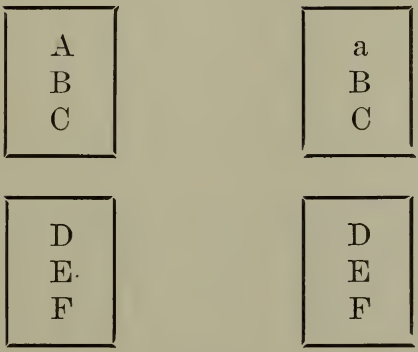


FIG. 2

Suppose, however, that a change in the germ plasm has occurred (Fig. 2) at some time or other. In one member of the first pair of chromosomes, determinant "A" has become "a." The mature germ cells differ from each other by one factor. For this reason the plant does not breed true, but gives a mono-hybrid Mendelian result.

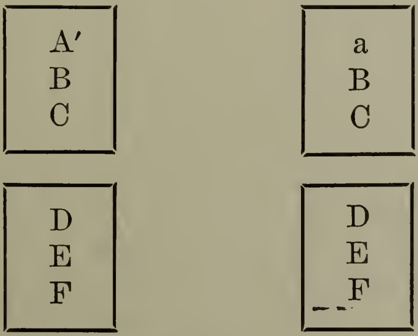


FIG. 3

Again, if such a change occurs that A becomes A′ (Fig. 3), a series of triple allelomorphs giving monohybrid results with each other, is formed. "A" is allelomorphic to "A′" or "a."

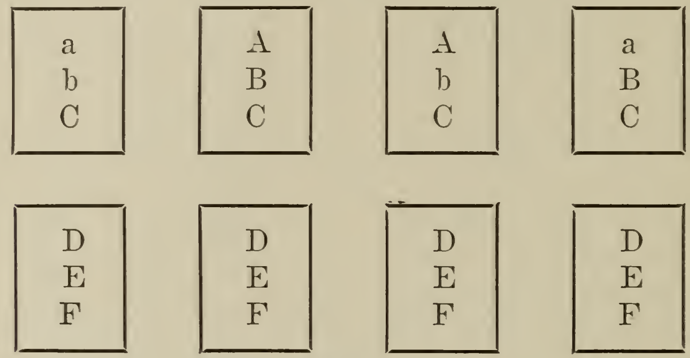


Fig. 4

But there are other character determinants in the first pair of chromosomes. What happens if both "A" and "B" become changed? There are two possibilities, as shown in the two parts of Fig. 4. If one of the members of the pair of homologous chromosomes becomes abC while the other remains ABC, there is a positive correlation between the inheritance of "A" and "B." On the other hand, if the change is such that the two chromosomes are aBC and AbC, there is a negative correlation between A and B. In other words, the determinants remain correlated in the same way they entered the combination. There may be breaks in these correlations, however, as Morgan has shown in *Drosophila;* and these breaks in correlation occur in a constant ratio. Diagrammatically, it may be said that A and B are always the same distance apart in the chromosome structure and that the determinants "cross over" from one member of a pair to the other every so often. All of the gametes in the first case are not ABC and abC, for example. Some of them will be AbC and aBC. And the same percentages of these cross overs are found in the second case where "A" and "B" are correlated negatively. Furthermore, if C should become c, and the chromosome pair take the form ABC and abc, there are definite relations between the three determinants. Breaks in correlation occur, and this ratio is constant, so that if given the percentage of breaks of correlation between "A" and "C" and "B" and "C," the percentage of breaks between "A" and "B" can be predicted. If there is a break in the correlation between "A" and "C" 30 times in 100, and a break between "B" and "C" 10 times in 100, then there will be breaks in the correlation between "A" and "B" 20 times in 100.

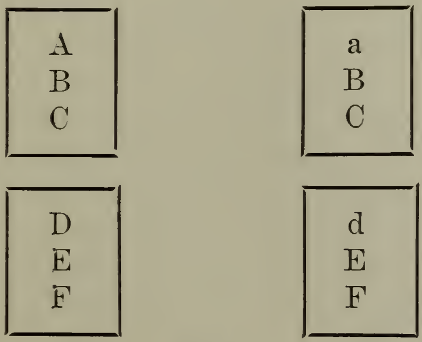


FIG. 5

Likewise, the determinants in the second pair of chromosomes are coupled together in their inheritance. D, E and F have each their peculiar linkage to the other, a linkage that remains comparatively constant. Yet the determinants in the second pair of chromosomes are entirely independent from those in the first pair in their inheritance. For example, if, as shown in Fig. 5, "A" should become "a" in either member of pair number one, and "D" should become "d" in either member of pair number two, Mendelian dihybridism would result. Furthermore, if "A" and "D" should each have the function of affecting the same general character complex in somewhat the same manner, there would be an apparent 15:1 ratio if dominance were complete or a series of types ranging from the type of one grandparent to that of the other, if dominance is lacking.

These are the main features that have been established by recent work on hybrids. We have *pictured* them as actual chromosome functions, because every part of the description has been actual fact as far as the breeding experiments go. Our picture, it is true, is fictitious, for we do not know absolutely that the heredity mechanism is of this nature. But the facts do fit perfectly all that is known of chromosome behavior. It seems impossible, therefore, that there should be so many coincidences.

There are also two other pieces of evidence that fit in and round out the case. Bridges has shown that females occasionally occur in *Drosophila* bearing the sex-linked characters borne by the mother but showing no influence of those borne in the father. Such exceptional females were found to inherit directly from their mother the power of producing like exceptions, and it was proven cytologically *after the prediction had been made from the breeding facts* that these females resulted from the non-disjunction of the X chromosomes at the maturation of the eggs from which they came, and that one half of their daughters did in fact contain a Y chromosome in addition to two X chromosomes. This appears to be definite proof that sex-linked genes are borne by the X chromosomes.

The other important basis for regarding the chromosomes as the material basis for heredity also comes from Morgan's work on *Drosophila ampelophila*, this being the only species upon which sufficient work has been done to give a reasonable basis for the conclusion. *All of the hundred and thirty or so mutations in this species upon which Morgan and his students have worked are so linked together in heredity that they form four groups corresponding to the four pairs of chromosomes found in the species. If one single character should be found that did not fit into one of these four groups, the whole theory would break down. But no such character has appeared.*

This completes the case for the chromosomes as regards the main facts, and it seems only proper that a fair-minded jury of scientists should render verdict for the plaintiff. No case is so bad, however, that a lawyer can find nothing to say for the defense and scientists in this respect resemble the men of the bar. Certainly there are some outlying facts, but they are comparatively unimportant. If a series of important facts should at any time be found which do not fit, the chromosome mechanism should be looked into. It is likely that the explanation will be found in an abnormal chromosome behavior as was the case in the aphis.

PRACTICAL CONCLUSIONS AND DISCUSSIONS

If now it be accepted as a reasonable premise that the chromosomes are the chief if not the sole bearers of hereditary determinants of body characters, and that their behavior is a rough indication of the mechanism of heredity; what cytological facts, if any, can be made useful at present or in the future to plant and animal breeders? If such data exist, they should be put to service; if it is likely that such facts can be found, investigations should be undertaken. The broad question may be divided into three parts which will be discussed in regular sequence:

1. What are the relations of chromosomes to somatic characters?
2. What are the relations of normal chromosome behavior to the transmission of characters?
3. What are the relations of peculiar or unusual chromosome behavior to the transmission of characters?

RELATIONS OF CHROMOSOMES TO INTERNAL CHARACTERS

Some very interesting observations have been made on the relations of internal and external characters to chromosome number.

Farmer and Digby in a comparative study of the cells of a fern of the genus *Athyrium* with similar cells of three of its varieties, found that the measurements were successively larger in the three varieties than in the species, and that there was a corresponding increase in the number of chromosomes, the gametic numbers for the species and its varieties being estimated at 76–80, 84, 90 and 100, respectively. Investigations on another fern, *Lastrea,* did not corroborate these results, however, in one variety the chromosomes being more numerous and the cells smaller than in the parent type.

Gates by comparing nuclei and cells of different tissues of *Œnothera Lamarckiana* and similar structures in its "mutant" *O. gigas* with double the number of chromosomes, found that the *O. gigas* cells and nuclei were always larger, varying from a comparative ratio of 1:1.5 to 1:3. At the same time, it would hardly be wise to maintain that this is always the case. for only a few individuals were investigated.

Primula sinensis has two forms in cultivation, similar except as to size. The giant form has flowers about one and one half times the size of those produced by the ordinary form. Gregory investigated these two forms cytologically to determine the cause of this increase. The nuclei and the chromosomes of the giant form were a little larger, though the difference was hardly a measurable one. The chromosome number was the same in both the forms. In a later investigation he has found that some exceedingly large plants with nuclei distinctly larger than those of the normal form had double the number of chromosomes normal to the species.

Boveri investigated this same relation of cells and nuclei to chromosome number in N, 2N and 4N larvæ of the sea urchin. From these studies, he concludes that chromatin is non-regulatory, and in the case of decrease, unregenerable, the cytoplasm in contrast showing the fullest regulatory activity. Further, the size of the larval cells is governed by the chromosome mass and the cell volume is directly proportional to the chromosome number. On the other hand, Conklin's investigations on annelids, mollusks and ascidians lead him to take a position opposed to that of Boveri. He says:

> The size of the nucleus, centrosomes and chromosomes is dependent upon the volume of the cytoplasm is clearly shown in *Crepidula,* where in large and small blastomeres, these structures are invariably proportional in size to the volume of cytoplasm.

Neither chromosomes nor nucleus control, the size of the cell in annelids, mollusks or ascidians.

Relations between Chromosomes and External Characters

Thus there seems to be no constant relationship even between nuclear or cell size and number of chromosomes, and bonds of union between external taxonomic characters and chromosome number seem to be still more tenuous. It is true that certain giant Primulas and Œnotheras had more chromosomes than were characteristic of the normal forms, but it is just as clear that all giant Primulas (and the same is probably true of Œnotheras, from the work of Heribert-Nilsson and of Geerts) do not have abnormal chromosome numbers.

Results on several species of both animals and plants are interesting in this connection.

The thread worm, *Ascaris megalocephala,* has two varieties, *bivalens* and *univalens,* the former having as a 2N number four chromosomes, the latter two chromosomes. Nothing is known as to the origin of these two forms. They are found parasitic in the same host individual and neither form is rare. According to Herla, they hybridize freely and produce embryos whose cells have three chromosomes, but no mature hybrids have ever been found. Meyer could distinguish no anatomical differences between the two varieties.

Rosenberg investigated the reproductive structures of two species of sundew and found one to have double the chromosome number of the other. A subsequent comparison of anatomical and taxonomic characters failed to show any sharply marked differences between them except in size. The form having the smaller chromosome number was smaller and less robust. They inhabit the same territory and produce natural hybrids which are sterile.

Rosa canina has two varieties which have the same taxonomic characters, but one form has thirty-four while the other has only sixteen chromosomes. The form with thirty-four chromosomes is apogamous and reproduces without fertilization, but that one must not conclude that apogamy is necessarily associated with a double or an increased chromosome number, is clear from the case of *Rumex*. *Rumex* was investigated by Roth; one species, *R. cordifolius,* having forty chromosomes as its 2N number, required fertilization to produce offspring; another species, with only sixteen chromosomes, was apogamous.

A short list of nearly related species or species with two varieties varying in their chromosome numbers with their character differences, if present, is given below.

Name	Date	N	2N	Characters	Investigator
Alchemilla Eualchemilla	1904	32	64	Apogamous	Strasburger, E.
“ *aphanes*	1904	16	32		“ “
Ascaris megalocephala	1883	2	4	Alike externally	Van Beneden
“ “	1895	2	4		Meyer, O.
“ “		1	2		“ “ and others
Ascaris lumbricoides	1887		24		Boveri, T.
“ “	1887		48		“ “
Dahlia variabilis	1911	16	32		Ishikawa, M.
“ “	1911	32	64		“ “
Drosera rotundifolia	1909	10	20		Rosenberg, O.
“ *longifolia*	1909	20	40	More robust, etc.	“ “
Echinus microtuberculatus .	1888	9	18		Boveri, T.
“ “ .	1902	18	36		“ “
Helix pomatia	1903	24	48	Alike externally	Ancel, P.
“ “	1896	12	24		v. Rath, O.
Nephrodium molle	1908	64	128	None mentioned	Yamanouchi, S.
“ “	1908	66	132		“ “
Œnothera lamarckiana	1911	7	14		Gates, R. R.
“ *gigas* form	1909	14	28	Large and coarser	“ “ “
Primula sinensis	1909	12	24		Gregory, R. P.
“ giant form	1909	12	24	More robust	“ “ “
“ “ “	1914	24	48	“ “	“ “ “
Rosa canina	1909		34	Apogamous	Rosenberg, O.
“ “	1904	8	16		Strasburger, E.
Thalictrum minus	1909	12	24		Overton, J. B.
“ *purpurascens*	1909	24	48	Apogamous	“ “ “
Zea Mays, “White Flint”.	1911	10			Kuwada, Y. “
“ “ , “Sugar”	1911	12			“

What conclusions can be drawn from these facts? Certain botanists have attempted to connect chromosome doubling with apogamy, as usually the chromosome number in apogamous species is higher than in the normal species of the same genus; but there is no evidence of apogamy in *Œnothera gigas,* and in *Rumex* the form with the low number of chromosomes is apogamous while the form with the high chromosome number requires fertilization. On account of these exceptions, therefore, it seems probable that the cause of apogamy is deeper than a mere doubling of the chromosomes, even though doubling may usually accompany such a change in reproductive habits.

Variation in chromosome number in the same species has been proposed as a cause of general variation in somatic characters, but the evidence is not clearly in favor of such a theory. In the fern *Nephrodium molle* Yamanouchi found spermatid cells to be of two sorts, those with sixty-six and those with sixty-four chromosomes. This would mean that *Nephrodium* has two gametophyte forms and two sporophyte forms, externally identical, so far as our present knowledge goes, but differing in their chromosome numbers.

Further, sporophytes developing from the prothallia of ferns without the intervention of a sexual process have the N instead of the 2N chromosome number, yet apogamously developed fern sporophytes, except as to chromosome number, are indistinguishable from normal sexually produced individuals of the same species.

Many writers have been tempted to postulate a causal relation between the numerical variation of chromosomes among the species of a genus and the genera of a family and their specific and generic characters. The thirty or more species of Compositæ investigated have shown a remarkable variation in their chromosome numbers, the 2N numbers ranging between six and sixty, and, as is well known, the Compositæ possess an infinite variety of sharply contrasting characters. But the lily family also has an enormous number of characters in its species and genera, and the genus *Lilium,* with its great variety of characters distributed among forty-five species, is typical of the other genera of the family, as far as present investigations go, in having the same chromosome number for all of its species. Others suggest that the more chromosomes a plant species possesses the greater is its variability. Thus Spillman[3] speaks of the low variability of rye, suggesting its small chromosome number (six or eight) as a possible reason; for maize, having probably from twenty to twenty-four chromosomes, is infinitely more variable than rye. However, Britton's "Manual" selects *Crepis virens* for special mention as an extremely variable species from among the four or five other species listed under that genus, and it is known that *C. virens* has only six chromosomes, while three other species of *Crepis* investigated all have higher numbers. Again, according to Wiegand, the *Canna* has only six chromosomes, yet every gardener is well acquainted with the infinite variety in Cannas.

THE CHROMOSOMES AND VARIABILITY

After a consideration of the above facts, one may well hesitate to state that there is even a high degree of correlation either between variability in chromosome number and general variability, or between high numbers of chromosomes and a high degree of variability in specific characters. On the other hand, it is not certain that the data upon which our discussion is based are relevant to the case in hand. We have discussed a possible relationship between chromosome numbers and species complexity and variability as found in the wild. This is not at all the same thing as discussing the relationship between chromosome number and true variability. It is true that complexity and specialization of plants and animals seem to have no connection with chromosome number, and that within a family a genus or a species profusion of taxonomic characters do not go hand-in-hand with high chromosome numbers. But in these cases our data come from persistent forms. What the actual inherent variability of the protoplasm is in most cases we do not know. *Drosophila ampelophila,* a species with only four chromo-

---

[3] Six according to Westgate's unpublished data; eight according to Nakao.

some pairs, is considered to be very constant in its characters from the taxonomist's standpoint, yet by careful continued observation Morgan has succeeded in detecting over 130 mutations.

From a strictly mathematical standpoint, it would seem that if other things are equal, variability would take place in proportion to the number of chromosome units. The difficulty is that in no case do we know anything whatever about the relative complexity of any particular chromosome unit. One must infer, however, that the 47–48 chromosomes in man are individually much more complex than the 128–132 chromosomes in the fern *Nephrodium molle.* If this inference be correct there are reasons why alteration in determinants may occur in direct proportion to the number of chromosomes or rather to the mass of chromatin without there being visible somatic variability in the same ratio. Let us construct an imaginary plan for preventing visible variation without preventing change in chromosome determinants. Unquestionably the simplest means is to double the chromosome number. Selecting, for example, a species with four chromosomes, let us suppose that fertilization occurs without a reduction division at some time or other. Then instead of a dual organism with two sets of chromosomes of similar function, one from the male and one from the female parent, there would be a quadruple organism with two sets of similar chromosomes from each parent. Any germinal change which would produce a *new dominant* character would be apparent immediately, but for a recessive change to appear—and these are many times as numerous as the others—it would be necessary to have identical changes occur in two chromosomes. Following out this line of reasoning, it is not hard to see what a great possibility for uniformity there is in further chromosome duplication, provided the actual fact of duplication makes no great change in the organism. That chromosome doubling has no decided visible effect we have seen from the cases already described; and since so many nearly related species and varieties have their chromosome numbers in series 1:2:3:4, etc., it seems by no means improbable that what we have imagined above has actually occurred many times. And if one may believe that the event has the result supposed, all the worry about relationships between chromosome number and height of species in the scale of evolution may be eliminated.

Normal Chromosome Behavior and Heredity

The second query, concerning the relation of normal chromosome behavior to the transmission of characters, is much more important than the one just examined, but it can be discussed more briefly. By normal "chromosome behavior" is meant a reduction division where maternal and paternal chromosomes approach each other in definite pairs (if homologous pairs are present), chance only governing the passage of either to a particular daughter cell. This is probably the usual behavior in the higher plants and animals, and upon this behavior depends Mendelian heredity in the narrow sense. The thesis to be submitted and scrutinized is the following: *The maximum possible difficulty in the improvement of animals and plants by hybridization usually depends directly upon the chromosome number.*

When a mutation in a single determinant takes place in the germ cells of a plant, such as may cause the loss of red color in the corolla, crosses between such a form and the normal give a monohybrid Mendelian result. Two mutations in non-homologous chromosomes gives in a similar way a dihybrid result. Such simple conditions, however, are not met with very frequently. For example, White found that a fasciated tobacco when crossed with the type from which it sprang and from which it probably differed only by this single determinant, gave a monohybrid Mendelian ratio in the F_2 generation; but when the fasciated type was crossed with other types the result was a complex F_2 population. This population was susceptible of analysis, nevertheless, and showed that the various varieties with which the fasciated type was crossed differed from it by several determinants, each of which was transmitted independently *though they every one affected the development of fasciation.* This illustration is not one of a rare phenomenon. It is what geneticists find constantly in their experiments. Presence or absence of a particular character may depend upon the presence or absence of a particular essential determinant, but, given this determinant, sooner or later the investigator finds several other determinants which modify the expression of the character. The existence of these modifiers has been the cause of a great deal of confusion in the analysis of breeding results, but in reality the inheritance is simple. The experience that all investigators who have worked intensively have had with them shows that practically all somatic characters are due to multiple determinants in the germ cells. It merely depends on the relative difference between the germ plasms brought together in crosses, how complex the resulting F_2 populations appear. Since even apparently simple characters are thus due to complex germinal interactions, that results of crosses made for the purpose of improving such intangible things as yield, size, quality, etc., should be complex, is not astonishing. In the comparatively extensive experience that the writer has had in breeding tobacco, maize, peas and beans the wide variability of the F_2 population in crosses between distinct varieties leads him to think that it is extremely common for such varieties to differ qualitatively in *every chromosome.* Furthermore, the relative complexity of the segregating populations is much greater in tobacco than in corn and greater in corn than in peas or beans. What can this mean but that when varieties are found that differ qualitatively in all of their chromosomes, the complexity of the result varies directly with the number of chromosomes present.

In Mendelian inheritance the number of actual types (both homozygous and heterozygous) present in the F_2 population when all are represented is 3^n, and the number of individuals that must be present to give an equal chance for the presence or absence of an individual of every type is 4^n, where n represents the number of allelomorphic pairs. This being true, if differences in all of the chromosomes are predicated in tobacco and in pea crosses, the maximum number of individuals necessary in the F_2 generation to allow for one reproduction of each of the grandparental forms is 4^{24} in the first case and 4^7 in the second case. It is clear that there is an absolutely overwhelming difference in the difficulty of recovering the grandparental forms in the two examples.

Now this is about what one wishes to do in many plant-breeding problems. It is desired to combine one or two characters from one parent with all of the other qualities of the second parent. And such has been my experience that I believe that this maximum possible difficulty in the operation as predicated by qualitative differences in all of the chromosomes often occurs. There can be no question on these grounds of the importance of determining the number of chromosomes in a species before beginning a complex plant-breeding problem, and thus being able to comprehend the maximum possible difficulties that may be encountered. How greatly these difficulties vary may be seen in the very incomplete list of chromosome counts in common plants that is given below.

Common Name	Scientific Name	N	2N	Date	Investigator
Banana.....	*Musa sapientum*, "dole".	8	"16"	1910	Tischler, G.
"	*Musa sapientum*, "Radjah Siam"......	16	"32"	1910	" "
"	*Musa sapientum*, "Kladi"	24	48	1910	" "
Bean........	*Phaseolus vulgaris*......	8	16	1904	Wager, H.
Calla lily....	*Richardia Africana*.....	8	16	1909	Overton, J. B.
Canna......	*Canna indica*..........	3	6	1900	Wiegand, K. M.
"	" "	8	more than 10	1904	Körnicke, M.
Corn........	*Zea Mays*, "yellow starchy" "amber rice pop," "black starchy," "golden broach field," "white flint"........	10	"20"	1911	Kuwada, Y.
"	*Zea Mays*, "red starchy," "red sugar".........	9–10	"18–20"	1911	" "
"	*Zea Mays*, early 8-rowed sugar...............	9–12		1911	" "

Common Name	Scientific Name	N	2N	Date	Investigator
"	*Zea Mays*, early sugar	12		1911	" "
Cotton	*Gossypium*, " hybrid"	28	"56"	1903	Cannon, W. A.
"	" , "Egyptian"	20		1910	Balls, W. L.
Currant	*Ribes* 2 sp.	8	"16"	1906	Tischler, G.
Dandelion	*Taraxacum confertum*	8	"16"	1909	Rosenberg, O.
"	" sp.	12 or 13	about 26	1905	Juel, H. O.
Elderberry	*Sambucus* sp.	18	38	1909	Lagerberg, T.
Evening primrose	*Œnothera grandiflora*	7	14	1909	Davis, B. M.
Evening primrose	*O. lamarckiana*	"7" 7	14	1907 1911	Geerts, J. M. Gates, R. R.
Evening primrose	*O. gigas*	14	28	1909	Gates, R. R.
Fern	*Nephrodium molle*	64 or 66	128 or 132	1908	Yamanouchi, S.
Flag	*Iris squalens*	12	24	1900	Strasburger, E.
Hawksbeard	*Crepis lanceolata* var. *platyphylum*	5	10	1911	Tahara, M., and M. Ishikawa.
"	*Crepis virens*	3	6	1909	Rosenberg, O.
"	*Crepis tectorum*	4	8	1905	Juel, H. O.
"	*Crepis japonica*	8	16	1910	Tahara, M.
Lily	*Lilium martagon*	12	24	1884	Guignard, L.
Lily-of-the-Valley	*Convallaria majalis*	18	"36"	1899	Wiegand, K. M.
Lily-of-the-Valley	*Convallaria majalis*	16	32	1909	Sauer, L. W.
Mulberry	*Morus alba*, "Shirowase"	17?	40–50	1910	Tahara, M.
"	*Morus indica*	14	28	1910	Tahara, M.
Nightshade	*Solanum nigrum*	36	72?	1909	Winkler, Hans
Onion	*Allium Cepa*	"8"	"16"	1898	Schaffner, J. H.
Peony	*Paeonia spectabilis*	12	"24"	1893	Overton, E.
Pea	*Pisum sativum*	7	14	1903	Cannon, W. A.
Persimmon	*Diospyros virginiana*		30 or more	1911	Hague, Stella M.
Pine	*Pinus laricio*	12	24	1899	Chamberlain, C. J.
Rice	*Oryza sativa*	12	24[4]	1910	Kuwada, Y.
Rose	*Rosa* sp.—3 species	8	16	1904	Strasburger, E.
Tobacco	*Nicotiana* sp.	24	48	1913	White, O. E.
Tomato	*Solanum lycopersicum*	12	24	1909	Winkler, Hans
Tulip	*Tulipa Gesneriana*	12	24	1901	Ernst, A.
Wake-robin	*Trillium grandiflorum*	6	12	1899	Atkinson, G. F.
Wheat	*Triticum vulgare*	8	16	1896	Körnicke, M.
"	" "	8	"16"	1893	Overton, E.
"	" "	8	"16"	1908	Dudley, A. H.

Among these figures are found four of our most important crops—wheat, tobacco, corn and cotton. They contrast strikingly in their chromosome numbers. Wheat and tobacco, species in which the flowers are naturally self-pollinated, have 8 and 24 chromosomes, respectively,

---

[4] "But we often find a larger number." Quotation marks refer to inferred numbers rather than actual countings.

in their gametes. Corn and cotton, species usually cross-pollinated, have 10-12 and 20-28 chromosomes, respectively, in their germ cells. These species all have been under cultivation since before there has been recorded history. Many varieties of each exist. It is not at all improbable that with thousands of years of cultivation and selection under diverse conditions, mutations in most of their chromosomes have persisted. If, then, *improvement* means working on character complexes that involve almost all of the plant functions, it does not seem improbable that the actual difference in the difficulty of improving wheat and tobacco is as $4^8:4^{24}$, or about 1 to 4,295,000,000. In like manner corn and cotton compare in the ratio $4^{10}:4^{28}$, or 1 to 68,720,000,000. And is it not true that modern improvement in most of these crops does involve nearly all the plant functions? Yield in wheat involves number and size of grain, and number of culms, with all that these things include in plant economy; yield of tobacco involves number, size and thickness of the leaves. Quality, a mystical word, is perhaps still more complex. In wheat, it takes in habit of growth of both root and stem and such other characters as go to make up strength and hardiness, thickness of pericarp, size of aleurone cells, and the physical and the chemical character of both endosperm and embryo, as well as their size ratios in regard to each other. In tobacco, it includes thickness and strength of leaf, color, texture and all chemical and physical characters that make for flavor and "burn."

One may say that this is all very well as a theory, but that it is all theory, and ask what support is given to it by practise. I have had personal experience with but two of these four crops. I have worked extensively and intensively with corn and tobacco for some ten years. But I have followed carefully the published experiments in breeding wheat and cotton and have seen several of the more important experiments. *And I may say that it was my observation of the extreme difficulty in the experiments with cotton and tobacco as compared with corn and wheat that led to this theory of the cause.*

In proposing this thesis, the chromosomes have been considered as pairs of freight boats loaded with character determiners, shifted bodily to the daughter cells by internal forces of which we are ignorant. Yet this is not the whole truth. The determiners in particular chromosomes seem to be tied together more or less tightly, but they are not always transferred as one package. They are coupled in their transmission to the next generation, but this coupling is not perfect. Breaks in the coupling occur and there is order and regularity in these breaks. Our knowledge on these matters rests upon the researches of Morgan on *Drosophila,* Bateson on the sweet pea, and Tanaka on the silkworm, so it is not certain whether these are common grounds for this regularity or whether each species has regular laws which control the breaks in correlation. But in either case, these breaks do not interfere with our proposition. They only complicate matters. In most of the cases in *Drosophila,* where they are best known, linkage is comparatively tight, *i. e.,* breaks are somewhat rare; but they may become so frequent as to simulate inheritance from separate chromosomes. In those cases our theory is of no value, but if *Drosophila* is any criterion by which to judge, such conditions are very unusual.

ABNORMAL CHROMOSOME BEHAVIOR AND HEREDITY

The third query concerning the relations of peculiar or unusual chromosome behavior to the transmission of characters may be passed over with a word. In certain insects, for example, bees, wasps, aphids, phylloxerans, etc., odd sex ratios and attendant complexities have long been known. These have been cleared up more or less completely by cytological studies. They depended upon chromosome behaviors that are not usual in animals or plants. Similar peculiar chromosome mechanisms may be present in many other species. Attention is merely called to the fact that if experiments on any plant species appear to show that its characters do not obey the laws that have been demonstrated for so many types, their cytological eccentricities should be looked into. In them will probably be found the key to the situation. The Œnotheras may be mentioned as a case in point. Their heredity in many cases is not what would be expected by analogy with other plants. We know that in some ways the behavior of their chromosomes is irregular. Further study will probably show that this is the sole cause of their anomalous heredity.

LITERATURE CITED

Allen, C. E.

1905. Nuclear Division in the Pollen Mother-cells of *Lilium canadense*. *Ann. Bot.*, 19: 189–258.

Atkinson, G. F.

1899. Studies on Reduction in Plants. *Bot. Gaz.*, 28: 1–26.

Balls, W. L.

1910. The Mechanism of Nuclear Division. *Ann. Bot.* 24: 653–665.

Baltzer, F.

1910. Ueber die Beziehung zwischen dem Chromatin und der Entwickelung und Vererbungsrichtung bei Echinodermenbastarden. *Archiv. f. Zellforsch.*, 5: 497.

Bateson, W.

1909. Mendel's Principles of Heredity. Cambridge, Cambridge University Press. See bibliography reported therein.

Bonnevie, K.

1909. Chromosomenstudien I. *Archiv. f. Zellforsch.*, 1: 450–514, 1908. II. *Ibid.*, 2: 201–278.

Boveri, Th.

1892. Die Entstehung des Gegensatzes zwischen den Geschlechtszellen und den somatischen Zellen bei *Ascaris megalocephala*. *Sitzber. Gesell. Morph. u. Physiol. München.*, Band 8.

1902. Mehrpolige Mitosen als Mittel zur Analyse des Zellkerns. *Verh. Phys. u. Med. Gesell. zu Würzburg.*, N. F., 35.

Bridges, C. B.

1914. Direct Proof Through Non-disjunction that the Six-linked Genes of *Drosophila* are Borne by the X-chromosome. *Science*, N. S., 40: 107–109.

Cannon, W. A.

1902. A Cytological Basis for the Mendelian laws. *Bull. Torr. Bot. Club*, 29: 657–661.

1903. Studies in Plant Hybrids: The Spermatogenesis of Hybrid Cotton. *Bull. Torr. Bot. Club*, 30: 133–172.

1903. Studies in Plant Hybrids: The Spermatogenesis of Hybrid Peas. *Bull. Torr. Bot. Club*, 30: 519–543.

Cardiff, I. D.

1906. A Study of Synapsis and Reduction. *Bull. Torr. Bot. Club*, 33: 271–306.

Chamberlain, C. J.
1899. Oögenesis in *Pinus laricio.* *Bot. Gaz.,* 27: 268–280.
Conklin, E. G.
1901. The Individuality of the Germ-nuclei During the Cleavage of the Egg of *Crepidula.* *Biol. Bull.,* 2: 257–265.
1905. The Mutation Theory from the Standpoint of Cytology. *Science,* N. S., 21: 525–529.
1908. The Mechanism of Heredity. *Science,* N. S., 27: 89–99.
Coulter, J. M., and Chamberlain, C. J.
1903. Morphology of the Angiosperms. N. Y., Appleton.
Davis, B. M.
1909. Cytological Studies on *Œnothera:* I. Pollen Development in *Œnothera grandiflora.* *Ann. Bot.,* 23: 551–571.
Delage, Yves.
1903. L'hérédité et les grands problèms de la biologie générale. 2^me^ ed., Paris, Reinwald.
DeVries, H.
1910. Intracellular Pangenesis: Including a Paper on Fertilization and Hybridization. C. S. Gager, trans. Chi. Open Court.
Dixon, H. N.
1894. Fertilization of *Pinus silvestris.* *Ann. Bot.,* 8: 21–34.
Driesch, H.
1899. Die Lokalisation morphogenetischen Vorgänge. Ein Beweis vitalistischen Geschehens. Leipzig, Engelmann.
Farmer, J. B., and Moore, J. E. S.
1905. On the Maiotic Phase (Reduction Division) in Animals and Plants. *Quart. Jour. Micr. Sci.,* N. S., 48: 489–557.
Farmer, J. B., and Digby, L.
1907. Studies in Apospory and Apogamy in Ferns. *Ann. Bot.,* 21: 161–199.
Fick, R.
1905. Betrachtungen über die Chromosomen, ihre Individualität, Reduktion und Vererbung. *Arch. Anat. u. Physiol.,* Anat. Abt., 179–228.
1908. Zur Conjugation der Chromosomen. *Arch. f. Zellforsch.,* 1: 604–611.
Gates, R. R.
1907. Pollen Development in Hybrids of *Œnothera lata* × *O. Lamarkiana,* and Its Relation to Mutation. *Bot. Gaz.,* 43: 81–115.
1909. The Stature and Chromosomes of *Œnothera gigas* DeVries. *Arch. f. Zellforsch.,* 3: 525–552.
1911. The Mode of Chromosome Reduction. *Bot. Gaz.* 51: 321–344.
Geerts, J. M.
1908. Beiträge zur Kenntnis der cytologischen Entwicklung von *Œnothera Lamarckiana.* *Ber. Deutsch. bot. Ges.,* 26a: 608–614.
1907. Ueber die Zahl der Chromosomen von *Œnothera Lamarckiana.* *Ber. deut. bot. Gesell.,* 25: 191–195.

Grégoire, V., and Wygaerts, A.

1904. La construction du noyau et la formation des chromosomes dans les cinèses somatiques. I. Racines de *Trillium grandiflorum* et télophase homœotypique dans le *Trillium cernuum*. *La Cellule,* 21: 7–76.

Grégoire, V.

1905. Les résultats acquis sur les cinèses de maturation dans les deux règnes. Revue critique de la Littérature. (I Mém.) *La Cellule,* 22: 221–376.

1907. Les fondements cytologiques des théories courantes sur l'hérédité Mendelienne. *Ann. Soc. Roy. Zool. et Malacol Belgique,* 42: 267–320.

1908. Les phénomènes de l'étape synaptique represéntent-ils une caryocinèse? *La Cellule,* 25: 87–99.

1910. Les cinèses de maturation dans les deux règnes. L'Unité essentielle du processus méiotique. (II Mém.) *La Cellule,* 26: 223–422.

Gregory, R. P.

1909. Note on the Giant and Ordinary Forms of *Primula sinensis. Proc. Cambridge Phil. Soc.,* 15: 239–246.

1909. The Mode of Pairing of Chromosomes in Meiosis. *New Phytologist,* 8: 146–153.

1914. On the Genetics of Tetraploid Plants in *Prunula sinensis. Proc. Roy. Soc.,* B. 87.

Guyer, M. F.

1911. Nucleus and Cytoplasm in Heredity. Am. Nat., 45: 284–305.

Haecker, V.

1907. Die Chromosomen als angenommene Vererbungsträger. *Ergebn. u. Fortschritte d. Zoologie,* 1: 1–136.

1910. Ergebnisse und Ausblicke in der Keimzellenforschung. *Zeitschr. Abstammungs. u. Vererbungslehre,* 3: 181–200.

Hague, S. M.

1911. A Morphological Study of *Diospyros virginiana. Bot. Gaz.,* 52: 34–42.

Hegner, R. W.

1911. Germ-cell Determinants and their Significance. Am. Nat., 45: 385–397.

Henking, H.

1891. Ueber Spermatogenese und deren Beziehung zur Eientwicklung bei Pyrrhocoris. *Zeitschr. wiss. Zool.,* 50: 1891.

Heider, K.

1906. Vererbung und Chromosomen. *Versamml. deut. Natur u. Ärtze.* Jena.

Herbst, C.

1909. Vererbungsstudien VI. *Arch. f. Entw.,* 27: Heft 2.

Hertwig, O.

1898. Die Zelle und die Gewebe. Jena, Fischer.

Hyde, E.

1909. The Reduction Division in the Anthers of *Hyacinthus orientalis. Ohio Nat.,* 9: 539–544.

Ishikawa, M.
1911. Cytologische Studien von Dahlien. *Bot. Mag.*, Tokyo, 25: 1–8.

Janssens, F. A.
1905. Spermatogenèse dans les Batraciens: Evolution des auxcytes mâles du *Batrahoseps attenuatus. La Cellule,* 22: 380–425.

Juel, H. O.
1897. Die Kernteilungen in den Pollen-Mutterzellen von *Hemerocallis fulva* und die bei denselben auftretenden Unregelmässigkeiten. *Jahrb. wiss. Bot.*, 30: 205–226.

Koernicke, M. Der heutige Stand der pflanzlichen Zellforschung.
1904. Ber. deut. bot. Gesell., 21: 66–134.

Kölliker, A.
1885. Die Bedeutung der Zellkerne für die Vorgänge der Vererbung. *Zeitschr. wiss. Zool.*, 52: 1–46.

Kuwada, Y.
1910. A Cytological Study of *Oryza sativa. Bot. Mag.*, Tokyo, 24: 267–281.
1911. Maiosis in the Pollen-mother Cells of *Zea Mays,* L. *Bot. Mag.*, Tokyo, 25: 163–181.

Lagerberg, T.
1909. Studien über die Entwickelungsgeschichte und systematische Stellung von *Adoxa moschatellina. Kungl. Sv. Vet. Akad. Handl.*, 44: 1–86.

Lawson, A. A.
1911. Nuclear Osmosis as a Factor in Mitosis. *Trans. Roy. Soc. Edinburgh,* 48: 137–161.
1911. The Phase of the Nucleus Known as Synapsis. *Trans. Roy. Soc. Edinburgh,* 47: Pt. III: 591–604.

Lotsy, J. P.
1906. Vorlesungen über Descendenz-theorien. Two vols. Jena, Fischer.

Lundegård, H.
1909. Ueber Reduktionsteilung in den Pollenmutterzellen einiger dikotyler Pflanzen. *Svensk. Bot. Tidskr.*, 3: 78–124.
1910. Ueber Kernteilung in den Wurzel-spitzen von *Allium cepa* and *Vicia faba. Svensk. Bot. Tidskr.*, 4: 174–196.

Lutz, Anne M.
1909. Notes on the First Generation of Hybrids of *O. lata* × *O. gigas. Science,* N. S., 29: 263–267.

Moenkhaus, W. J.
1904. The Development of Hybrids between *Fundulus heteroclitus* and *Menidia notata* with Especial Reference to Behavior of Maternal and Paternal Chromosomes. *Am. Journ. Anat.*, 3: 29–64.

Montgomery, Jr., T. H.
1906. Chromosomes in the Spermatogenesis of the *Hemiptera heteroptera. Trans. Am. Phil. Soc.*, N. S., 21: 97–173.
1908. On the Morphological Difference of the Chromosomes of *Ascaris megalocephala. Arch. f. Zellforsch.*, 2: 66–75.

Morgan, T. H.
1910. Chromosomes and Heredity. AM. NAT., 44: 449–496.

1913. Heredity and Sex. N. Y., Columbia University Press.

Mottier, D. M.

1907. The Development of Heterotypic Chromosomes in Pollen Mother-cells. *Ann. Bot.*, 21: 309–347.

Nakao, M.

1911. Cytological studies on the nuclear division of the pollen mother cells of some cereals and other hybrids. Jour. Col. Agr. Sapporo (Japan), 4: 173–190.

Nawaschin, Sergius.

1910. Näheres über die Bildung der Spermakerne bei *Lilium Martagon. Annales d. Buitenzorg, 31ème* Supplément, 2e Partie: 871–904.

Němec, B.

1909. Zur Mikrochemie der Chromosomen. *Ber. deutsch. Bot. Gesell.*, 27: 43–47.

1910. Das Problem der Befruchtungsvorgänge und andere cytologische Fragen. Berlin, Borntraeger.

Overton, J. B.

1909. On the Organization of Nuclei in the Pollen-mother Cells of Certain Plants with Special Reference to the Permanence of the Chromosomes. *Ann. Bot.*, 23: 19–61.

Rabl, C.

1885. Ueber Zelltheilung. *Morphol. Jahrb.*, 10: 214–330.

Remak, R.

1858. Ueber die Theilung der Blutzellen beim Embryo. *Müller's Arch.*, S. 178–188.

Rosenberg, O.

1905. Zur Kenntnis der Reduktionsteilung in Pflanzen. *N. Bot. Not.*, S. 1–24.

1906. Cytological Investigations in Plant Hybrids. Rpt. 3d Intern. Conf. on Genetics, pp. 289–291.

1907. Experimental and Cytological Studies on the Apogamy in *Hieracium. Svensk. Bot. Tidskr.*, 2: 143–170.

1909. Ueber den Bau des Ruhekerns. *Svensk. Bot. Tidskr.*, 3: 163–173, Taf. 5.

1909. Ueber die Chromosomenzahlen bei *Taraxacum* und *Rosa. Svensk. Bot. Tidskr.*, 3: 150–162.

1909. Cytologische und morphologische Studien uber *Drosera longifolia* × *D. rotundifolia. Kungl. Svensk. Vetensk. Handl.*, 43: 1–64.

1909. Zur Kenntnis von den Tetradenteilungen der Compositen. *Svensk. Bot. Tidskr.*, 3: 64–77.

Sargent, E.

1896. The Formation of Sexual Nuclei in *Lilium Martagon.* I. Oogenesis. *Ann. Bot.*, 10: 445–477.

1897. The Formation of Sexual Nuclei in *Lilium Martagon.* II. Spermatogenesis. *Ann. Bot.*, 11: 187–224.

Sauer, L. W.

1909. Nuclear Divisions in the Pollen Mother-cells of *Convallaria majalis. Ohio Nat.*, 9: 497–505.

Schaffner, John H.

1909. Chromosome Difference in *Ascaris megalocephala*. *Ohio Nat.*, 9: 506–508.

Stevens, N. M.

1905. Studies in Spermatogenesis with Especial Reference to the "Accessory Chromosome." Carnegie Inst., Wash., Pub. 36, I.

1906. Studies in Spermatogenesis, II. A Comparative Study of the Heterochromosomes in Certain Species of Coleoptera, Hemiptera and Lepidoptera, with Especial Reference to Sex Determination. Carnegie Inst., Wash., Pub. 36, II.

Stomps, T. J.

1911. Kerndeeling en Synapsis by *Spinacea oleracea*. S. 1–162. 1910. *Review Biol. Centralbl.*, 31: 257–320.

Strasburger, E.

1894. Periodic Reduction of Number of Chromosomes in the Life History of Living Organisms. *Ann. Bot.*, 8: 281–316.

1904. Ueber Reduktionsteilung. *Sitzber. K. Preuss. Akad. Wiss.*, 18: 587–614.

1905. Typische und allotypische Kernteilung. Histologische Beiträge zur Vererbungsfrage. *Jahrb. wiss. Bot.*, 52: 1–71.

1907. Ueber die Individualität der Chromosomen und die Pfropfhybriden Frage. *Jahrb. f. wiss. Bot.*, 44: 482–555.

1907. Die Ontogenie der Zell seit 1875. *Progressus rei Botanicæ*, 1: 1–138.

1908. Chromosomenzahlen, Plasmastrukturen, Vererbungsträger, und Reduktionsteilung. *Jahrb. f. wiss. Bot.*, 45: 479–570.

1909. Meine Stellungnahme zur Frage der Pfropfbastarde. *Ber. Deutsch. Bot. Gesell.*, 27: 511–528.

1909. Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktionsteilung. *Histologische Beiträge*, Heft 7, S. 1–124. Jena.

1909. The Minute Relation of Cells in Relation to Heredity. Darwin and Modern Science, pp. 102–11. Cambridge, Cambridge University Press.

1910. Chromosomenzahl. *Flora*, 100: 398–446.

Sutton, W. S.

1902. On the Morphology of the Chromosome Group in *Brachystola magna*. *Biol. Bul.*, 4: 24–39.

1903. The Chromosomes in Heredity. *Biol. Bul.*, 4: 231–251.

Tahara, M.

1910. Ueber die Kernteilung bei *Morus*. *Bot. Mag.*, Tokyo, 24: 281–289.

1910. Ueber die Zahl der Chromosomen von *Crepis japonica*, Benth. *Bot. Mag.*, Tokyo, 24: 23–28.

Tahara, M., and Ishikawa, M.

1911. The number of chromosomes of *Crepis lanceolata* var. *platyphyllum*. *Bot. Mag.*, Tokyo, 25: 119–121.

Tanaka, Y.

1913. A Study of Mendelian Factors in the Silkworm, *Bombyx mori*. *Journ. Col. Agr.*, Sapporo, 5: 91–113.

Tennent, D. H.

1908. The Chromosomes in Cross-fertilized *Echinoid* Eggs. *Biol. Bul.*, 15: 127–134.

Tischler, G.

1906. Ueber die Entwicklung des Pollens und der Tapetenzellen bei Ribes-Hybriden. *Jahrb. f. wiss. Bot.*, 42: 558.

1908. Zellstudien an sterilen Bastardpflanzen. *Arch. f. Zellforsch.*, 1: 3–151.

1910. Untersuchungen über die Entwicklung des Banana-Pollens. *Arch. f. Zellforsch.*, 5: 622–670.

Wager, H.

1904. The Nucleolus and Nuclear Division in the Root-apex of *Phaseolus*. *Ann. Bot.*, 18: 29–55. (Number of chromosomes determined by White from a study of Wager's figures.)

Weismann, A.

1892. Das Keimplasma. Jena.

White, O. E.

1913. The Bearing of Teratological Development in *Nicotiana* on Theories of Heredity. Am. Nat., 52: 206–228.

Wilson, E. B.

1904. The Cell in Development and Inheritance. New York, Macmillan.

1901. Experimental Studies in Cytology. A Cytological Study of Artificial Parthenogenesis in Sea Urchin Eggs. *Arch. f. Entw.*, 12: 529–596.

1909. Studies on Chromosomes, V. The Chromosomes of *Metapodius*. A Contribution to the Hypothesis of the Genetic Continuity of Chromosomes. *Journ. Exp. Zool.*, 6: 147–205.

1910. The Chromosomes in Relation to the Determination of Sex. *Science Progress*, 5: 570–592.

1911. The Sex Chromosome. *Arch. mikr. Anatomie*, 77: 249–271. (Bibliography on accessory chromosome.)

Winkler, Hans.

1908. Ueber Parthenogenesis und Apogamie im Pflanzenreiche. *Progressus rei Botanicæ*, 2: 293–454.

1910. Ueber die Nachkommenschaft der Solanum-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. *Zeitschr. Bot.*, 2: 1–38.

Yamanouchi, S.

1908. Sporogenesis in Nephrodium. *Bot. Gaz.*, 45: 1–30.

Ziegler, H. E.

1906. Die Chromosomen-Theorie der Vererbung in ihrer Anwendung auf den Menschen. *Arch. Rassen-Gesellsch. Biologie*, 3: 797–812.

Zoja, R.

1895. Sulla independenza della cromatina paterna et materna nel nucleo delle cellule embrionali. *Anat. Anz.*, 11: 289–293.

THE CONNECTICUT

AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 188, SEPTEMBER, 1915

FURTHER EXPERIMENTS ON INHERITANCE IN MAIZE

BY

H. K. HAYES and E. M. EAST.

CONNECTICUT AGRICULTURAL EXPERIMENT STATION.

OFFICERS AND STAFF.

BOARD OF CONTROL

His Excellency, Marcus H. Holcomb, *ex-officio, President.*
Prof. H. W. Conn, *Vice President* .... Middletown
George A. Hopson, *Secretary* .... Wallingford
E. H. Jenkins, *Director and Treasurer* .... New Haven
Joseph W. Alsop .... Avon
Wilson H. Lee .... Orange
Frank H. Stadtmueller .... Elmwood
James H. Webb .... Hamden

Administration.	E. H. Jenkins, Ph.D., *Director and Treasurer.*
	Miss V. E. Cole, *Librarian and Stenographer.*
	Miss L. M. Brautlecht, *Bookkeeper and Stenographer.*
	William Veitch, *In charge of Buildings and Grounds.*
Chemistry.	
Analytical Laboratory.	John Phillips Street, M.S., *Chemist in Charge.*
	E. Monroe Bailey, Ph.D., C. B. Morison, B.S.
	C. E. Shepard, G. L. Davis, *Assistants.*
	Hugo Lange, *Laboratory Helper.*
	V. L. Churchill, *Sampling Agent.*
	Miss E. B. Whittlesey, *Stenographer.*
Proteid Research.	T. B. Osborne, Ph.D., D.Sc., *Chemist in Charge.*
	Miss E. L. Ferry, M.S., *Assistant.*
Botany.	G. P. Clinton, Sc.D., *Botanist.*
	E. M. Stoddard, B.S., *Assistant Botanist.*
	Miss E. B. Whittlesey, *Herbarium Assistant.*
	G. E. Graham, *General Assistant.*
Entomology.	W. E. Britton, Ph.D., *Entomologist; State Entomologist.*
	B. H. Walden, B.Agr., *First Assistant.*
	Q. S. Lowry, B.Sc., I. W. Davis, B.Sc. M. P. Zappe, B.S. } *Assistants.*
	Miss G. A. Foote, *Stenographer.*
Forestry.	Walter O. Filley, *Forester; also State Forester and State Forest Fire Warden.*
	A. E. Moss, M.F., *Assistant State and Station Forester.*
	Miss E. L. Avery, *Stenographer.*
Plant Breeding.	Donald F. Jones, B.S., *Plant Breeder.*
	C. D. Hubbell, *Assistant.*
Vegetable Growing.	Howard F. Huber, B.S.

FURTHER EXPERIMENTS ON INHERITANCE IN MAIZE.

BY

H. K. HAYES * AND E. M. EAST.

This paper is a report on the inheritance of certain differences in the endosperm of various maize races that have been made the basis of a division into the subspecies *everta, indurata, indentata* and *amylacea*. To these investigations, a genetic study of the shape of seed which characterizes the socalled rice pop corns is added.

The writers take pleasure in acknowledging the efficient aid of Mr. A. F. Schultze, assistant botanist at the Connecticut Agricultural College, and Mr. C. D. Hubbell, assistant at the Connecticut Agricultural Experiment Station, in the considerable amount of field work involved.

MATERIAL AND METHODS.

The parental races used in the crosses were self-fertilized for several years before any hybrids were made, and are believed to have been homozygous for the characters studied. The material from which these races originated was described in a previous publication (See East and Hayes, 1911), but the following additional points regarding it should be noted:

1. *Zea mays everta*. The pop corns.

No. 64. White rice pop.

This white pop is one of the lines which has been produced from No. 23, (East & Hayes, 1911). It breeds true to the "rice" type of seed,—sharply pointed where the style

---

* Mr. Hayes resigned January 1,. 1914, to take charge of plant breeding work in the Experiment Station and College of Agriculture of the University of Minnesota. The experimental work here reported was carried on at the Connecticut Station as an Adams Fund Project. The Minnesota Experiment Station and the Bussey Institution of Harvard, should be given credit for time spent in the preparation of this paper for publication.

(silk) was attached,—although there is some variation in the degree to which this character is expressed. The seeds contain only very small amounts of soft starch.

No. 65. A white, flint-like pop.

This is a strain produced from No. 26, of our previous publication. Its seeds resemble those of a typical flint variety in shape, and contain only very small amounts of soft starch.

2. *Zea mays indurata.* The flint corns.

No. 5. Watson's white flint.

This variety is a true white flint which developes a red pericarp in full sunlight. The depth of tint which developes naturally is therefore inversely proportional to the thickness of the husk. The seeds contain a larger proportion of corneous starch than many races of flint corn, though less than that shown by the two pop varieties just described. As in all flints, however, there is a small zone of soft starch in the center of the seed.

3. *Zea mays indentata.* The dent corns.

No. 6. Leaming dent.

This is a vigorous strain of a famous yellow dent. Like all varieties of its group, the soft starch extends over the whole summit of the seeds, yet the layer is thin enough to allow the race to be classified as a smooth dent (i. e. not beaked).

4. *Zea mays amylacea.* The flour corns.

No. 10. White flour.

This is a floury race with seeds resembling the average 8 rowed flint in shape. Though the seeds usually contain only floury starch, sometimes an almost imperceptible layer of corneous starch developes in the exterior of the endosperm. It seems likely that this variation is an effect of external conditions rather than of gametic impurity.

The plantings have always been made from the original seed envelope, and pains have been taken to prevent the misplacement of seeds.

The different families were marked in the field by heavy stakes to which wired tree labels were attached, but to prevent error through their misplacement a planting plan was made each year showing the exact location and the number of hills of each strain.

Classification of seeds was made only from hand pollinated ears, although the remaining ears of a selection were always examined, and in the case of those seed characters not immediately affected by pollination, were used in determining the range of variation.

The various races were given different numbers as No. 10 flour corn and No. 5 flint corn. A cross between 10 and 5 was then written as 10 x 5 the female parent appearing first. Different self-pollinated ears obtained from growing the cross between (10 x 5) were labeled (10 x 5)-1, (10 x 5)-2, etc. Later generations were labeled as (10 x 5)-1-2, (10 x 5)-1-3, (10 x 5)-2-4, etc. If the F_1 generation was pollinated with pollen from the flint parent, this ear received the label (10 x 5)-1 x (5-2)-8-3, as the case might be. This back cross was planted the following year as (10 x 5 x 5). Thus we had complete records of the parents and ancestry of our various lines.

The field technique has been described in previous publications.

For convenience the various crosses will be considered under special headings.

FAMILY (10 x 5), FLOUR x FLINT.

A cross between the floury race No. 10 and flint race No. 5 was made in 1910, the resulting seeds resembling the female parent. As indicated above, the characteristic difference between these races is the amount of soft starch in the seeds. The flint race produces a small quantity of soft starch in the center of the seed, surrounded by a large layer of corneous starch, while the flour race produces only an occasional trace of corneous starch around the exterior of the endosperm. No immediate effect of pollination through double fertilization was expected, as both our own earlier results and those of other investigators (Correns and Lock) were thought to imply that these differences in the starchy character of the endosperm behaved in heredity as if they pertained to the plant rather than to the endosperm. On growing this cross in 1910, however, we were much surprised to find a clear segregation of seeds on each ear. This fact showed that the physical condition of the starch in these races was not a maternal character, since in that case we should have expected a uniform population of seeds on the F_1 ears, resembling either the male or female parents or intermediate between them.

A classification of the seeds from the ears of the F_1 generation plants, is given in Table 1. Only two classes could be made; corneous seeds like the flint parent, and floury seeds resembling the floury parent. There was no difficulty in dividing the seeds into these two classes. Of the thirteen ears shown in Table 1, some contained a greater proportion of flint or of floury seeds than others, but all gave close approximations to a 1 to 1 ratio. This being a novel F_1 ratio, further experiments were made to find a genetic interpretation of it.

TABLE 1.

SELF-POLLINATED EARS FROM THE F_1 GENERATION OF A CROSS BETWEEN NO. 10 FLOUR AND NO. 5 CORNEOUS FLINT.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-1	145	186
" -3	208	142
" -4	169	161
" -5	156	169
" -6	181	166
" -7	189	172
" -8	175	203
" -9	168	165
" -10	213	213
" -11	209	205
" -12	238	237
" -13	190	197
" -14	252	223
Total	2493	2439

The floury seeds of (10 x 5)-7 and (10 x 5)-8 were labeled (10 x 5)-7S and (10 x 5)-8S to distinguish them from the corneous (flint-like) seeds 'of the same ears, which were labeled (10 x 5)-7C and (10 x 5)-8C respectively. The data from sev-

---

[1] The word hybrid in these discussions is used in a peculiar sense to avoid longer descriptions. It means a cob bearing a population of seeds belonging to more than one phenotype.

eral self-fertilized ears obtained by growing the floury seeds are given in Table 2. Of a total of 11 hand-pollinated ears, 8 were hybrid[1], and gave 1 to 1 ratios with a total of 748 corneous to 691 floury seeds. The other 3 ears bred true for the floury habit.

Of the open field or naturally pollinated ears, 28 were hybrids and 23 pure floury. This gives a total of 36 hybrids to 26 pure floury, which, considering the number grown, is a reasonable approximation of a 1 to 1 ratio.

TABLE 2.

SELF-POLLINATED EARS OBTAINED THROUGH GROWING FLOURY SEEDS OF EARS (10 x 5)-7 AND (10 x 5)-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-7 S-1	108	125
" -7 S-2	76	59
" -7 S-4	162	126
" -7 S-7	58	55
" -8 S-5	100	97
" -8 S-6	53	48
" -8 S-7	91	89
" -8 S-8	100	92
" -8 S-2		Pure Floury
" -8 S-3		" "
" -8 S-4		" "
Total in hybrid ears	748	691

Table 3 gives the results of planting the corneous seeds of ears (10 x 5)-7 and (10 x 5)-8. Of a total of 9 self-fertilized ears, 5 proved to be hybrids and 4 were pure corneous. The ratio of corneous to floury seeds in these 5 hybrid ears was 464 corneous to 482 floury, a close approximation of 1 to 1. Of the open field ears 38 were corneous and 34 hybrids. Thus in this case the hybrid and the pure corneous ears are clearly in a 1 to 1 ratio.

TABLE 3.

SELF-POLLINATED EARS OBTAINED THROUGH GROWING CORNEOUS SEEDS OF EARS (10 x 5)-7 AND (10 x 5)-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-7C-6	30	29
" -7C-9	73	101
" -8C-3	97	81
" -8C-8	191	211
" -8C-10	73	60
" -7C-5	Pure corneous	
" -7C-8	" "	
" -8C-5	" "	
" -8C-6	" "	
Total in hybrid ears	464	482

Table 4 gives the results of pollinating ears of the F_1 plants with pollen from the parental strains No. 10 flour, and No. 5 flint, respectively. Only 1 ear was obtained from the back cross between (10 x 5) and the No. 10 parent. This ear had 156 corneous and 184 floury seeds. Three ears resulted from crossing plants of (10 x 5) with the flint, or No. 5 parent. These ears showed various ratios of corneous to floury seeds, but the deviations from 1: 1 ratios were not all in the same direction. Of the total number of seeds in the four ears, 544 were corneous and 543 floury.

TABLE 4.

EARS OF THE FIRST GENERATION CROSS OF (10 x 5) POLLINATED WITH POLLEN FROM THE PURE PARENTS, NO. 10 FLOUR AND NO. 5 CORNEOUS FLINT.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-13 x (10-3)-14	156	184
" - 3 x (5-3)-1	102	79
" - 1 x (5-3)-3	107	79
" - 5 x (-5-3)-7	179	201
Total	544	543

Table 5 gives the results obtained from planting floury seeds of ears (10 x 5)-5 x (5-3)-7 and (10 x 5)-1 x (5-3)-3 of Table 4. It was expected that such seeds would be hybrids between the corneous and floury types and should therefore give hybrid ratios when grown. The table shows 10 self-pollinated ears which gave a ratio of 1014 corneous to 850 floury seeds. Seventy-nine naturally pollinated ears were all hybrids showing a definite segregation. The corneous seeds of ears (10 x 5)-5 x (5-3)-7 and (10 x 5)-1 x (5-3)-3 were also tested. A total of 13 self-fertilized and 87 open field ears were pure corneous flints like the corneous flint parent, No. 5.

TABLE 5.

SELF-POLLINATED EARS OBTAINED FROM PLANTING FLOURY SEEDS OF EAR (10 x 5)-5 x (5-3)-7 AND EAR (10 x 5)-1 x (5-3)-3.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5) x 5-7S-6	102	116
" -5	125	137
" -1	77	48
" -8	126	110
" -2	128	106
" -7	67	36
(10 x 5) x 5-3S-2	93	58
" -8	74	71
" -1	126	92
" -6	96	76
Total	1014	850

Table 6 gives the results obtained from planting corneous seeds of ears (10 x 5)-13 x (10-3)-14. As these seeds were assumed to be the result of a cross between corneous and floury types, it was to be expected that all resulting ears would show segregation. Five self-fertilized ears evidently came from hybrid seeds as they gave a total ratio of 653 corneous to 620 floury seeds. Of 57 open field ears, 56 came from hybrid seeds. One ear which was somewhat immature probably was a pure soft floury ear. This result may be explained by assuming that one floury seed was planted by mistake.

Of the 7 self-fertilized ears obtained from planting the floury seeds of the cross between (10 x 5)-13 x (10-3)-14, all were pure floury. Of the open pollinated ears, 11 were unquestionably pure floury while 2 indicated segregation. These ears may have come from corneous seeds planted by mistake, although it is possible that a few stalks were mislabeled at harvesting time, as the stalks bearing the open pollinated ears all were shocked on the same field.

TABLE 6.

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF EAR NO. (10 x 5)-13 x (10-3)-14.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5) x 10-3-14C-4	127	116
" " -9	200	172
" " -7	70	71
" " -6	73	94
" " -10	183	167
Total	653	620

Table 7, gives the results of planting seeds of Ear No. (5-3)-20, pure corneous flint, which was pollinated with pollen from F_1 generation cross (10 x 5). There was no immediate effect of the pollen of (10 x 5)-6 upon the pure flint ear (5-3)-20. Of 5 self-fertilized ears obtained from growing this cross, 4 showed segregation, giving a total of 528 corneous to 508 floury seeds, and 1 was pure corneous. Of the open field ears 24 were pure corneous and 34 showed segregation. These results show that the pollen grains carry the factors for corneous and floury starch in the ratio of 1 to 1.

Table 8 gives the results of planting seeds of ear (10-3)-13, which was pollinated with pollen from an F_1 ear (10 x 5)-14. There was no visible effect on the endosperm of (10-3)-13 due to crossing. Three of the self-fertilized ears obtained from this cross had a total of 397 corneous to 377 floury seeds; 6 self-fertilized ears were like the floury parent. Of the open field ears, 32 were homozygous floury and 30 were hybrids.

TABLE 7

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF EAR NO. (5-3)-20 x (10 x 5)-6.

Ear Number	Corneous Seeds	Floury Seeds
5 x (10 x 5)-2	116	113
“ -3	116	116
“ -5	126	120
“ -8	170	159
“ -9	Pure corneous	
Total in hybrid ears	528	508

TABLE 8.

SELF-POLLINATED EARS OBTAINED FROM PLANTING FLOURY SEEDS OF EAR NO. (10-3)-13 x (10 x 5)-14.

Ear Number	Corneous Seeds	Floury Seeds
10 x (10 x 5)-6	158	156
“ -7	84	79
“ -4	155	142
“ -1	Pure floury	
“ -2	“	
“ -3	“	
“ -4	“	
“ -5	“	
“ -6	“	
Total in hybrid ears	397	377

Table 9 gives the results of planting the corneous seeds of (10 x 5)-8C-8 and (10 x 5)-8S-8. This F_3 generation was grown to determine whether a constant splitting into a 1 to 1 ratio in the hybrid ears could be expected. The results show no great deviations from this ratio. On 9 selfed ears showing segregation there were 996 corneous and 954 floury seeds.

The total progeny of (10 x 5)-8C-8 consisted of 12 hybrid ears and 15 corneous ears, while the progeny of (10 x 5)-8S-8C included 17 hybrid and 10 pure corneous ears. Considering the few individuals grown the data corroborate those of the previous generation.

TABLE 9.

SELF-POLLINATED EARS OBTAINED FROM PLANTING CORNEOUS SEEDS OF F_2 GENERATION EARS (10 x 5)-8C-8 AND (10 x 5)-8S-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-8C-8C-1	150	116
" -3	116	133
" -2	Pure corneous	
" -5	"	
" -7	"	
" -8	"	
(10 x 5)-8S-8C-1	114	132
" -2	96	115
" -4	103	98
" -5	142	104
" -6	114	95
" -7	89	101
" -8	72	60
" -3	Pure corneous	
Total in hybrid ears	996	954

Table 10 gives the results of planting floury seeds of ears (10 x 5)-8C-8 and (10 x 5)-8S-8. In 8 self-pollinated ears there were a total of 966 corneous and 997 floury seeds. Among the progeny of (10 x 5)-8C-8S there were 17 segregating ears and 16 floury ears, while the progeny of (10 x 5)-8S-8S gave a total of 12 segregating and 10 floury ears. The data in these two tables show that the progeny of an ear which is a cross between floury and corneous may be expected to give a ratio in F_2 of 1 corneous, 2 segregating to 1 floury ear.

TABLE 10.

Self-pollinated Ears Obtained From Planting Floury Seeds of (10 x 5)-8C-8 and (10 x 5)-8S-8.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 5)-8C-8S-1	112	132
" -2	157	174
" -5	155	150
" -6	100	98
" -7	150	150
(10 x 5)-8S-8S-2	98	107
" -3	96	100
" -4	98	86
" -1	Pure Floury	
" -4	"	
(10 x 5)-8C-8S-8	"	
" -3	"	
Total in hybrid ears	966	997

To test the purity of apparently homozygous segregates the seeds of pure corneous ear (10 x 5)-8C-6 were planted. A total of 63 ears were all pure for the corneous habit. Pure floury ear (10 x 5)-8S-2 gave a progeny of 78 ears. All were of a similar character and contained seeds which were nearly filled with soft starch. There were traces of corneous matter in some seeds, but under Connecticut conditions the floury parent also produces traces of corneous matter in a few seeds.

Summary and Interpretation of Results.

In general, no matter which variety was used as the female parent, there was no immediate visible effect of the male parent in the endosperm of crosses between No. 5 flint and No. 10 floury maize. The F_1 generation plants produced ears in which there was a clear segregation of corneous and floury seeds in a 1 to 1 ratio. This ratio was unaffected whether the F_1 ears were pollinated with pollen from either the pure flint or the pure floury parent. The progeny of a cross between F_1 and the flint parent gave a ratio of 1 hybrid ear to 1 pure flint ear. Likewise the progeny of a cross between F_1 and the floury parent gave a ratio of 1 floury ear to 1 hybrid ear. Seventy-six

F_2 ears produced from a self-fertilized F_1 ear of cross (10 x 5), gave a ratio of 1 pure flint ear, 2 hybrid ears and 1 pure floury ear. The flint and the floury ears bred true in later generations.

A total of 69 self-fertilized ears showing segregation gave a ratio of 8,803 corneous seeds to 8,562 floury seeds. This is a ratio of 1 to .961 or approximately 1 to 1.

The above results prove that the visible endosperm character of a seed shows the potentiality of the female gamete which entered into that particular seed, and that the male gametes have no immediate effect on the endosperm to determine whether they be corneous or floury. Data from later generations, however, show that the pollen grains of plants from hybrid seeds transmit both the corneous and the floury condition, approximately ½ carrying a factor for corneous seeds and the other half a factor for floury seeds.

Two hypotheses will explain the facts: either there is no fusion between the female endosperm nucleus and the so-called second male nucleus of the pollen grain, in which case the endosperm developes wholly from the endosperm nucleus of the embryo sac and therefore exhibits the gametic character of the egg cell: or, there is dominance of the condition of the mother. As ordinarily two female polar nuclei unite with a single male nucleus to produce the endosperm it might be expected that this double dose of the female character should predominate over a single dose of the male character, so that by inspection the seeds would be classed as of the mother type. Correns (1901) used the second hypothesis to account for certain results in his study of the inheritance of color in the aleurone cells, where there appeared to be a dominance of the maternal condition. Although East and Hayes (1911) were able to show that Correns' assumption was unnecessary in the case of aleurone color, the aberrant ratios obtained being due to the interaction of several factors, it does appear to fit the facts in the crosses just described.

A cross between a yellow corneous race and a white floury race would show the correct explanation of the results of the floury-flint cross, for if in F_2 the ratio of yellow to white was 3 to 1, and of corneous to floury, 1 to 1, it would then be established that there was a fusion of the female polar nuclei with a male generative cell. Emerson suggested that the same test could be made by pollinating ears which were expected to give a 1 to 1 ratio with pollen from a yellow corneous flint. At the time this test was to be made no seeds of the immediate cross between the corneous and floury races were available, but a number of seeds of hybrid ears (10 x 5)-8C-8S-6 were planted and the resulting plants crossed with pollen from a corneous yellow flint known to breed true. Four ears were obtained of a cross between (10 x 5)-8C-8S-6C (the corneous seeds) and the yellow flint. They proved to be yellow corneous flints. Of the naturally pollinated ears obtained from (10 x 5)-8C-8S-6C, 12 were pure corneous flints and 18 hybrids. Five ears of (10 x 5)-8C-8S-6S (the floury seeds) were also pollinated with pollen from the yellow corneous race. All five ears were yellow and four were yellow floury ears. One ear was a definite hybrid, however, and gave a ratio of 55 floury seeds to 59 corneous seeds. Of the open field ears of (10 x 5)-8C-8S-6S, 13 were pure floury and 14 hybrids.

The ear which *had all yellow seeds* and yet showed a ratio of 55 floury to 59 corneous, seems sufficient evidence for concluding that the apparent dominance of the condition of the mother is due to the fact that the endosperm is produced from a union between two female polar nuclei and one male cell. Thus two doses of a flour corn factor dominates one dose of the corneous factor and *vice versa. This fact has an important bearing on the multiple factor hypothesis for interpreting the inheritance of quantitative characters, for it shows that a series of factors may have cumulative somatic effects.*

FAMILY (10x6), FLOUR x DENT.

This cross was made in 1909 between self-fertilized strains of Leaming No. 6 and floury No. 10. An F_1 generation was grown in 1910, and an F_2 generation from the seeds of F_1 ear (10 x 6)-1 was produced in 1911. There was no appreciable effect on the physical condition of the starch in the seeds of No. 10 due to the pollen of No. 6. On the F_1 ears the seeds were intermediate between No. 10 and No. 6 in size, and were rather uniformly dented. As regards the appearance of the starch in the seeds, there was definite segregation, but classification was difficult due to the fact that all seeds contained soft starch at the cap and sides and were dented. The seeds of the self-fertilized F_1 and F_2 ears were all examined carefully against a strong light, however, and were classified as accurately as possible. The results of this classification are given in Table 11. Considerable variation in the ratios on the different ears is exhibited, but as a rule there is an indication of a 1 to 1 ratio.

Although this seed classification may not have been as accurate as might be desired owing to the difficulties involved, the division of the total population of F_2 ears into corneous, hybrid and floury types as shown in Table 12, is exact and serves as a complete corroboration of the theory. Thirty-six ears were classed as pure corneous, eighty as hybrids and thirty-seven as pure floury. This is certainly a close approximation of a 1:2:1 ratio.

An examination of the F_2 ears showed that there was considerable range of variation between the different ears which were classed as corneous or floury types. There was a little variation among the seeds of the same ear, but this was not greater than could be explained by differences in development due to physiological causes. The pure corneous or pure floury ears, however, differed from each other by a considerable amount, and it seemed likely that some of this variation would be inherited. Of the ears of Table 11, (10 x 6)-1-13, (10 x 6)-1-3 and (10 x 6) 1-4 bred true to the floury type.

The corneous seeds of ear (10 x 6)-1-5 produced 13 hybrid and 17 pure corneous ears, while the floury seeds yielded 19 pure floury and 16 hybrid ears. Corneous ear (10 x 6)-1-5-2 was grown the following year and produced dented ears which bore seeds containing a fair proportion of corneous starch.

Ears (10 x 6)-1-6, (10 x 6)-1-9, (10 x 6)-1-12 and (10 x 6) -1-14 of Table 11 were grown in 1912. All produced ears having seeds with a considerable proportion of corneous starch, the progeny of No. (10 x 6)-1-6 and No. (10 x 6)-1-12 having about the same proportion, and of No. (10 x 6)-1-9 and No. (10 x 6)-1-14, having a greater proportion of corneous starch than the dent parent.

TABLE 11.

Record of Self-Fertilized Ears of F_1 and F_2 Generation of Cross Between No. 10 and No. 6.

Ear Number	Corneous Seeds	Floury Seeds
(10 x 6)-5	104	75
(10 x 6)-2	159	226
(10 x 6)-1-1	123	48
“ “-2	157	152
“ “-3a	199	145
“ “-4a	307	250
“ “-5	242	208
“ “-6a	149	94
“ “-7	199	182
“ “-8	124	77
“ “-9a	259	202
“ “-10	226	196
“ “-11	212	209
“ “-12a	182	106
“ “-13a	107	108
“ “-14a	42	30
“ “-15	72	85
“ “-16	hybrid ear, immature	
“ “-6	considerable corneous starch in all seeds	
“ “-9	all seeds very corneous	
“ “-10	some varibility, no seeds as No. 10 (variation probably due to immaturity)	
“ “-11	pure corneous	
“ ”-12	pure corneous	
“ “-14	all seeds very corneous	
“ “-15	pure corneous	
“ “-3	as No. 10	proved pure floury in 1912
“ “-4	probably as No. 10	
“ “-16	“	
“ “-17	as No. 10	
“ “-18	“	
“ “-19	“	
“ “-13	“	
“ “-20	“	
“ “-21	Probably as No. 10	
“ “-22	“	
“ “-23	“	
“ “-24	“	
Total in hybrid ears	2863	2393

TABLE 12.

F_2 EARS OBTAINED FROM GROWING EAR (10 x 6)-1.

Parent Stock	Pure corneous	Hybrids	Pure Floury
[Hand pollinated ears]	7	16	12
Dark yellow seeds of (10 x 6)-1	11	16	8
Light yellow seeds of (10 x 6)-1	7	24	8
White seeds of (10 x 6)-1	11	24	9
Total	36	80	37

All ears obtained from ear No. (10 x 6)-1-9 selfed had small seeds with traces of dent. On some ears there were merely traces of dent, but other ears showed the dented condition in all seeds. Selections were made to determine whether these variations were inherited. In 1914 a self-fertilized ear which bore seeds with only a few traces of dent was grown, also an ear with all seed dented. The progeny of these ears is given in Table 13.

TABLE 13.

THE PROGENY OF EARS NO. (10 x 6)-1-9-1 AND (10 x 6)-1-9-2.

Condition of Parent Ear	Progeny Classes.			
	¾ seeds dented	½ seeds dented	Few seeds dented	No seeds dented
Few seeds dented	9	12	14	1
¾ seeds dented	11	7	20	3

These results show that little progress was made by the selection.

Of the self-fertilized ears obtained from ear No. (10 x 6)-1-14, one showed no trace of dent, all of the seeds containing a large proportion of corneous starch. This ear was grown and compared with another self-fertilized ear which showed traces of dent in nearly all seeds. The results are given in Table 14.

TABLE 14.

THE PROGENY OF EARS NO. (10 x 6)-1-14-1 AND (10 x 6)-1-14-2.

Condition of Parent Ear	Progeny Classes		
	½ Seeds dented	Few seeds dented	No seeds dented
No seeds dented		4	27
Half seeds dented	5	11	19

In this case there seems to be some effect of selection, although the number of individuals grown is not very large.

CONCLUSIONS.

There seems to be a close agreement between the results of the cross between 10 and 6 and those reported for the cross between 10 and 5. It was, however, more difficult to classify the seeds in the (10 x 6) cross as in No. 6 corneous starch is produced only on the sides of the seed, the cap and the immediate vicinity of the embryo being filled with soft starch.

The essential difference between No. 10 and No. 6 in type of starch produced is evidently one factor, yet since different F_3 families showed variations in the amount of corneous starch produced, there must be several minor factors which modify its development. There is good evidence that at least some of these minor factors are factors which have a direct effect on totally different tissues. For example, the size and shape of the seed which is at least partly controlled by the type of pericarp (a maternal character) has considerable influence upon the appearance of the starch. To put the matter roughly, in plants which fundamentally have the same zygotic possibilities as regards the type of starch in the endosperm, the amount of soft starch actually developed is directly proportional to the size of the seed.

FAMILY (10 x 64), FLOURY x RICE POP (VERY CORNEOUS.)

The No. 10 parent had been self-fertilized for three years and the No. 64 parent had been self-fertilized for two years prior to 1909 when the cross was made. There was no visible effect of the pollen of No. 64 on No. 10. F_1 ears were grown in

1910, but in no case was there a clear segregation among the seeds like that occurring in the F_1 ears of crosses (10 x 5) and (10 x 6). This may have been due to the fact that the ears were somewhat immature. The seeds of three F_1 ears were separated into two classes; first, seeds as floury as No. 10; second, all remaining seeds. These partially corneous seeds showed a range of variation from very corneous seeds to those which contained only a little more corneous matter than the No. 10 flour parent. The result of this classification is shown in Table 15.

TABLE 15.

F_1 Ears of Cross Between (10 x 64).

Ear Number	Floury Seeds	Corneous Seeds
(10 x 64)-7	93	216
(10 x 64)-10	82	349
(10 x 64)-12	168	353
Total	343	918

The seeds of (10 x 64)-7 and (10 x 64)-10 were planted in 1911. Those which had been classed as of the floury type like No. 10 were planted as (10 x 64)-7S and (10 x 64)-10S. The remainder of the seeds of the same ears were planted as (10 x 64) -7C and (10 x 64)-10C respectively. The results obtained from a classification of the progeny of these ears are given in Table 16.

TABLE 16.

Ears Obtained From Planting (10 x 64)-7C and 7S and (10 x 64)-10C and 10S.

Parent Type	Progeny Classes				
	Pure Floury	Intermediate Floury	Definite Hybrids	Intermediate Corneous	Pure Corneous
(10 x 64)-7S	4	15	11	6	
(10 x 64)-10S	6	13	17	2	
(10 x 64)-7C			16	7	13
(10 x 64)-10C		1	15	6	10

There is a similarity in the variability of the populations obtained from the floury seeds of (10 x 64)-7S and (10 x 64)-10S; the progeny of the corneous seeds of (10 x 64)-10 and (10 x 64) -7 also show about the same percentage of ears in the different classes.

Two self-fertilized F_2 ears (10 x 64)-10S-5 and (10 x 64) -10C-4 were classed as definite hybrids. The corneous seeds of these ears gave a range of variation from purely corneous to definitely hybrid ears, there being 3.3 times as many corneous, intermediate, and definitely hybrid ears, as there were pure corneous ears. The floury seeds of (10 x 64)-10S-5 and (10 x 64)-10C-4 produced 4.2 as many hybrid and intermediate ears as pure floury ears. Thus these two F_2 ears showed as variable a progeny in F_3 as had been found in F_2.

Five self-fertilized F_2 ears of the intermediate floury class from the progeny of (10 x 64)-10S gave a total population of 165 ears; of which 19 approached pure corneous but contained a larger percentage of soft starch than the corneous parent, 12 approached the floury parent, and 134 were intermediate. Many of these intermediate ears showed some variation among the seeds, but no clear segregation.

F_2 corneous ears, (10 x 64)-10C-9, (10 x 64)-7C-9, and (10 x 64)-7C-1 bred true for the corneous habit in F_3. (10 x 64) -10C-9 was grown in F_4 and again bred true.

Pure floury ear (10 x 64)-7S-13 bred true in F_3 and F_4 for the floury habit.

One self-pollinated intermediate F_2 ear, (10 x 64)-7C-2 proved to be a hybrid and gave in F_3 15 corneous ears, 32 definitely hybrid ears showing clear segregation, and 18 intermediate corneous ears which showed some variation. This is a 1:2:1 ratio.

Two F_4 ears bred from the intermediate class, (10 x 64)-7C-2-10 and (10 x 64)-7C-2-1, together produced 14 ears approaching pure corneous, 68 intermediate variable ears and 4 approaching pure floury. These ears are probably all intermediates, the variation being due to maturity and possibly due to the effect of other inherited factors. Of 3 other F_2 ears classed as intermediate, 2 gave intermediate progeny and 1 proved to be a definite hybrid. Self-pollinated ears of selections (10 x 64)-7S-1 and (10 x 64)-7S-7 from the intermediate class were grown the following year. These results are given in Table 17.

TABLE 17.

PROGENY OF EARS NO. (10 x 64)-7S-1 AND (10 x 64)-7S-7 WHICH WERE CLASSED AS INTERMEDIATE VARIABLE EARS.

Ear No.	Parent type	Classification of Progeny: Approaching Corneous	Classification of Progeny: Variable Intermediate	Classification of Progeny: Approaching Floury
(10 x 64)-7S-1-2	Most corneous ear	2	35	
(10 x 64)-7S-1-6	" floury ear		40	1
(10 x 64)-7S-7-10	Intermediate ear	3	35	
" -2	"		48	
" -4	"		47	
" -8	"	2	‡46	

‡ Of this population, 25 open field ears were very variable and showed definite segregation. The self-fertilized ears were comparatively uniform.

The data in Table 17 show that intermediate variable ears tend to give intermediate variable progeny. The ears did not all become thoroughly mature, and this may be the explanation of their variable endosperms. There is also the possibility that other heterozygous factors may have influenced development in such a way as to produce variation. (East & Hayes 1911).

F_3 ear (10 x 64)-10C-1-6 produced intermediate and corneous seeds in a ratio approaching 1:1. The corneous seeds of this ear gave a progeny of 28 purely corneous and 24 definitely hybrid ears, while the intermediate seeds gave a progeny of 2 corneous ears, 17 definite hybrids and 23 intermediate variable ears. This is a close approximation of a 1:2:1 ratio. That only 1 factor determined whether corneous or intermediate seeds were to be produced in this ear is further indicated by the separation of seeds from five self-pollinated ears which were classed as definite hybrids. The results are given in Table 18. The total number of corneous seeds in these five ears were 514 and of intermediate seeds 491. This clearly approaches a 1 to 1 ratio.

TABLE 18.

CLASSIFICATION OF SEEDS OF HYBRID EARS OBTAINED FROM PLANTING INTERMEDIATE AND CORNEOUS SEEDS OF EAR (10 x 64)-10C-1-6.

Ear Number	Corneous Seeds	Intermediate Seeds
(10 x 64)-10C-1-6I-2	101	84
“ -9	78	92
“ -8	80	67
(10 x 14)-10C-1-6C-8	135	124
“ -10	120	124
Total in hybrid ears	514	491

SUMMARY AND INTERPRETATION OF RESULTS.

The pollen of No. 64 pop apparently had no effect on the character of the endosperm of No. 10 flour. This is in agreement with the results of the crosses (10 x 5) and (10 x 6). The F_1 ears showed the results of segregation, although in this case there was a range of variation from the floury to the corneous type. Seeds of this F_1 generation (F_2 seeds) produced a population of ears ranging from the pure corneous to the pure floury type.

One uniformly floury ear bred true in F_3 and F_4 for the floury habit; three ears with purely corneous seeds also bred true.

Two F_2 ears (10 x 64)-10S-5 and (10 x 64)-10C-4 gave as variable an F_3 progeny as had been found in F_2. The ratio in this case was approximately 1 pure corneous ear to 6.2 intermediates and definite hybrids to 0.8 pure floury ears.

Other F_2 ears gave a 1:2:1 ratio in F_3 as was the case in the (10 x 5) and (10 x 6) crosses. An example of such a ratio is that obtained from F_2 ear (10 x 64)-7C-2, which produced 15 corneous ears, 32 definitely hybrid ears and 18 intermediate ears.

Several self-fertilized intermediate F_2 ears bred comparatively uniformly, giving a progeny which contained more corneous starch than the No. 10 parent but less than the No. 64 parent. Thus intermediate ear (10 x 64)-7S-1 produced 41 ears of the intermediate type none being either purely corneous, definitely hybrids, or clearly floury. A self-fertilized ear (10 x 64)-7S-1-2 which contained more corneous starch than other self-fertilized ears, yielded a progeny of 35 variable intermediate ears and 2 ears approaching the corneous condition although they were not truly corneous ears like No. 64. Self-fertilized ear (10 x 64)-7S-1-6 which approached the floury type, produced 40 intermediate variable ears and 1 ear with somewhat more floury matter, though it did not compare with No. 10. Thus in a total of 119 ears from this intermediate line (10 x 64)-7S-1 there were no pure corneous, pure floury or definitely hybrid ears. This variation may largely be due to differences in the maturity of the seeds and ears, as the amount of corneous starch is directly dependent on the maturity of the seeds, although of course the hereditary constitution determines the amount which can be produced under favorable conditions, but there is also considerable likelihood that what one may call minor inherited factors modify the expression of the character. Whether more than one major factor affecting the endosperm is involved is still a question. The ratio obtained among the progeny of ears (10 x 64)-10S-5 and (10 x 64)-10C-4, the facts that certain F_2 ears produced an F_3 progeny similar to the 10 x 5 cross, and that others bred approximately true to the intermediate, the pure floury, or the pure corneous types might seem to indicate two such factors, but analysis is so difficult that this is only a reasonable guess, as will be shown by a consideration of all of the facts.

The following conclusions we hold to be justified by the data at hand.

1. The factors directly responsible for the differences in the physical condition of the starch exhibited by the so-called starchy sub-species of maize, the flour, dent, flint and pop corns are as truly endospermal in their inheritance as endosperm color characters. They partake of the nature of the *embryo* and not of the *plant* on which they are borne.

2. These characters appear superficially to be maternal for the following reasons. The endosperm nuclei are triploid due to the fusion of two nuclei from the female gametophyte with one nucleus from the male gametophyte. In the characters under discussion, the presence of two factors always dominates the presence of one factor. Thus corneous female (CC) x floury male (F) is phenotypically corneous, while floury female (FF) x corneous male (C) is phenotypically floury. These characters,

therefore, *appear* to be inherited in a different manner from endosperm colors where the presence of *one* color factor is sufficient to cause perfect development of color. This is the first proof of a cumulative somatic effect of factors.

3. From the fact that in these crosses, as well as in numerous others involving the same subspecies of maize that we have examined, the F_2 reproduces the grandparental and no types more extreme than the grandparental types (with possibly a rare exception), it follows that a large series of multiple allelomorphs affecting the starchy condition of the endosperm exists.

4. From the facts (a) that where no complications such as differences in shape and size of seed exist (viz. cross 10 x 5) segregation is simple and definite, (b) that where such differences in shape and size of seed do exist segregation occurs but is difficult to demonstrate clearly until these complications have been eliminated, it follows that although only the presence of factors in the endosperm affect these characters directly, the maternal zygotic constitution has an indirect effect. This effect is roughly a direct correlation of size of seed with floury condition of the endosperm.

Having these facts in mind, let us see what difficulties obstruct analysis if it be assumed that two factor differences may differentiate the endosperms of certain maize varieties in respect to starch as seemed possible in the case of cross (10 x 64).

The simplest assumption would be that each of these factors has a similar effect, and when one sees the difficulties thus involved, and considers that such a simple assumption is less probable than one in which each factor has a different effect, it is clear why we do not wish to assert dogmatically that two such factors are involved in the cross between the flour and the pop-corn.

Let the flour corn be AABB and the pop corn aabb, it being understood that the phenomenon of dominance is in this case wholly a quantitative reaction. The F_1 generation in the cross and its reciprocal would be

AAa BBb
and
aaA bbB

In each case, the predominant influence of the mother would be such that any effect of the father would scarcely be noticeable. Four types of gametes would be formed in the F_1 generation as usual, AB, Ab, aB and ab,—but the appearance and breeding qualities of the zygotes formed would be peculiar, as is shown in the following table, due to the fact that the "gametes" of the embryo sac are the fusion cells AABB, AAbb, aaBB and aabb.

1	AAABBB	Appear alike breed differently
1	AAABBb	
1	AAaBBB	
1	AAaBBb	
1	AAAbbB	Appear alike breed differently
1	AAAbbb	
1	AAabbB	
1	AAabbb	
1	aaABBB	Appear alike breed differently
1	aaABBb	
1	aaaBBB	
1	aaaBBb	
1	aaAbbB	Appear alike breed differently
1	aaAbbb	
1	aaabbB	
1	aaabbb	

The grandparental types have appeared of course and will breed true, but other individuals will look like the grandparents though they will breed differently and will ultimately give the whole series if crossed together. Other complications will occur to any one who takes the trouble to study the table.

Family (65 x 64), White Pearl Pop x White Rice Pop.

In 1910 a cross was made, between white rice pop No. 64 and pearl pop No. 65 for the dual purpose of determining the probable value of such a cross for the commercial production of first generation hybrid pop corn, and to study the inheritance of the pointed seed characteristic of the rice pop corns.

The F_1 plants were considerably more vigorous than either parent. The seeds produced approached the length of those of the longer type, the white rice pop, and the width of those of the broader parent, the pearl pop. Thus the F_2 seeds (those borne on F_1 plants) were considerably larger than those of either parent, and since the pericarp was weaker rather than stronger than that of the pure types, they did not pop as well.

TABLE 19.

INHERITANCE OF SEED SHAPE IN A CROSS BETWEEN WHITE RICE POP NO. 64 AND PEARL POP NO. 65.

Ear Number	Parent Type	Condition of Progeny			Ratio of Pointed ears to intermediate and non point
		Pure Point	Intermediate Point	Non Point	
64-4	Pure pt.	147			
65-8	Non pt.			200	
(65 x 64) F_1			132		
(65 x 64)-1 F_2	Int. pt.	6	64	1	1:10.8
" -3 "	"	5	49	5	1:10.8
" -5 "	"	9	55	3	1:6.5
" -6 "	"	4	58	2	1:15
" -1-13 F_3	Int. or non pt.		*21		

* Possibly non-point as the point was scarcely perceptible.

The data on the cross are given in Table 19. The F_1 generation was of intermediate habit,—there being some projection of the seeds at the point of attachment of the silk. Four selfed F_1 ears furnished F_2 generations. The progeny of these ears was variable, the seeds of some ears being as completely pointed as the white rice pop parent, the seeds of others non-pointed like the pearl pop parent, while the greater number were of various intermediate types. Of a total progeny of 263 individuals, 24 ears were classed as pure pointed like the white rice parent. This is an indication of a 15:1 ratio, although one can not be certain that the classification was correct because these ears were not selfed and could not be tested by the type of progeny produced. A number of F_2 ears were self-pollinated, but none happened to be obtained which could be classed as typically pointed. One ear having seeds but slightly pointed (possibly non-pointed) was grown in F_3. The twenty-one ears produced were like the parent ear, showing only slight projections on the seeds at the tip of the ear.

The difference between the pointed seed characteristic of the white rice pop corn and the normal shape of seed typical of other varieties can not be explained by a single factor. If, however, we assume that there is a difference in two factors, that each factor is allelomorphic to its own absence and is inherited independently of the other, that both are necessary for the production of the pure pointed condition, and that either of them alone may produce a tendency to a pointed condition (intermediate point), the data accord fairly well with the theory. But since on this hypothesis it is assumed that a factor in the heterozygous condition, produces only half as great an effect as when homozygous, one can appreciate the difficulty of classifying the ears correctly by inspection, and since classification must be exact to prove such a case merely by the ratios obtained it must be admitted that our evidence is open to some criticism. On the other hand, we believe that the facts are clear enough to make them of some value in practical plant breeding, and we do not believe that the case is sufficiently important to make it worth while overcoming the difficulties that stand in the way of a more acceptable proof. Furthermore, the data on the next cross appear to corroborate our earlier facts.

Family (64 x 6), White Rice Pop x Leaming Dent.

This cross was made in 1909 between self-bred Leaming and white rice pop strains. The purpose of this cross was a further study of the mode of inheritance of quantitative differences in seed size, of the proportion of corneous to soft starch, and of the pointed habit of the white rice pop.

The results on inheritance of seed shape are given in Table 20. These results again indicate that two factors are involved. Furthermore, examination of Table 20 and Table 21, shows that the pointed character is inherited independently of the position of starch in the seeds.

TABLE 20.

INHERITANCE OF SEED SHAPE IN A CROSS BETWEEN NO. 6 LEAMING DENT AND NO. 64 WHITE RICE POP.

Ear Number		Parent Type	Condition of Progeny		
			Pure Point	Intermediate Point	Non Point
64-4	P_1	Pure pt.	147		
6-3-4	P_1	Dent non pt.			107
6 x 64	F_1			112	
(6 x 64)-4	F_2	Int. pt.	47	65	20
“ -6	F_2	“	35	44	17
“ -6-6	F_3	Pure pt.	26		
“ -6-3	F_3	“	21	2	
“ -4-8	F_3	Pure (?) pt.	44	20	
“ -4-9	F_3	“	41	11	
“ -6-4	F_3	Int. pt.	4	44	1
“ -4-6	F_3	“	13	31	
“ -4-4	F_3	“	13	37	2
“ -6-5	F_3	Non pt.	4 (?)	53	4
“ -6-7	F_3	“	3	34	
“ -4-3	F_3	“	2	41	17
“ -4-7	F_3	“	11	45	7
“ -4-10	F_3	“		52	13
“ -4-5	F_3	“	6	37	3
(6 x 64)-6-6-4	F_4	Pure pt.	35		
“ -6-6-1	“	Pure or int. pt. (?)	27a		
“ -4-8-8	“	Pure pt.	61b	1 (?)	
“ -6-3-6	“	“	43		
“ -6-5-4	“	Int. pt.	1 (?)	38	5
“ -6-5-3	“	“	1 (?)	35	11
“ -6-7-8	“	“	26	11	
“ -4-8-3	“	“	16	40	
“ -4-3-7	“	“	5	72	
“ -4-10-5	F_4	“		47	22
“ -4-10-3	F_4	Non or int.		48	17
“ -4-3-5	F_4	Non			60

a—4 ears with points not as strongly developed as the remaining ears.
b—1 ear with points not as strongly developed as the remaining ears.

The F_1 generation was intermediate as regards the pointed condition, and there was segregation into pointed, non-pointed and intermediate ears in F_2. Thirteen self-pollinated F_2 ears were grown in F_3. Of these, the following F_2 ears were classed as pure pointed, (6 x 64)-6-6, (6 x 64)-6-3, (6 x 64)-4-8, (6 x 64) -4-9. Two of these ears, (6 x 64)-6-6 and (6 x 64)-6-3, bred true in F_3, while (6 x 64)-4-8 and (6 x 64)-4-9 showed segregation in F_3 with a total of 85 pointed and 31 intermediate pointed ears. Two self-fertilized ears, (6 x 64)-4-8-8 and (6 x 64) -4-8-3, were grown in 1914. One proved to be a pure pointed ear and the other again gave pure pointed and intermediate pointed seeds. These results might have been obtained if ear (6 x 64) -4-8 were homozygous for one factor for point and heterozygous for a second factor.

Three self-fertilized F_2 ears of the intermediate class showed a range of variation in F_3 from pure pointed to non-pointed ears. Six F_2 ears classed as non-pointed were proved to have been hybrids by the F_3 results. One of these, (6 x 64)-4-7, produced 52 intermediate and 13 non-pointed ears. As no typically pointed ears were obtained it seems fair to conclude that the parent ear (6 x 64)-4-7 was heterozygous for 1 factor for pointed seeds.

Two self-fertilized F_3 ears of line (6 x 64)-6-6 which bred true for the pointed habit in F_3 were grown in F_4. Ear (6 x 64) -6-6-4 gave a progeny of 35 ears, all of which were pure pointed; while (6 x 64)-6-6-1 had a progeny of 23 pure pointed ears and 4 with points more strongly developed than the intermediate class, but not so strongly developed as the 23 pure pointed ears. This may be a physiological variation or it may possibly be due to chance pollination. As these four were open field ears, it is impossible to determine the matter by further breeding.

The results are an excellent illustration of the old Vilmorin Isolation Principle,—in modern times the genotype hypothesis,—for they show that the only sure method to determine the breeding value of an ear is to grow and examine its progeny. A part of the pure pointed class gave a pure pointed progeny; other ears proved to be hybrids. There was also considerable difference in the progeny of different intermediate ears; some being apparently homozygous for one factor for point and heterozygous for another, while others appeared to be heterozygous for a single factor.

These results, as did those in the case of the (65 x 64) cross, indicate that two factors are involved in the production of strongly pointed maize seeds.

Table 21 gives the results of a study of the dented condition and the proportion of corneous to floury starch in the same cross. The white rice pop parent contains only a small amount of floury starch, while the dent variety has corneous starch at the sides of the seed and floury starch at the cap and next the embryo. There was no effect on the development of the amount of corneous starch in No. 6 dent due to the pollen from No. 64 pop. The F_1 generation cross produced ears with intermediate sized seeds. These ears would have to be classed as dents.

TABLE 21.

INHERITANCE OF DENTED HABIT AND PROPORTION OF CORNEOUS TO FLOURY STARCH.

Ear Number	Parent Type	Condition of Progeny				
		Pure dent	Nearly pure dent	Half seeds dented	Few seeds dented	Non-dented
64-4	pop, non-dent					107
6-3-4	dent	147				
6 x 64 F_1			112			
(6 x 64)-4 F_2	nearly pure dent	15	27	27	20	3
“ -6 “	“ “ “	38	34	21	8	
“ -4-4 F_3	pure dent	29	1	15	5	1
“ -4-5 “	“ “	1	11	24	6	
“ -4-8 “	“ “		39	9		
“ -6-6 “	“ “	24		2		
“ -6-5 “	“ “	25	19	13	4	
“ -6-7 “	nearly pure dent	3	11	15	5	2
“ -6-4 “	“ “ “	2	2	35	8	2
“ -4-7 “	half seeds dented	14		24	5	3
“ -4-9 “	“ “ “	30	3	8	2	
“ -4-6 “	few seeds slightly dented		12	7	11	14
“ -6-3 “	“ “ “ “	2	2	35	8	2
“ -4-10 “	non-dented				17	48
“ -4-3 “	“ “				26	34
“ -6-3-6 F_4	pure dent	2	5	12	21	2
“ -6-5-3 “	“ “	32	1	4		
“ -6-5-4 “	“ “	6	23	12	3	
“ -6-6-1 “	“ “	2	3	9	12	1
“ -6-6-4 “	“ “	15	14	4	2	
“ -6-7-8 “	half seeds dent		1	4	9	23
“ -4-8-8 “	half seeds slightly dent		6	21	16	18
“ -4-8-3 “	seeds slightly dent		4	28	12	13
“ -4-3-7 “	few seeds dent		1	8	29	40
“ -4-3-5 “	no seeds dent				5	44
“ -4-10-5 F_4	few traces of dent				5	63
“ -4-10-3 “	non-dent					67

Two F_1 ears (6 x 64)-4 and (6 x 64)-6 were grown in F_2. Both populations showed a wide range of variation. The ears were classed as pure dent, nearly pure dent, half seeds dent, few seeds dent and non-dent. Ear (6 x 64)-4 had progeny of each class, while (6 x 64)-6 produced progeny in all classes except the non-dent class. Thirteen F_2 ears were grown in F_3. Two non-dented ears gave a progeny of non-dented ears and ears with a few seeds slightly dented. No ears bred true in F_3 or F_4 for the pure dented condition, although some selections gave a progeny with a much larger proportion of dented ears than others.

Twelve F_3 ears were grown in F_4. Ear (6 x 64)-6-5-3 produced the greater proportion of its progeny in the pure dent class. Ear (6 x 64)-4-10-3 bred true to the non-dented character, and the corneous non-pointed condition. Ear (6 x 64)-6-5-3 bore seeds which approached the size of those of the No. 6 Leaming parent, although the range of variation was somewhat greater. Ear (6 x 64)-4-8-3 gave a uniform progeny in 1914, and bred comparatively true to the seed size of the pop parent.

The seeds of those ears which were classed as non-dents and those with a few seeds dented, popped perfectly when tested. The condition of the other families is shown in the table.

Summary and Interpretation of Results.

The data from these two crosses indicate strongly that two independently inherited factors are necessary for the production of a strongly pointed seed. The rice pop point can be transferred from the pop parent to dented seeds by crossing and selection; the inheritance of these characters being entirely independent of each other.

A study of the proportionate amount of corneous and floury starch in the 6 x 64 cross shows a wide variation in F_2. One ear (6 x 64)-4-10-3 bred true for about the same amount of corneous starch in F_4 as that of the No. 64 parent. Other ears were again as variable as F_2, while still others showed a smaller range of variability. It is impossible to state how many factors are involved in producing these somatic differences, but it is a fact that the parental types can be recovered easily and will breed true.

CONCLUSION.

Since a summary of the results obtained for each cross has been given in its proper place, it seems unnecessary to repeat them here. If the reader will refer to them he will find an abstract of the paper.

LITERATURE CITED.

CORRENS, C.

1901. Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenien. Bibliotheca Botanica. 53:1-161.

EAST, E. M. and HAYES, H. K.

1911. Inheritance in Maize. Connecticut Expt. Sta. Bull. 167:1-142.

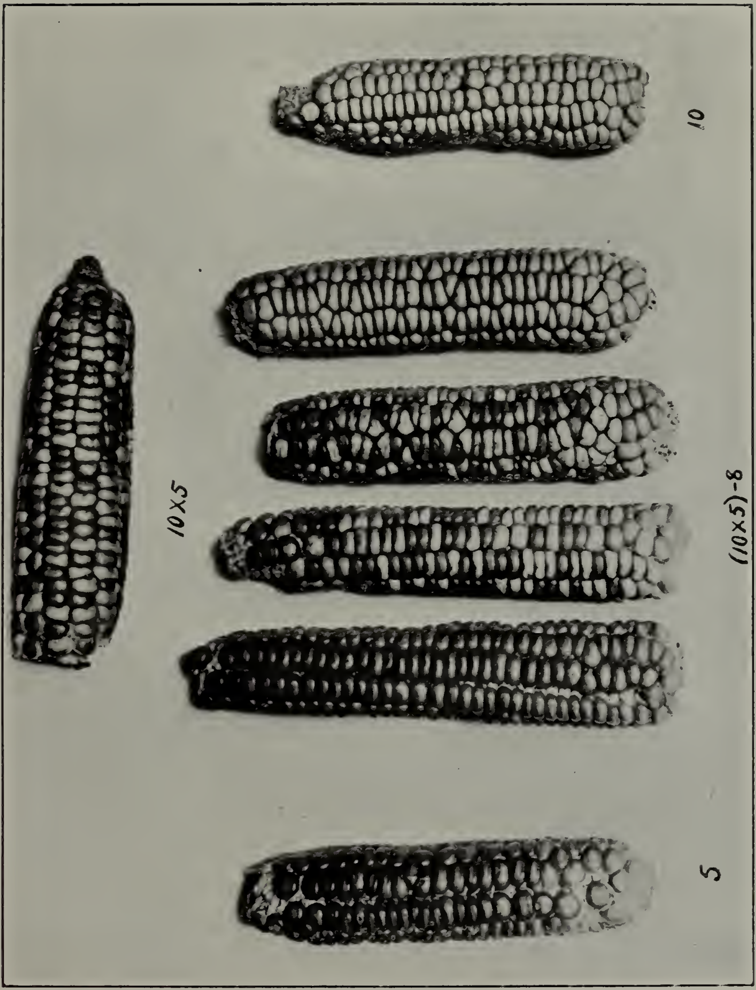
EMERSON, R. A. and EAST, E. M.

1913. The Inheritance of Certain Quantitative Characters in Maize. Nebraska Station Research Bull. 3:1-120.

SHULL, GEORGE HARRISON.

1914. Duplicate Genes for Capsule-form in Bursa bursa-pastoris. Zeitschrift für induktive Abstammungs-und Vererbungslehre XII: 97-149.

PLATE I.

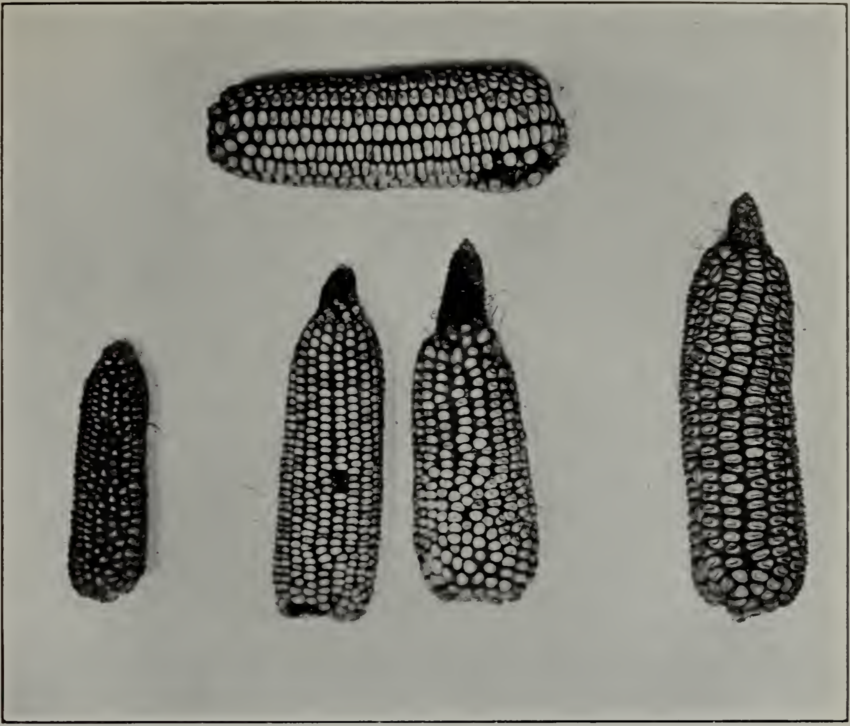


No. 5, corneous flint at bottom, No. 10 flour at top and F_1 at left. The two lower center ears show the result of planting corneous F_1 seeds and the two upper center ears show the result of planting floury F_1 seed.

a. No. 10 flour at left. No. 6, Leaming dent at right. The four other ears represent the F_3 generation of cross. They are uniformly very corneous with slight traces of dent. The seeds are smaller than those of either parent and of uniform size.

b. Average ears of No. 65 pearl pop at left, No. 64 rice pop at right with average F_1 in center. The two remaining ears represent the extremes of F_2.

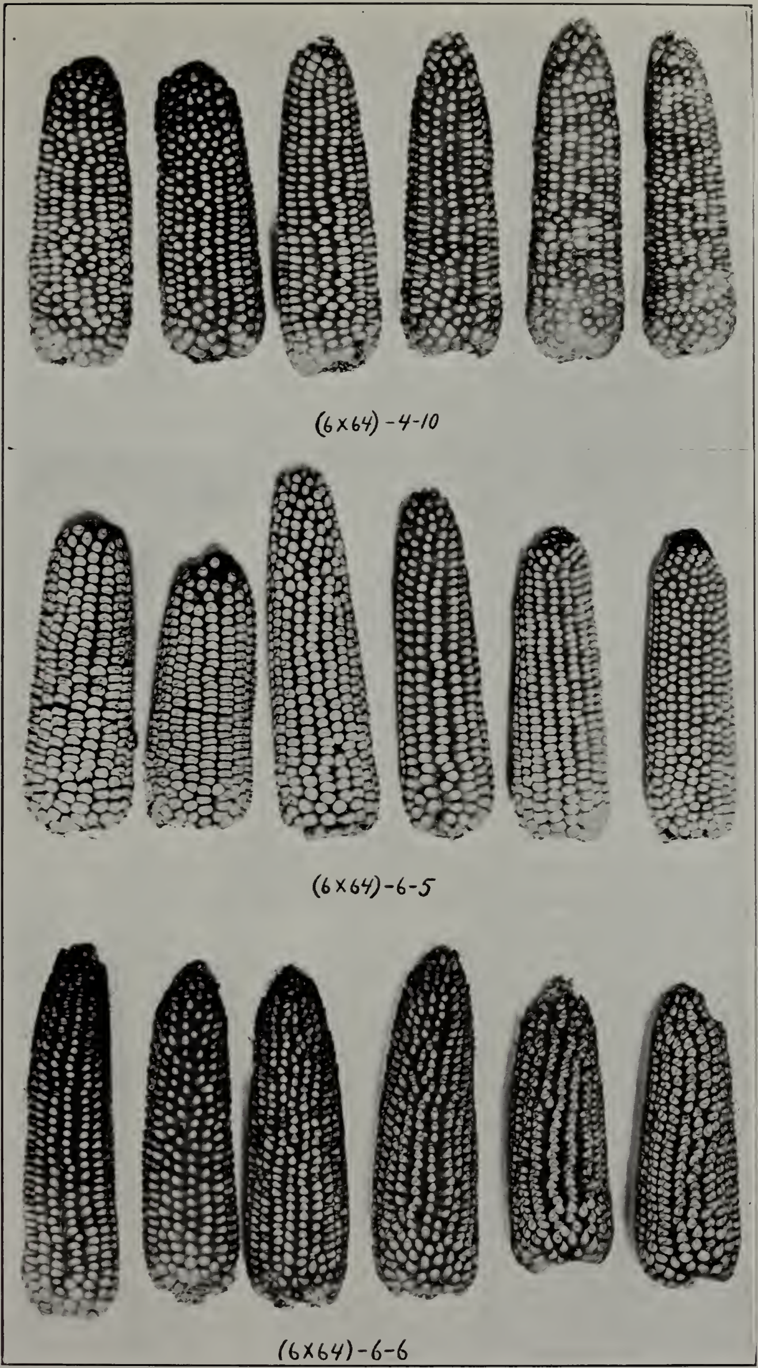
PLATE III.



a. No. 6 Leaming dent at right, No. 64, rice pop at left and immediate cross, (6 x 64), above. The two central ears show the variation in seed size and condition of point of the F_1 generation.

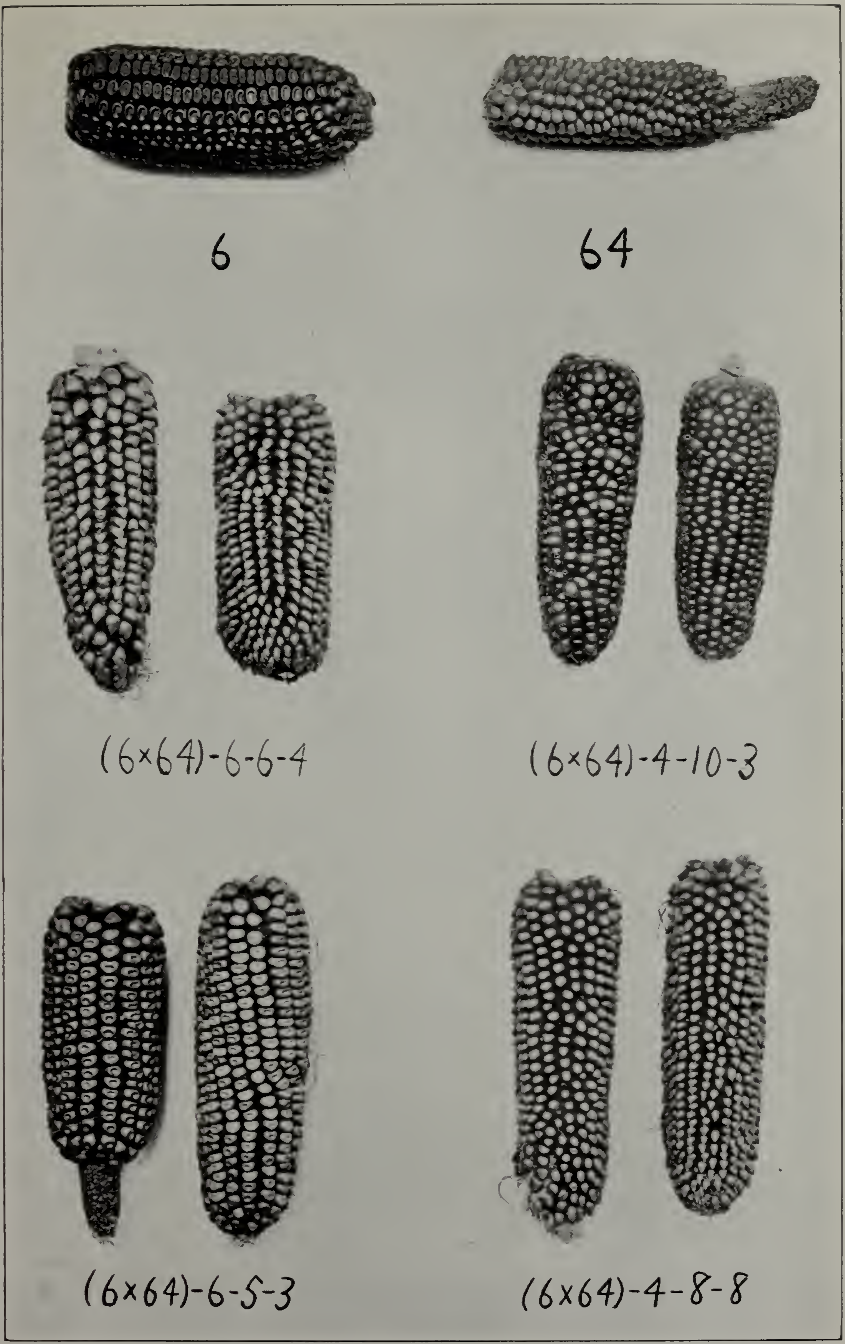
b. F_2 generation of cross (6 x 64). Note the segregation of characters.

PLATE IV.



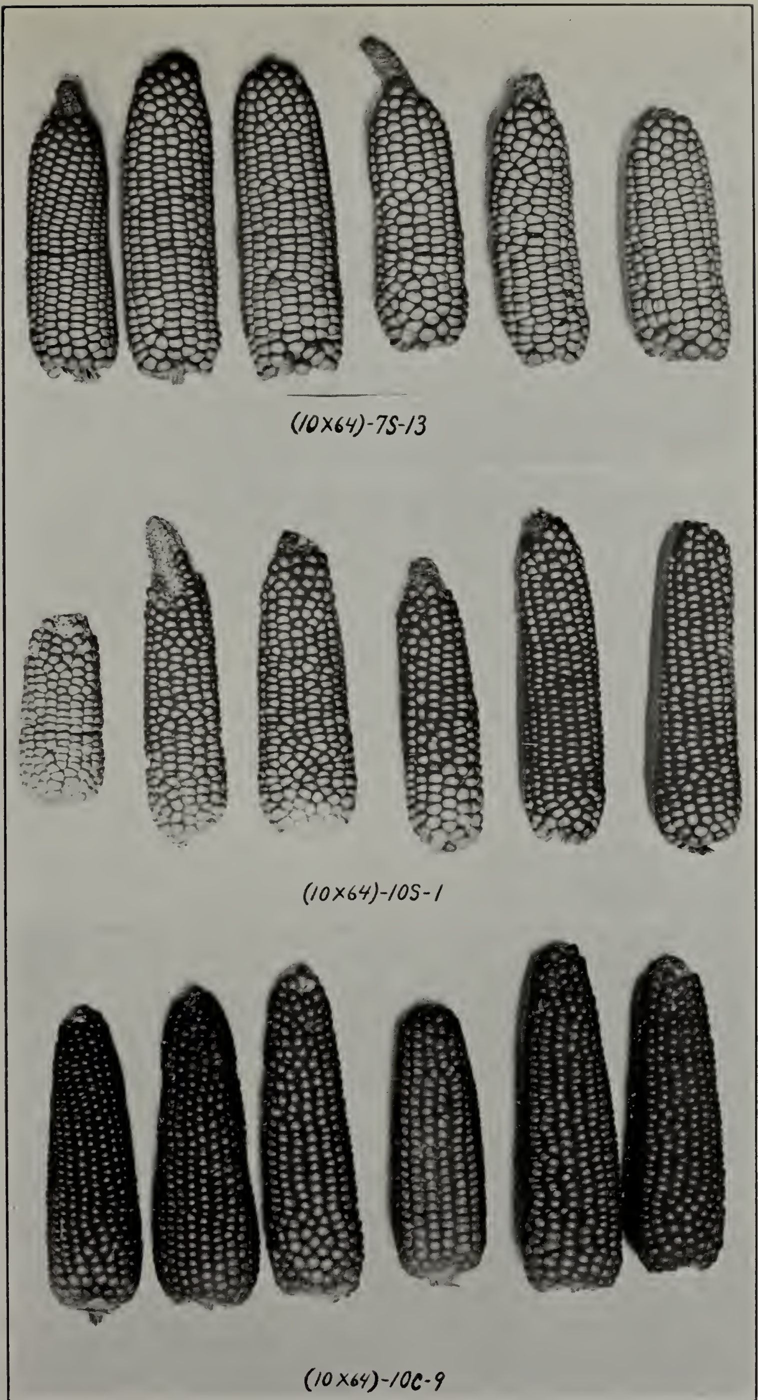
Upper row, F_3 generation ears, with large amount of corneous starch. Some ears with slight trace of dent. Middle row, average progeny of F_2 ear which bore good sized dented seeds. Lower row, average progeny of F_2 ear which bore intermediate dented seeds with a well-developed point.

PLATE V.



Average ears of parental types No. 6, Leaming dent and No. 64, white rice pop above. The ears below represent the variation in 4 F_4 families. (6 x 64)-6-6-4 bred true for the rice point, (6 x 64)-4-10-3 bred true for corneous, non-dented seeds, (6 x 64)-4-8-8 is a small-seeded selection and (6 x 64)-6-5-3 is a large-seeded selection. (Photo by Walden.)

PLATE VI.



Upper row, F_3 generation of cross between No. 10 flour and No. 64, rice pop, which bred true for the floury habit.

Middle row, F_3 generation of same cross which bore seeds of intermediate type.

Lower row, F_3 generation of same cross which bred true for the corneous habit.

PLATE VII.

a. F_3 generation of cross between No. 10 and No. 64 which bred true for the seed size of No. 10.

b. F_3 generation of cross between No. 10 and No. 64 which bred true for the seed size of No. 64. The corneous seeds popped perfectly.

STUDIES ON SIZE INHERITANCE IN NICOTIANA

E. M. East

Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS 1:164-176, March, 1910

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

---

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916 at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SIZE INHERITANCE IN NICOTIANA

E. M. East

Harvard University, Bussey Institution, Forest Hills, Massachusetts

STUDIES ON SIZE INHERITANCE IN NICOTIANA

E. M. EAST
Harvard University, Bussey Institution. Forest Hills, Massachusetts

[Received January 6, 1916]

As various writers have pointed out, all Mendelizing characters probably are due to the interaction of several genes, and presumably every gene may exhibit several somatic effects, yet no one doubts that the Mendelian notation describes the inheritance of such things as color accurately and concisely. It is strange, therefore, that some geneticists still refuse to believe that the inheritance of size characters can be described in the same way, without further assumptions.

Various reasons are assigned for this disbelief.

It is held that one should not assume the absence of dominance, as has been done by those who have investigated size characters. But as a matter of fact, absolute dominance is rare. A heterozygous gene very seldom produces an effect identical with that of homozygous genes. Full dominance is the extreme, the limiting condition, not the common condition. Even with such simple and possibly superficial characters as colors, careful examination usually shows incomplete dominance.

A further misconception of the phenomenon of dominance is the objection to the assumption of genes having cumulative effects. As stated in the first sentence, most Mendelizing characters have been shown to be due to the interaction of several traceable factors, in addition to an ever present factorial residue of which nothing is known. This unexplored ground may be reduced in its extent by new mutations affecting the character in question, but proof can never be offered that it has been entirely eliminated. For the same reasons it follows that one should not assume that the simplicity of the known facts proves actual simplicity in the hereditary transmission of any character. This complexity in the germinal basis of characters, is, of course, general proof of the cumulation effect of genes, but in addition a specific case has recently been found in maize (HAYES and EAST, 1915). When reciprocal crosses of "floury" and "flinty" maize races are made, the *maternal* endosperm character is dominant. This dominance has been proved to be due to the fact that the endosperm is produced by the union of *two maternal* and one paternal nuclei. Thus two genes of either kind dominate the effect of one.

The only other criticisms worthy of notice are directed against assumptions of gametic purity and of factorial constancy. As criticisms of the Mendelian interpretation of quantitative characters they come no nearer the mark, for they apply to Mendelism as a whole.[1]

The true reason for objecting to the theory, therefore, seems to be—as is often the case—that those who disapprove of it have not given it sufficient study to be convinced that any real evidence in its favor can be cited. For example, CASTLE (1914) says:

> "When races are crossed that differ widely in size, the first filial (F_1) generation is intermediate between the parents and often not more variable than one of the parent races. But the second filial (F_2) generation, though still intermediate, commonly shows increased variability, the range of which may even extend into or include the size range of one or both parent races. This increased variability of the F_2 generation is the only evidence of Mendelism in size crosses."

With this view I cannot agree. It is true that one may not expect dimorphic phenotypes in simple ratios in the F_2 generation. Somatic appearance is not so highly correlated with genetic constitution that definite ratios always appear when characters like color are studied. Even in such cases one must *prove* the classification of the phenotypes by further breeding. By carefully studying what actually occurs in simple and obvious Mendelian phenomena, however, the mathematical requirements where size characters are involved can be worked out. If these requirements are independent,—i.e., if they are not restatements of the same conditions,—and if the breeding facts meet them fairly and squarely, the case is good.

At least eight such requirements, most of which are independent mathematically, should be met by the pedigree-culture data when all populations succeeding the original cross are obtained by self-fertilization.

1. Crosses between individuals belonging to races which from long-continued self-fertilization or other close inbreeding approach a homozygous condition, should give F_1 populations comparable to the parental races in uniformity.

2. In all cases where the parent individuals may reasonably be presumed to approach complete homozygosis, F_2 frequency distributions arising from extreme variants of the F_1 population, should be practically

---

[1] The question of the validity of these criticisms when directed against the entire Mendelian theory, is not under discussion.

identical, since in this case all F_1 variation should be due to external conditions.

3. The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

4. When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

5. In certain cases individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent. This phenomenon was predicted by the writer (EAST, 1910) as an expected result of Mendelian recombination before actual cases had been discovered.

FIGURE 1. At left, young plant of *Nicotiana longiflora* var. (383); at right, young plant of *N. longiflora* (330).

6. Individuals from various points on the frequency curve of an F_2 population, should give F_3 populations differing markedly in their modes and means.

7. Individuals either from the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parents to that of the F_2 generation.

8. In generations succeeding the F_2, the variability of any family may be less but never greater than the variability of the population from which it came.

Not all of these eight conditions are met by the data to be presented in this paper, but all of them have been met many times in the course of other experiments, and not one fact has been discovered directly opposed to them.

FIGURE 2. Average flowers of parents with an average flower of the F_2 generation (383 × 330) in the center.

The data to be considered here were obtained by measuring the length of the corolla in a cross between two varieties of *Nicotiana longiflora* Cav. The seed of No. 330, which is probably the type, was obtained from Prof. W. A. Setchell (see Setchell 1912, pp. 21-22). The seed of No. 383 was received from the Instituto Sperimentale per le Cultivazioni dei Tabacchi at Scafati, Italy, through the kindness of Dr. A. Splendore. It was known there as *N. plumbaginifolia* Viv., but seems to be merely a small variety of *N. longiflora*.

Each corolla length recorded is expected to represent the phenotype of a single plant. The method of recording them and the accuracy that

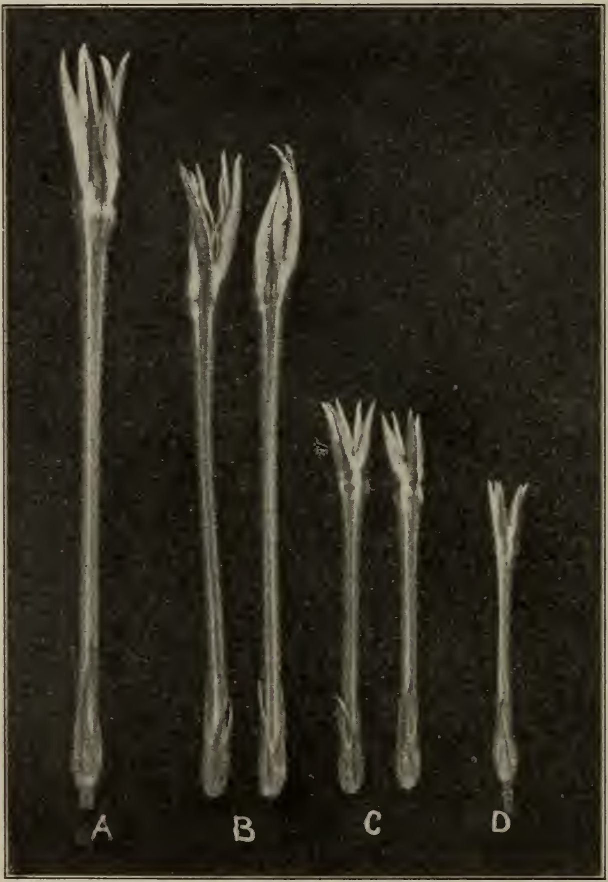


Figure 3. Average flowers of parents at A (330) and D (383); extreme segregates of the F_2 generation at B and C.

TABLE I

Frequency distributions for corolla length in a cross between varieties of Nicotiana longiflora Cav.

Designation	Year	Generation	Parent size	Class centers in millimeters																						
				34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100
No. 383	1911	—	—	—	13	80	32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 383	1912	—	—	1	4	28	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 383	1913	—	—	—	4	32	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. 330	1911	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	22	49	11	—
No. 330	1912	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	16	32	6	1
No. 330	1913	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	7	10	2	—
No. 383 × 330	1911	F_1	—	—	—	—	—	—	—	—	4	10	41	75	40	3	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 1	1912	F_2	61	—	—	—	—	—	—	1	5	16	23	18	62	37	25	16	4	2	2	—	—	—	—	—
No. (383 × 330) 2	1912	F_2	61	—	—	—	—	—	—	2	4	2	24	37	31	38	35	27	21	5	6	1	—	—	—	—
No. (383 × 330) 1–1	1913	F_3	72	—	—	—	—	—	—	—	—	—	4	20	25	59	41	19	2	—	—	—	—	—	—	—
No. (383 × 330) 1–2	1913	F_3	46	—	—	—	1	4	26	44	38	22	7	1	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 1–3	1913	F_3	50	—	—	—	6	20	53	49	15	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 1–4	1913	F_3	60	—	—	—	2	3	9	25	37	70	19	10	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 2–1	1913	F_3	77	—	—	—	—	—	1	0	1	1	1	2	16	33	43	34	20	6	1	—	—	—	—	—
No. (383 × 330) 2–3	1913	F_3	81	—	—	—	—	—	—	—	—	—	1	1	8	16	20	32	41	17	3	3	1	—	—	—
No. (383 × 330) 2–4	1913	F_3	80	—	—	—	—	—	—	—	—	—	2	8	14	21	39	39	32	10	1	—	—	—	—	—
No. (383 × 330) 2–5	1913	F_3	50	—	—	—	—	7	25	55	55	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 2–6	1913	F_3	82	—	—	—	—	—	—	—	—	—	—	—	3	5	12	20	40	41	30	9	2	—	—	—
No. (383 × 330) 1–2–1	1914	F_4	44	—	—	8	42	95	38	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 1–3–1	1914	F_4	43	—	—	2	23	122	41	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 2–6–1	1914	F_4	85	—	—	—	—	—	—	—	—	—	—	—	—	—	4	9	38	75	59	6	3	1	—	—
No. (383 × 330) 2–6–2	1914	F_4	87	—	—	—	—	—	—	—	—	—	—	—	4	5	6	11	21	33	41	29	8	5	1	—
No. (383 × 330) 1–3–1–1	1915	F_5	41	3	6	48	90	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
No. (383 × 330) 2–6–2–1	1915	F_5	90	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	8	14	20	25	25	20	8	—

may be expected of the method have been discussed in another paper (EAST 1916).

Both of the varieties used as parents may reasonably be supposed to be homozygous in most of their characters for they are generally self-pollinated naturally. Whether either or both of them had been self-pollinated artificially before I obtained them is not known, but they had been self-pollinated for two generations after I received them before the cross was made. The crosses and the succeeding selfings gave full capsules, and the germination of the seeds was almost perfect.

As shown by the tables, if the frequency distributions of the pure varieties for 1913 are excluded on account of the small number of plants grown, the average mean of No. 383 is 40.54 mm and of No. 330, 93.30 mm. The species has corollas over twice the length of the variety. The average of both parents is 66.91 mm, and since the mean length of the F_1 generation is 63.53 mm, it is clear that the vigor induced by heterozygosity, which was fairly well marked in the vegetative characters, had no effect on the flowers. This fact is in keeping with previous observations, since it has been shown that corolla length is very slightly influenced by external conditions, and that heterozygosity effects a result comparable to favorable external conditions.

The variability of the F_1 population appears to be exactly the mean of variety No. 383 (the more variable parent) for the two years 1911 and 1912, though considerably higher than the variability of variety No. 330 for the same period. Theoretically one ought to expect this only when both parental varieties are completely homozygous, therefore the data might be supposed to show such a condition. But, while the two varieties used here probably approach a homozygous condition, the similarity of the two constants obtained is possibly more apparent than real. The measurements have been thrown into three-millimeter classes for convenience, but these classes are manifestly too large for small flowers like those of No. 383. If one-millimeter classes are used there is less distortion of the figures and the percentage variability is smaller. For this reason I believe that it is fair to conclude that the variability of the F_1 population is slightly larger than that of either parent. The proponents of the Mendelian theory may maintain that this merely shows a slight degree of heterozygosity in the parents, therefore, while its opponents may see in the results indication of a slight increase in variability due to the cross itself. No one can object to this view when considered apart from other facts, but it should be pointed out that the difference to be accounted for is very small in either case.

TABLE 2

Statistical constants of the frequency distributions shown in table 1.

Designation		No. Ind.	Mean	S. D. in mm	C. V. in percent
No. 383—1911		125	40.46±.11	1.75±.07	4.33±.18
No. 383—1912		49	40.61±.19	2.00±.14	4.92±.34
No. 383—1913		37	39.76±.12	1.09±.09	2.74±.21
No. 330—1911		88	93.22±.16	2.29±.12	2.46±.13
No. 330—1912		57	93.37±.20	2.23±.14	2.39±.15
No. 330—1913		24	92.12±.37	2.70±.26	2.93±.30
No. (330 × 383)	F_1	173	63.53±.15	2.92±.11	4.60±.17
No. (330 × 383) -1	F_2	211	67.51±.27	5.91±.19	8.75±.29
No. (330 × 383) -2	F_2	233	69.78±.30	6.79±.21	9.73±.30
No. (330 × 383) 1-1	F_3	170	73.14±.20	3.82±.14	5.22±.19
No. (330 × 383) 1-2	F_3	143	53.47±.21	3.74±.15	6.99±.28
No. (330 × 383) 1-3	F_3	147	50.20±.18	3.17±.12	6.31±.25
No. (330 × 383) 1-4	F_3	175	56.34±.21	4.07±.15	7.22±.26
No. (330 × 383) 2-1	F_3	159	73.04±.27	5.00±.19	6.85±.26
No. (330 × 383) 2-3	F_3	143	76.34±.29	5.06±.20	6.63±.26
No. (330 × 383) 2-4	F_3	166	74.01±.25	4.85±.18	6.55±.24
No. (330 × 383) 2-5	F_3	160	52.97±.16	3.04±.11	5.74±.22
No. (330 × 383) 2-6	F_3	162	80.20±.25	4.76±.18	5.93±.22
No. (330 × 383) 1-2-1	F_4	184	45.71±.12	2.37±.08	5.18±.18
No. (330 × 383) 1-3-1	F_4	189	46.25±.09	1.87±.06	4.04±.14
No. (330 × 383) 2-6-1	F_4	195	82.25±.16	3.30±.11	4.01±.14
No. (330 × 383) 2-6-2	F_4	164	82.86±.31	5.83±.22	7.04±.26
No. (330 × 383) 1-3-1-1	F_5	161	41.98±.12	2.30±.09	5.49±.21
No. (330 × 383) 2-6-2-1	F_5	125	87.88±.33	5.52±.24	6.28±.27

Examination of the F_2 frequencies shows that only one individual reaches the lower size limit of No. 330 and that no individual comes within two classes of the upper size limit of No. 383. Viewed from this standpoint the results are less in accord with Mendelian theory than any of those obtained in the numerous size studies I have made. At the same time, one may say that this is because the numbers are too small to expect an exact duplication of the grandparents in a species which in all probability has 24 chromosomes in its germ-cells and in which grandparental duplication should be expected only once in 265 million millions of F_2 individuals. The difficulty here would be not to account for the non-appearance of the grandparental sizes in F_2 populations of about 200 individuals, but to conceive how extremes differing by 36 millimeters had arisen. One appears to have but a single alternative: either the differences between types that give fertile F_1 generations are due to relatively few factors, the remaining germ-plasm being identical, or the extremes recovered are not like the grandparents but merely resemble them.

From another standpoint the variability of the F_1 and the F_2 generations is very different. Theoretically if recombination is possible, the number of classes between the extremes varies directly with the square root of the number of individuals involved. The coefficients of variability of the two populations, however, should not change with larger numbers except as regards the confidence to be placed in the calculated constants. The coefficient of variability of the F_1 generation is 4.60 ±.17 percent and the coefficients of variability of the two F_2 populations grown are 8.75 ±.29 percent and 9.73 ±.30 percent, respectively. Thus the average variability in F_2 is just double that of the F_1 generation.

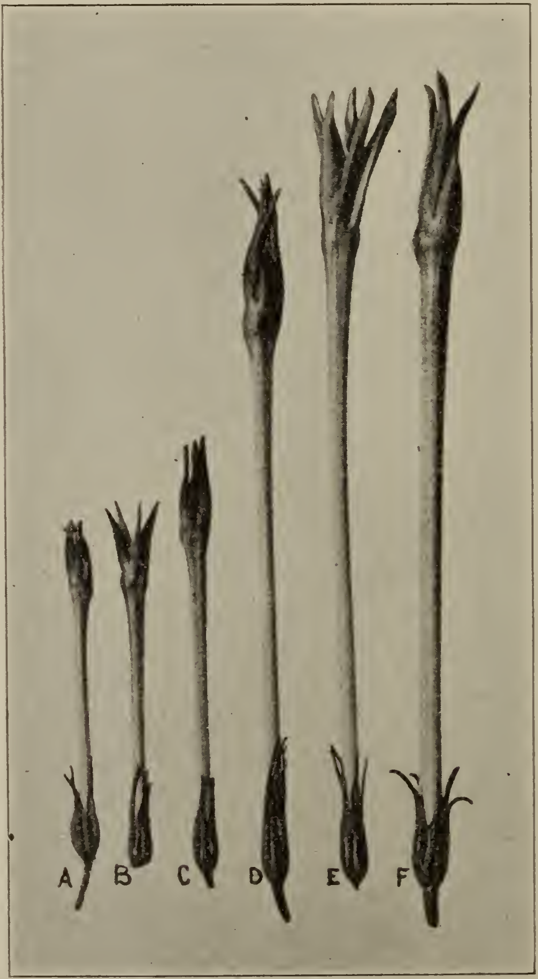


FIGURE 4. Average flower of No. 383 (A) compared with modal condition (C), and with an extreme (B), of F_3 family (383 × 330) 1-3; and, ditto No. 330 (F) compared with modal condition (D), and with an extreme (E), of F_3 family

One can scarcely appreciate the significance of this immense difference until he recalls that the difference between the means of the pure varieties and the mean of the F_2 generation is only about four times the standard deviation of the latter, while the difference between the means of the varieties and the mean of the F_1 generation is about nine times its standard deviation.

Let us now examine the means of the populations that have resulted from selfing selected individuals of the F_2, F_3 and F_4 generations. Whether one can isolate rapidly lines with markedly different mean values after a blend such as occurred in the F_1 generation is a question of considerable practicable importance. Nine F_3 populations were grown. The extreme parental types from which they were grown were 46 mm and 82 mm, a difference of 36 mm. The greatest mean difference between the F_3 populations was 30 mm, although it happened that the difference between the parents that produced these two lines was only 32 mm.

From the F_3 generation two "short corolla" and two "long corolla" lines were grown. In this generation it was possible to select extremes a little farther apart, 43 mm to be exact. The difference between the means of the most extreme resulting populations was 37 mm.

Only two F_5 populations were grown, one from a plant with flowers 41 mm long and the other from a plant with flowers 90 mm long. The families to which they gave rise had means of 42 and 88 mm in round numbers. Thus a relatively small number of selections has given a type averaging but two millimeters longer than the smaller parent, and a type averaging less than five millimeters under that of the larger parent. To attain these ends only twelve families from extreme parents were grown. It is impossible to say just how many selections of F_2 individuals would have had to have been made to reach the same goal on the recombination theory, but one can estimate the probability of the occurrence of individuals of the desired size in F_2 from which to select. Consider the F_2 generation in which the standard deviation is 6.79 mm. Assuming this distribution to be normal the expected frequency beyond the distance from its mean represented by one-half the mean of No. 330 minus mean of No. 383 is .0619 percent. In other words, one might expect an F_2 individual with the size of the modal class of either grandparental variety about once in every 1600 plants.

These facts indicate clearly the proper procedure of the plant breeders in such cases, as has already been brought out by EMERSON and EAST (1913). If it is technically possible to grow an F_2 large enough to be reasonably certain of obtaining several individuals with the desired combination, the breeder is tolerably sure of success. But the numbers are often prohibitive in practice, and at the best the work involved is great. On the other hand, though success is not so certain because the plants with the gametic possibilities desired may be dropped out at any point, selection continued for several generations gives a high probability of success with comparatively little work.

A study of these means with reference to their bearing on GALTON'S Law of Regression is also interesting.

In thirteen out of the fifteen fraternities descended from the two F_2 populations there was regression towards the mean of the fraternity from which the parent came; these two individuals, however, produced populations with means further removed from the means of the parental population than were the parent individuals themselves. Further, the deviations of the parents from the mean of their fraternity show no correlation with the deviation of the mean of the progeny from the parental value. In other words, in selfed lines of this kind an extreme variant is almost as likely to produce a type like itself as is a slight variant. This is to be expected with the hypothesis of plural segregating factors but not with the old Galtonian hypothesis in which somatic resemblance is the sole measure of heredity. Our observation is not new since Galtonian regression in the original sense is now entirely discredited, but our data illustrate the point.

The remaining arguments are based upon the variabilities of the fifteen fraternities whose means have just been considered.

In the first place, it is essential that one should know whether he may expect to obtain fraternities that breed as true as the parental varieties at once, after long continued selection, or not at all. These data do not show fraternities comparable to either parent variety in variability among the nine F_3 families, but out of the four F_4 families two show as narrow a variability as No. 383.

A more important question, however, is that of continuous reduction of the coefficient of variability due to the automatic tendency toward complete homozygosis produced by continued self-fertilization. Theoretically, a fraternity produced by self-fertilization may be as variable as the fraternity from which its parent came, but it can never be more variable, provided breaks in any linkage between characters are equally probable in both cases. Of course when dealing with small populations one should not place too much confidence in the probable error calculated for any particular biometrical constant. If one could be certain that the calculated coefficient of variation represented the true values in

TABLE 3

The pedigrees of the families and their coefficients of variation.

F_2	F_3	F_4	F_5
8.75±.29	5.22±.19		
	6.99±.28	5.18±.18	
	6.31±.25	4.04±.14	**5.49±.27**
	7.22±.26		
9.73±.30	6.85±.26		
	6.63±.26		
	6.55±.24		
	5.74±.22		
	5.93±.22	4.01±.14	
		7.04±.26	6.28±.27

a series of populations of this kind a single coefficient of variation higher than that of the preceding generation would be a critical failure of the theory of plural Mendelian determiners to meet the breeding facts. In small populations from one hundred to three hundred, however, the matter can only be tested by induction from a large number of experiments. Table 3 is a contribution toward this end. Among the fifteen families reported there are two exceptions to the rule which are noted by bold-faced type. The remainder of the families all show lower variabilities than the families from which they came.

Considering these data apart from other known facts, one may say that the evidence tends to justify the use of plural segregating factors in interpretating size inheritance, nevertheless the writer believes that dogmatic conclusions on such a broad question should not be drawn from a single set of experiments. Only when the numerous size studies of such investigators as BELLING, CASTLE, DAVENPORT, EAST, EMERSON, HAYES, HERIBERT-NILSSON, KAJANUS, MACDOWELL, NILSSON-EHLE, PEARL, PHILLIPS, PUNNETT, SHULL, TAMMES, and TSCHERMAK are considered together, is it possible to make a reasonable judgment of the mechanism by which such characters are transmitted. The volume of this work is large and the data reported, without exception, can be interpreted as Mendelian. Furthermore, such an interpretation is not merely formal, as some writers have stated, but is as genuinely helpful to the breeder as is any Mendelian data.

In view of these facts many biologists may question the desirability of increasing the literature by papers of the same type. They may hold with considerable justice that the case has been proven. At the same time, though one may not question the value of any of these investigations, it must be admitted that the material used in most of them is undesirable for a critical test of the theory involved. In all of the zoölogical researches, bisexuality introduces a constant error into the results. Many of the races of plants involved were markedly heterozygous. The difficulty of drawing just conclusions from the botanical investigations was also increased by the use of characters affected strongly by environmental differences. For these reasons, I hope to report the results of several other studies of this kind in which the constant errors are reduced to a minimum, believing that the theory must be proven or disproven under such critical conditions. If with such material the Mendelian notation is justified—as I believe is true when one considers the work of BELLING, EMERSON, HAYES and myself on plants naturally self-fertilized—then it will be impossible to criticize its use in those experiments where some allowance must be made on account of the peculiarities of the material involved.

LITERATURE CITED

CASTLE, W. E., 1914 Multiple factors in heredity. Science, N. S. **39**: 686-689.

EAST, E. M., 1916 Significant accuracy in recording genetic data. Amer. Jour. Bot. (in press).

EMERSON, R. A., and EAST, E. M., 1913 The inheritance of quantitative characters in maize. Neb. Agr. Exp. Sta., Research Bull. No. 2, pp. 1-120.

HAYES, H. K., and EAST, E. M., 1915 Further experiments on inheritance in maize. Conn. Agr. Exp. Sta., Bull. 188, pp. 1-31.

SETCHELL, W. A., 1912 Studies in Nicotiana I. Univ. of Cal. Pub. Botany **5**: 1-86.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with cover, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

TABLE OF CONTENTS

A CO-OPERATIVE EFFORT

Genetics has been founded through the coöperative effort of many persons interested in the discovery of the principles of heredity and in their application. The plans for this journal do not contemplate any financial gain from its publication. As soon as the subscriptions pay the cost of manufacture and distribution on the basis of plans already announced, the income from additional subscriptions will be devoted to increasing the size or the frequency of issue, and to improving the quality of the journal. Subscribers are urged therefore to assist in extending the subscription list as rapidly as possible, in order that Genetics may be enabled to publish an increasingly large share of the work of American investigators in this field.

SIGNIFICANT ACCURACY IN RECORDING GENETIC DATA

E. M. East

Reprinted from the AMERICAN JOURNAL OF BOTANY, 5: 211–222,
May, 1916.

[Reprinted from the AMERICAN JOURNAL OF BOTANY, 5: 211–222, May, 1916.]

SIGNIFICANT ACCURACY IN RECORDING GENETIC DATA

E. M. EAST

In 1913, I contributed a paper to the Botanical Gazette (55: 177–188) on the inheritance of flower size in a cross between *Nicotiana alata grandiflora* Comes, and a type thought to be *Nicotiana forgetiana* Hort. Sand. Corolla size had been selected for study because in this genus it is "so comparatively constant under all conditions attending development"—something which could not be said of any other size character that had been under observation. Since other investigations of the same kind were under way, and a larger amount of data might be reported later, the "liberty of asserting the truth of this statement" with only the following data in its support was requested. This paragraph followed.

"During the past four years, I have grown about 20 species of Nicotiana in considerable numbers. They have been grown under very diverse conditions. Some have been starved in four-inch pots, others have had the best of greenhouse treatment; some have had poor field conditions, others have had all field conditions practically at their best. The height of the plants, the size of the leaves, and similar size complexes have varied enormously, but the size of the corollas has scarcely varied at all. For example, plants of *Nicotiana sylvestris* Speg. & Comes, grown to maturity in four-inch pots, produced no leaves longer than 7 inches. On the other hand, sister plants of the same pure line produced leaves 30 inches long in the field. Both series, however, produced flowers with the same length and spread of corolla. Furthermore, cuttings from 20 of the field plants reported in this study were rooted and grown in small pots (6 inch) in the greenhouse. Their blossoms were the same size as those of the field grown plants from which they came."

[The **Journal** for April (3: 135–210) was issued April 18, 1916.]

Recently Goodspeed and Clausen have published in this Journal (2: 332–374. 1915) an immense amount of data on the influence that certain environmental factors have on flower size in Nicotiana. The conclusions they draw are eight in number based upon 25,000 measurements of the length and spread of the corollas of *Nicotiana tabacum* var. *macrophylla* and three hybrids between *N. tabacum* varieties and *N. sylvestris*, and run somewhat as follows:

1. Both length and spread of corolla decrease during the flowering season to such an extent that at the end of six weeks the average spread may drop 6 mm. and the average length 4.5 mm.
2. The F_1 *N. tabacum* × *N. sylvestris* hybrids are short-lived perennials, and the flowers of the second season are of approximately the same size as those of the first season.
3. Removal of open flowers during the normal flowering season prevents nearly all decrease in size.
4. Flowers apparently fully opened are smaller before than they are after anthesis, even though the anthers are partially sterile.
5. Flowers on pot-grown cuttings are smaller than those borne on the field plants from which they were taken.
6. Under favorable and unfavorable greenhouse conditions, flower size varies distinctly and in the same direction as the vegetative characters.
7. Length of corolla is more stable than spread of corolla under environmental stimuli.
8. "The only true distribution representing the flower size of a population must be based upon measurements which, for each plant, extend over the greater part of the period of flowering normal for the given species or hybrid group, or cover an identical portion of the flowering period of each plant."

The data were collected and these conclusions drawn, the authors say, "to establish tentative criteria in keeping with which flower size investigations, in Nicotiana at least, should be carried on and interpreted."

The statements of Goodspeed and Clausen and those quoted from my own paper seem at first sight to be irreconcilable. Indeed, the authors have done me the honor of devoting a considerable portion of their paper to criticizing my views and methods. For example, because it was maintained that flowers are constant under different environments compared with the changes exhibited by vegetative organs, they have assumed that no precautions whatever were taken to eliminate environmental differences. Since the statement was made that plants were grown under diverse conditions, a fact mentioned merely in connection with the question of the effect of stimuli on corolla size, they seem to have concluded unjustly and unreasonably that the data from *these* experiments were used in the paper under consideration.

On the other hand, Goodspeed and Clausen are perfectly justified in asking for a description of the way in which my data were taken. I wish to make such a statement, therefore, in order to support my former paper and some other studies on the inheritance of flower size which are to be published in the near future, and because of the opportunity presented to illustrate a question of considerable general interest. This question, which as a teacher of genetics I have found neglected by research students more than any other, is: *What is significant accuracy in recording data?*

The seemingly opposed statements of Goodspeed and Clausen and of myself serve to illustrate the thought in mind. The two allegations are not wholly discordant. Although I do not wish to withdraw or to modify my own statements, at the same time I am willing, in a broad sense, to accept most of their conclusions. Excluding certain differences in our data that are undoubtedly due to dissimilar conditions at Berkeley, California, and at Boston, Massachusetts, my own results are similar to theirs except as to the magnitude of the changes caused by environmental differences. The point upon which we differ decidedly is the *significance* of the results in relation to the problem at hand—the inheritance of differences in corolla size in Nicotiana.

One of my college instructors once said to me: "It is seldom necessary, in the interests of scientific accuracy, to weigh a ton of hay on an analytical balance." That statement might be made the basis of a course on Precision of Measurements. One is hardly ever required to impress mechanical accuracy upon really earnest students. They will weigh and measure material with the utmost pains (in spirit at least). What is difficult is to impress an idea of true précision. It is not uncommon to see measurements recorded to tenth millimeters after the random use of two scales having a one percent difference, or material for analysis weighed to the fourth decimal place with weights that have never visited the Bureau of Standards, on a balance with very unequal arms. It is rare to find students who think of these errors and endeavor to correct them, although such correction is as necessary in biology as in physics. Let us see how our biological problem fits the rules for the treatment of errors in use in experimental physics.

It was desired to record, in such a manner that they would be comparable, numerics that represented the phenotypes of series of plants of species of Nicotiana in regard to corolla length and spread, sufficiently accurately that genetic analysis of the results might be made.

The investigation was initiated by a series of preliminary measurements designed to show the practical physical limits to the precision of the direct measurements. Repeated measurements of the same flowers showed that there were residual errors beyond one millimeter in the case of length and two millimeters in the case of spread of corolla. Measurement to millimeters was adopted, therefore, although these measurements were afterwards thrown into larger classes for reasons that can be justified biometrically.

Then came a study of ontogenetic variation in order that the factors affecting such variation might be detected. The factors that would naturally occur to anyone who had had experience in growing plants were time of planting, physical and chemical condition of the soil, moisture, age of plant, flowering period, age of flower, position of inflorescence on plant and position of flower in the inflorescence. To determine the effect of each of these factors, it was necessary of course to eliminate the influence of all the others as far as possible. Since the cultures to be compared were nearly always planted at the same time, and since this variable is somewhat dependent upon others that were under consideration, it was neglected. My cultures have also been grown in well-drained soil very uniform in its fertility, but it was thought wise to determine how much effect extreme soil conditions might have. Several species growing outside in soil of good tilth were compared with greenhouse pot cultures. Three-inch, four-inch, five-inch and six-inch pots were used in various species, but the treatment was uniform for each species. The species were *N. tabacum* (several varieties), *N. rustica* (several varieties), *N. longiflora* (two varieties), *N. sylvestris*, *N. paniculata*, *N. acuminata*, *N. forgetiana* and *N. alata grandiflora*. Since only from ten to twenty plants could be grown in the greenhouse in most cases, statistical constants were not calculated, for I have not the faith of Goodspeed and Clausen in probable errors based on nine or ten observations (see their tables II *a*, *b* and III *a*, *b*). Averages of five flowers per plant taken when first in full flower, however, indicated means within a millimeter of each other for length and within two millimeters of each other for spread of corolla for over half of the species, when compared with the sister plants in the field. The greatest difference was in a *N. alata grandiflora* test where the starved plants showed an average of about 5 mm. shorter and 7 mm. narrower flowers. Hybrids were also tested. As I do not consider it necessary to cite figures endlessly where they serve so little purpose, however, only a table of results on a cross between two varieties of *N. longiflora* is given, the field records and the pot records being made by different observers. The general effect of starvation can be seen even without having the means calculated. A comparatively small number of observations were made on each population, but they serve as samples of the frequencies found. Certainly no marked decrease in size is apparent, and since the vegetative organs of the pot-grown plants varied from one half to one fifth the size of those in the field (linear dimensions), it seems that one

TABLE I

Frequency Distribution for Length of Corolla in Cross between N. longiflora Varieties

Designation	Class Centers in Millimeters																				
	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97
No. 383 field..	4	32	1	...	...	...	...	...	...	...	...	...	...	...	...	...	.	.	.	...	.
No. 383 pots..	3	15	1	...	...	...	...	...	...	...	...	...	...	...	...	...	.	.	.	...	.
No. 330 field..	.	...	.	...	...	...	...	...	...	...	...	...	...	...	...	...	.	5	7	10	2
No. 330 pot...	.	...	.	...	...	...	...	...	...	...	...	...	...	...	...	...	.	1	4	3	1
(383 × 330) F_3A field....	.	...	.	...	...	...	...	...	...	4	20	25	59	41	19	2	.	.	.	...	.
Ditto, pot.....	.	...	.	...	...	...	...	...	...	...	1	3	4	1	...	...	.	.	.	...	.
(383 × 330) F_3B field....	.	...	6	20	53	49	15	4	...	...	...	...	...	...	...	...	.	.	.	...	.
Ditto, pot.....	.	...	.	2	6	4	...	...	...	...	...	...	...	...	...	...	.	.	.	...	.
(383 × 330) F_3C field....	.	...	2	3	9	25	37	70	19	10	...	...	...	...	...	...	.	.	.	...	.
Ditto, pot.....	.	...	.	...	...	2	3	3	...	...	...	...	...	...	...	...	.	.	.	...	.
(383 × 330) F_3D field ...	.	...	.	...	...	...	...	...	2	8	14	21	39	39	32	10	1	.	.	...	.
Ditto, pot.....	.	...	.	...	...	...	...	...	...	...	1	...	3	3	2	3	.	.	.	...	.
(383 × 330) F_3E field....	.	...	.	...	1	...	1	1	1	2	16	33	43	34	20	6	1	.	.	...	.
Ditto, pot.....	.	...	.	...	...	1	1	...	...	...	...	1	4	1	2	...	.	.	.	...	.

should be justified in stating that comparatively starvation had no effect on the flowers.

Both sets of these plants had a sufficient supply of moisture to keep them healthy. When this is not the case there is some difference in flower size. For example, some *N. rustica* plants each showing a mean flower length of 20 mm. with extremes of 18 mm. and 22 mm. at the first of the season, decreased in their mean flower length to 18.8 mm. after being in flower for four weeks during which very little rain fell. Then came four inches of rain within forty-eight hours. After this, stout vigorous laterals arose from the lower part of the main stems bearing flowers with a mean length of 21.1 mm. (extremes were 19 mm. and 23 mm.). Thus a marked difference in activity of cell division shows its effect on the flower.

This factor is probably the cause of the greater size shown by flowers on lateral branches when compared with those on terminal branches in Goodspeed's and Clausen's work (Tables XIII, XIV, XV). These authors also found that the flowers on new vigorous branches after "cutting back" were increased in the same way.

These facts should be taken into consideration when examining the conclusion of the California botanists that flower size decreases markedly as the length of the flowering season increases. Their data, as well as my own, proving that flower size may keep up to that of the first of the season and even increase if the weather conditions remain favorable for the production of vigorous new lateral branches, show that it is questionable whether a significant decrease in flower size occurs during the time that data would be likely to be taken. Their data showing marked decreases from the first of the season to mid-season are from populations of 9 and 10. During similar periods I have found no measurable decrease in flower length in *N. tabacum*, *N. longiflora*, *N. paniculata* and *N. rustica*. I have found a mean decrease of 1.0 mm. to 1.5 mm. which possibly is due to this factor in certain cultures of *N. langsdorffii*, *N. acuminata*, *N. forgetiana* and *N. alata grandiflora*, but I think the true occasion of the decrease was lack of moisture. On the other hand, there seems to be evidence in Goodspeed's and Clausen's data that toward the end of the season there is likely to be a decrease in flower size. My own data have shown a drop of from 4 mm. to 8 mm. in both corolla length and spread in various species in the last dozen or two flowers produced. This shows as a sudden change which is evidently due to physiological reasons. The true state of affairs is masked, therefore, when this decrease is treated as a gradual drop in flower size during the season. If measurements on greenhouse cultures grown in proper sized pots are taken daily over a long period, they simply show comparative uniformity in flower size until about the end of the flowering season. Then a decrease which produces a sharp bend in the curve occurs.

As to variation in size owing to age of the flower, I have found that this is largely a mechanical difficulty. There is no difference in length between flowers before and after anthesis, for anthesis takes place normally either before or within 10 hours after the flower opens in all species of Nicotiana under Boston conditions. A flower if unpollinated may open for as many as 5 successive days, and there is a slight increase in both length and spread of the corolla. But a pollinated flower seldom opens on more than two successive days. The flower becomes less firm however and the *spread* of the corolla may *appear* to increase.

Flowers of the same relative position on vigorous branches are the same size whether they be on the main stalk or on laterals in species like *N. forgetiana* and *N. alata grandiflora* which are characterized by vigorous lateral branches from the base of the stem. Flowers on lateral branches in species like *N. tabacum* where the main stem is so much more vigorous, average (in my counts) slightly less (under 1 mm.) than those on the main stem.

After about the sixth flower on the species having racemes, and on the flowers coming out after the first full glory of the panicled species, there is also a slight decrease in size owing to decrease in the conducting channels of the fibro-vascular system.

What information do these observations, which are the preliminary "qualitative" tests made in every investigation, give us? They show that to record the phenotypes of flower size of a series of Nicotiana plants, the seeds should be sown at the same time in uniform soil, the plants should be pricked out uniformly and set at the same time in a plot of uniform fertility. The flower records should be made within two or three weeks of each other at the first of the season, allowing no marked climatic change to intervene if possible. The flowers recorded should be the vigorous flowers (as stated in the last paragraph) of vigorous branches, and should be measured on the same day that they open.

This procedure should be followed where it is physically possible, and any departure noted in order that a correction for any constant error due to it may be calculated, if it be advisable. But, one might ask, would not any trained geneticist have taken these precautions anyway? What has been gained?

The advantages are real. Unsuspected constant errors often come to light through such preliminary investigations. The good fortune that none appeared here certainly makes it no less satisfactory. It showed that control of conditions in such a manner that constant errors will be negligible in the end result is technically possible. It gave a definite idea of the magnitude of the error produced when various environmental factors do vary, and this is very necessary in determining the probable limits of error.

There is a way of testing the conclusion that with the conditions controlled as suggested the constant error is negligible. If the same plants are measured during *similar portions* of successive periods of flowering activity, there is but one other obvious variable—total age of plant. If the latter has no measurable effect the two frequency distributions should duplicate. On this point I have no data, but Goodspeed and Clausen have corroborated the expectation in their conclusion number two. I do have some data on random samples of the same pure line grown in different years. This will be taken up later, however, as another point is involved.

Now the question arises: If records are made in this uniform manner, how many records from each plant are needed to obtain a measure of that plant with the precision necessary for a genetic investigation? Goodspeed and Clausen say that twenty-five flowers is the minimum. At the beginning of my Nicotiana investigations (1908), I used the same number, curiously enough. But I soon found that this was "accuracy with no significance," and the number was reduced to five. I now use but one measurement per plant. This is done because the precision is so nearly that of using twenty-five flowers, that it would be a waste of labor to try to attain the other. Furthermore the precision obtained by measuring twenty-five flowers is only appreciably greater when it can be done in a short time, otherwise *constant* errors may become very much greater.

The precision attained by measuring one flower per plant is all that is required for the use to which the data are to be put, and it is a rule of experimental physics not to strive for greater accuracy.

This matter can and has been tested in two ways. The first is to compare random frequency distributions of the corolla size of single plants with frequency distributions of the flowers when selected from vigorous branches and measured on the same day they have opened. This procedure gives a measure of the accuracy of single flower selections. To illustrate this, data from two species with very different sized flowers are submitted.

TABLE II

Comparison of Random Samples of Corolla Length on Single Plants and Samples in which Constant Errors have been Largely Eliminated

Name	Class Centers in Millimeters											
	20	21	22	23	24	25	26	27	28	29	30	31
N. paniculata, Random					1	3	16	2	3			
" " Selected						4	18	3				
" " Ran.				2	4	14	4	1				
" " Sel.					5	17	3					
" " Ran.							4	16	5			
" " Sel.							3	20	2			
" " Ran.				2	3	15	4	1				
" " Sel.					3	22						

Name	Class Centers in Millimeters										
	70	73	76	79	82	85	88	90	94	97	100
N. alata gr., Ran.			1	3	16	4	1				
" " " Sel.				2	22	1					
" " " Ran.				1	6	14	3	1			
" " " Sel.					3	18	4				
" " " Ran.					2	3	17	3			
" " " Sel.						2	23				

These plants are among the most uniform and the most variable respectively, and give an idea of the range of variability involved.

The other test made was to select fifteen flowers on a plant at random, and determine the mean to the nearest millimeter; then to find the deviation from this mean when single flowers were selected. In 100 tests of flowers shorter than thirty millimeters 88 selections were made within the 3 millimeter class to which the mean belonged. The remainder were in contiguous classes. On flowers between 70 and 100 millimeters long 82 out of 100 selections were within the 6 millimeter class to which the mean belonged. The remainder with 2 exceptions were in contiguous classes.

From these tests it will be seen that the probable error of the selection (equal chances) is not over plus or minus 2 percent. If this were a constant error it would be considerable. But it must be remembered that it belongs to the class of accidental errors and that in the long run the minus errors are compensated by the plus errors.

Such compensation can be clearly seen and the accuracy of the method perhaps most clearly demonstrated by comparing frequency distributions of the same pure line, daughters of the same plant, during successive seasons. In a number of cases populations of sister plants were grown for two and three years. The seed in each case came from single 1909 or 1910 plants, and since the percentage germination remained practically constant, the different populations are in the nature of duplicate and triplicate determinations. If then the frequency distributions are sufficiently alike that they may be presumed to be random samples of one population, the method is accurate enough for genetic purposes. A sample of the result is shown in Table III.

Table III

Random Samples of the Same Population Grown in Different Seasons

Name	Class Centers in Millimeters												Means
	34	37	40	43			85	88	91	94	97	100	
N. longiflora, var. *A*, 1911	...	13	80	32	...	...	...	...	...	...	...	...	40.46±.11
" " " " 1912	1	4	28	16	...	...	...	...	...	...	...	...	40.61±.19
" " " " 1913	...	4	32	1	...	...	...	...	...	...	...	...	39.76±.12
N. longiflora, var. *B*, 1911	...	...	...	...	...	...	...	6	22	49	11	...	93.22±.16
" " " " 1912	...	...	...	...	...	...	...	2	16	32	6	1	93.37±.20
" " " " 1913	...	...	...	...	...	...	...	5	7	10	2	...	92.12±.37

When one takes into consideration the difference in size of corolla among Nicotiana species and varieties that will cross and give fertile hybrids—*i. e. N. langsdorffii* 21 mm. and *N. alata grandiflora* 85 mm., it is scarcely necessary to enter into a biometrical argument on the precision of the method. Here are two small samples of the same population of *N. langsdorffii* grown in 1911 and 1914:

Designation	Class Centers in Millimeters				
	19	20	21	22	23
1911 plants	...	3	12	1	2
1914 plants	1	9	33	7	1

Can it be doubted that the phenotype for corolla length to which *N. langsdorffii* belongs is shown here with an accuracy much greater than is necessary when an analysis of the hybrid progeny of it and *N. alata grandiflora* is contemplated? Biometrical methods are much too imperfect to demand more. There is no intention to discuss here the reasons why the biometrical methods in general use in genetics are imperfect. But it must be emphasized that they are merely used in default of better, since many of them cannot be defended either mathematically or biologically. For example, common sense tells us that equal-sized classes should not be used for the two very different species shown in Table III, where the corolla of one is three times that of the other, yet no satisfactory method has been proposed which does away with the difficulties involved. Since it is necessary to use such poor methods in calculating our end results in genetic studies of size, however, one should remember that labor to record data far more precisely than these methods require is *labor wasted.*

At the same time, though one may believe that biometrical methods are imperfect for certain purposes, they are founded on the theory of probability and when used should be used with this in mind. Having recorded his data with the precision desired, one should not try to analyze them until he has collected a sufficient number of observations to make calculations of residual errors have meaning. Just what the minimum number should be varies with the problem and cannot be discussed in this paper. There are several textbooks on the Theory of Measurements in which the matter is treated in detail. All I wish to point out here is that in every problem capable of biometrical analysis there is such a minimum, and if the data to be analyzed are far under this required minimum, no over precision (in cases where this is possible) in making the records will give them value.

An excellent illustration of this is found in Goodspeed's third article on Quantitative Studies of Inheritance in Nicotiana Hybrids.[1] The author used his method of recording measurements of flowers through a considerable portion of the flowering season in order to determine the phenotypes to which the plants belong, and yet has made analyses of frequency distributions having such a small number of entries that they possess no meaning whatever. Among 44 frequency distributions, 29 have less than 12 plants recorded. He recognizes the fact that the number of plants involved is too small, but feels that this deficiency is balanced by the accuracy of his records.

[1] Univ. Cal. Pub. Bot. 5: 223–231. 1915.

He says: "Data which have been submitted, however, leave no room for doubt in my own mind that investigations on the inheritance of flower-size demand the recognition of certain definite criteria and that the results of such investigations are vitally influenced by inherent as well as externally induced physiological states peculiar to the plant. Thus it remains to be seen if as many as 800 plants are necessary to establish the validity of an expanded Mendelian notation in F_2 of a flower-size hybrid, whether the 40,000 to 80,000 measurements, seemingly essential to a fair expression of results, can be accumulated. In other words, the experiment with which this paper deals has been a partially successful effort to measure many flowers on a few plants with the thought that the conception of flower-size would thus be approximately perfect for a few, rather than certainly imperfect for many plants. It is undeniably true that the number of plants is smaller than it should be, and it is perfectly evident that if the flowers on a larger number of plants cannot be correctly measured the attempt is not worth making."

One could hardly find a better illustration of "accuracy without significance." These views are absolutely indefensible mathematically. It has been shown that the method used by Goodspeed in making his records has only a fallacious claim to great precision; but, granting that the method is extremely accurate, it is an accuracy unnecessary to the end result. On the other hand, it should be clear that records in sufficient number to make probable errors significant is positively essential for a biometrical analysis. This end can only be attained by recording larger numbers of plants and not by over-refinement in the plant records. The plant records should have the precision required by the end result, but greater precision does not influence this result.

HARVARD UNIVERSITY

INHERITANCE IN CROSSES BETWEEN *NICOTIANA LANGSDORFFII* AND *NICOTIANA ALATA*

E. M. East
Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS **1**: 311-333, July, 1916

INHERITANCE IN CROSSES BETWEEN *NICOTIANA LANGSDORFFII* AND *NICOTIANA ALATA*

E. M. EAST

Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received March 14, 1916]

TABLE OF CONTENTS

INTRODUCTION

In a rather intensive genetic study of the genus Nicotiana including some sixty inter-specific crosses, the writer has found very few fertile crosses between species whose status would not be questioned by taxonomists. Of these, the one showing the most perfect fertility is to be described in this paper.

Nicotiana Langsdorffii Weinm. and *Nicotiana alata* Lk. and O. are so different from each other in their characters that they were placed by GEORGE DON in the different sections of the genus, that he called Rustica and Petuniodes, and have been kept there by COMES, the most recent monographer of the Nicotianas. The writer agrees with the suggestion of LOCK (1909) that *N. Langsdorffii* should be removed from the Rustica section to the Petuniodes section on the basis of its genetic behavior when crossed with *N. alata,* but the very fact that taxonomists without access to genetic data have seen fit thus to separate them is an indication of a specific distinction not to be questioned except by those who would fuse all types giving fertile hybrids.

Nicotiana Langsdorffii was described by WEINMANN (ROEM. &

GENETICS **1**: 311, Jy 1916

Schult. Syst. iv. p. 323) from Brazil. It probably has a wide distribution in South America as it has been found in Chile (Comes 1899). The immediate sources of my plants were Setchell (1912, his $\frac{22}{02}$) and A. Splendore, Scafati, Italy. I do not know where Setchell obtained his plants, and the two strains may be from the same stock. At any rate they are practically identical, both corresponding with the plate in the Botanical Magazine (1825 pl. 2555).

Figure 1

Figure 2

Figure 1. A young flowering plant of *Nicotiana alata* Link and Otto, var. *grandiflora* Comes.

Figure 2. A young flowering plant of *Nicotiana Langsdorffii* Weinm.

The plants are from 120—145 cm in height, vigorous, profusely branched, the branches erect. The basal leaves are 20—30 cm long, obtuse, ovate, sessile, narrowed and decurrent at the base. Upper leaves are lanceolate, and all are extremely rugose above. Inflorescence racemo-paniculate. Flowers are about 20 mm long, very uniform in size; corollas funnel-shaped, a gibbous ring above, the limb concave, spreading, and very slightly notched; greenish yellow, pendulous. The pollen is blue.

Nicotiana alata as described by LINK and OTTO (see Ic. Pl. Rar. I, 63, t. 32. DC. Prodr. XIII. I. p. 567. GARTENFLORA tab. 1010. COMES 1899, p. 35) from Brazil (found in Uruguay and Paraguay according to COMES), I have never seen. The type used in these experiments is the common *N. affinis* Moore (GARDN. CHRON., 1881, p. 141) referred by COMES to the variety *grandiflora*. The variety seems to have no points by which it can be distinguished from the species. It is described as having larger flowers with more perfume, more zygomorphism and less gibbosity than the species, but these are very indefinite and inconstant qualities.

The strain with which our crosses were made has plants 110-130 cm high, appearing shorter because of the loosely spreading habit. Basal leaves are acute, ovate, quickly narrowed to a slightly decurrent base, slightly rugose; upper leaves lanceolate to linear. Inflorescence is a raceme. Flowers are 75—95 mm long, tube gradually enlarging toward the limb and slightly gibbous at the top, light greenish yellow faintly lined with purple; limb broadly expanded into obtuse, ovate lobes the lower two being distinctly smaller than the other three and giving the flower a decidedly zygomorphic form. The corolla limb is pure white on the inside and cream with sometimes a tinge of purple on the outside. One anther is usually somewhat shorter than the others. The pollen is white or yellowish. Some plants are self-fertile, others are completely self-sterile.

EARLY WORK

These two species were crossed and studied by at least three of the earlier hybridizers, NAUDIN, GODRON and FOCKE. Concerning their results, I quote FOCKE (1881):

> "*N. alata* Lk. × *Langsdorffii* Weinm. GÄRTNER found no foreign species with which he was able to fertilize *N. Langsdorffii*. Reciprocal crosses between *N. alata* and *N. Langsdorffii* are not difficult, however; NAUDIN obtained especially good, well filled capsules by fertilizing *N. Langsdorffii* with pollen from *N. alata,* and although only one pollination of *N. alata* with *N. Langsdorffii* pollen was successful, in this case also a large capsule full of seeds matured. I found no difficulty with either cross. Of *N.*

Langsdorffii ♀ × *N. alata* ♂ (*N. Persico-Langsdorffii* Naud. l. c. p. 74) NAUDIN produced 118, and of *N. alata* ♀ × *N. Langsdorffii* ♂ (*N. Langsdorffii-Persica* Naud.) 53 examples; all of which were exactly like one another. They were 130—160 cm high (*N. Langsd.* ca. 100; *N. alata* 60 cm) and because of their spreading branches more nearly resembled *N. Langsdorffii.* The blossoms were medium large, greenish white, with the limbs distinctly rounded. Pollen bluish gray. Fruitfulness perfect. I have made the same crosses with like results. Pollen was plentiful and the grains well-formed. The capsules contained in the neighborhood of 500 seeds.

"NAUDIN's hybrids were to be distinguished from *N. commutata* by their higher stature, their larger and more greenish flowers, and their darker leaves.

"*Later generations.* Through continued self-fertilization, NAUDIN's hybrid plants gradually returned toward the condition of the parent species, although this was never fully reached. GODRON received from ALEX. BRAUN of Berlin, seed of *N. alata-Langsdorffii* (as well as of *N. Langsdorffii* ♀ × *N. alata* ♂) and raised many forms from it; among others were varieties with yellow, with cream, and with pure white flowers. The leaves were variable, the decurrence at the stem being sometimes very pronounced, sometimes just traceable and sometimes lacking.

"Two varieties in which crossing had been prevented by gauze produced fruits whose seeds reproduced the mother form exactly."

From this extract, it is clear that FOCKE was familiar with the facts that in the cross under consideration—as well as in other crosses—the F_1 generation is more vigorous than either of the parent species, that the population is uniform and the individual plants fertile, and finally that the F_2 and following generations are variable and may produce plants having a striking resemblance to the original parents. In this he was merely copying NAUDIN. Both NAUDIN and GODRON perceived the essential facts of inheritance in hybrids much more clearly than other contemporary hybridizers, and we may be assured that had NAUDIN had an opportunity of reading MENDEL's paper, as did NÄGELI, he would have appreciated its significance. He came very close to an enunciation of what we now know as the Mendelian laws, but either he lacked the ability for mathematical analysis that characterized MENDEL because of the latter's training in physics, or was prevented from making such an analysis by the greater complexity of the hybrids he studied.

NAUDIN (1865) says of his cross, *Nicotiana Persico-Langsdorffii:*

"The two plants here united, although very different at first sight, have distinct analogies in their habit of growth, the form of their leaves, their general aspect, and up to a certain point, in their long, tubular, pendent flowers. One feels these analogies more strongly if he remembers that there exists a form exactly intermediate between the two (*N. commutata,* Fisch.), of which I shall speak later. As well as I can judge by the descriptions, *N. Persica,* of which there is a pretty good figure in the BOTANICAL REGISTER, pl. 1592, appears to be identical with the *N. alata* of DUNAL;

not being sure, however, I have preserved the name that it carried at the Museum."

NAUDIN wished to see whether *N. commutata* was a natural hybrid and if he could reproduce it by this cross. He obtained 118 plants from his cross, "all of the most uniform appearance" and from 130-160 cm high. He concludes that *N. commutata* is not the hybrid *N. Persico-Langsdorffii,* "at least of the first generation." Since he made this conclusion solely on account of the greater height and vigor of his artificial hybrids, it must be that he suspected that he might have duplicated *N. commutata* when by inbreeding his plants had lost their hybrid vigor. I have duplicated plants of *N. commutata* grown from seed received from Dr. SPLENDORE of Scafati, Italy, several times in my own crosses and have obtained F_3 families that bred as true to the form (intermediate between *N. alata grand.* and *N. Langsdorffii*) of the so-called *N. commutata* as did the species (?) itself.

NAUDIN found that the reciprocal cross was so nearly like the other that "without the labels the two lots would have been taken the one for the other." Unfortunately, however, although these crosses were perfectly fertile, NAUDIN did not self them and continue his observations. On the other hand, he did obtain some information regarding later generations by a consideration of the volunteer seedlings that appeared during the next few years on the plat that had borne the original cross. He says:

> "Without having given these hybrids of the second and the third generations the attention they merited, I have noticed that their forms became more and more divergent, some approaching *N. Persica* and others distinctly tending toward *N. Langsdorffii.*"

Some of these plants he potted, and obtaining seed from one that resembled *N. Langsdorffii* he grew a population that bred true to a type that could scarcely be distinguished from *N. Langsdorffii.* These experiments were continued, and from seed of this generation, he raised in 1863, fifty plants nearly all of which "had returned to the type well known as *N. Langsdorffii.*"

Thus it is seen that NAUDIN observed nearly all the essential facts of Mendelian heredity in this one cross,—a uniform F_1 generation, a segregating F_2 generation, and a later generation which showed that certain of the extreme segregates bred true. But the observations on this particular cross are not so important as the general conclusions to which NAUDIN was led by his broad experience as a hybridizer. Under the heading "Physionomie des hybrides," he says:

"In order to have a correct idea concerning the phenomena presented by hybrids, it is essential to distinguish between the first generation and those that follow.

"I have always found, in the hybrids I have made myself or of whose origin I was certain, a great uniformity of aspect between individuals of the first generation and originating from the same cross no matter what their number. This fact we have seen exemplified in *Petunia violaceo-nyctaginiflora, Datura Tatulo-Stramonium* and *D. Stramonio-Tatula, D. Meteloido-Metel, D. Stramonio-lœvis,* etc., *Nicotiana Texano-rustica* and *rustico-Texana, N. Persico-Langsdorffii,* etc.; having already emphasized these resemblances it is useless for me to dwell upon them."

"In fact, one may say that hybrids of the first generation resemble each other as much or nearly as much as the individuals that come from a single legitimate species."

(It is well to note that the hybrids with which NAUDIN supports his thesis here are all between solanaceous species that are generally self-pollinated naturally, and may be presumed to approach homozygosis.)

"Beginning with the second generation, the aspect of hybrids is changed in a remarkable manner. Ordinarily, the perfect uniformity of the first generation is succeeded by a regular medley of forms, some approaching the specific type of the father, others that of the mother, a few returning suddenly and entirely to the one or the other form. At other times, this progress toward the original types is by degrees and slowly, and sometimes one sees a whole collection of hybrids incline toward the same side. The important fact, however, is, that it is the second generation, in the great majority of cases (and perhaps in all), that starts this dissolution of the hybrid forms, a phenomenon recognized by many investigators, doubted by others, but which appears to me to-day to be established beyond argument. We shall explain the cause in the following paragraph."

"All of the hybrids of which I have studied the second generation with some care, have shown these changes in appearance and have manifested this tendency to return to the forms of the original species, and this when conditions have been such that the pollen of the species themselves could not have been the cause. We have seen striking examples of it in *Primula officinali-grandiflora,* in all of the hybrids of *Datura Stramonium,* in *D. Meteloido-Metel,* in the reciprocal hybrids of *Nicotiana angustifolia* and *macrophylla, N. Persica* and *Langsdorffii, Petunia violacea* and *nyctaginiflora,* in *Luffa acutangulo-cylindrica,* and further in *Linaria purpureo-vulgaris.* In the second generation of several of these hybrids there has been a complete return to one or the other or to both of the parent species together with individuals approaching each species in varying degrees; in other cases also we have seen intermediate forms continued at the same time that other specimens from the same family have effected the return of which I speak. Moreover, we have observed cases (*Linaria purpureo-vulgaris* of the third or fourth generation) of actual retrogression toward the hybrid form, sometimes a plant that had apparently returned entirely to one of the two species, has even given rise to individuals that very nearly resembled the other species. All of these facts are explained naturally by the *segregation* (disjunction) *of the two specific essences* in the pollen and the ovules of the hybrid."

Space may not be claimed to show just how NAUDIN's views differed from those of MENDEL, except the bare statement that he did not grasp the idea of a unit-character inheritance. Our quotations are already somewhat lengthy. They may well be pardoned, however, since they are taken from a paper not readily available to most geneticists, and have a considerable theoretical and historical interest. But it was not for this alone that I have used them, nor because they contain observations upon the particular cross that is the subject of this paper. And in passing let me say that there is scarcely a doubt but that NAUDIN's *Nicotiana Persica* and *N. Langsdorffii* are the same as our own *N. alata grandiflora* and *N. Langsdorffii.* The particular reason for the citations is this: While it is to be hoped that with the fruitful hypotheses of modern biology as guides, contemporary genetic research is to be more productive than that of the early nineteenth century hybridizers, it must not be forgotten that very often we are merely repeating more carefully, more quantitatively and with a better idea of relative values, the experiments of these pioneers. The observations of such men as NAUDIN have been confirmed and as far as they go are usually correct. For this reason I think that we may accept their facts until the same experiments have been repeated more carefully and have given us more precise data. This being true, there is no question but that these numerous observations on hybrids between species belonging to so many different groups, showing as they do all the essential phenomena of Mendelian inheritance, go far toward proving Mendelian heredity in quantitative characters.

The only recent work upon *N. Langsdorffii-alata* hybrids is that of LOCK. LOCK made a number of crosses between species of Nicotiana in the years 1906-8, but published only one paper (1909) on the subject. He crossed *N. alata* and *N. Langsdorffii* reciprocally, made several back-crosses, and studied the selfed progeny of the F_1 generation. He noted the uniformity of the F_1 generation and the variability of the F_2 generation and reported a few measurements of the flowers. He established the dominance of blue pollen over yellow and of yellow corollas over white. He also believed that the facts indicated the dominance of gibbous over funnel-shaped corollas.

INHERITANCE OF POLLEN COLOR AND OF FLOWER COLOR

In a cross such as this between two distinct species it is important to know whether any distinct qualitative difference shows a Mendelian behavior. I found only two such differences, pollen color and flower color, and have corroborated the results of Lock in regard to them. I was not able to corroborate his conclusions in regard to corolla shape, as F_2 plants all showed some development of the gibbous condition. And it seems to me that this was to be expected for it is characteristic of both species.

N. alata has yellow pollen and *N. Langsdorffii* blue pollen. No matter which way the cross is made the pollen is blue. The pollen of the heterozygotes is often lighter than that of the pure *N. Langsdorffii,* but not invariably so. Microscopical examination showed no distinctly yellow grains on the F_1 plants so that, like pollen shape in Lathyrus, the color is a sporophytic character. This is less astonishing than the phenomenon in the sweet pea, for it is well known that pollen color is a tapetal deposit. One F_2 consisted of 342 plants with blue pollen and 100 plants with yellow pollen. Counts of smaller segregating populations corroborated these results, though there was an excess of blues in all but one case, an F_3 family consisting of 39 blue and 22 yellow. Just what this excess of blue-pollened plants means, I am unable to say. It may be only a technical difficulty, as the anthers of both species are blue. At any rate, there seems to be no possibility of other factors being concerned directly. Yellow-pollened plants have never given blues.

The flower of *N. Langsdorffii* is greenish yellow both outside and inside the corolla. *N. alata,* on the other hand, though slightly greenish yellow with sometimes a faint tinge of purple on the outside of the corolla, is pure white on the inside of the limb. Apparently the cells just beneath the epidermis on the inside of the limb of these flowers contain no colored chromatophores and very few plastids of any sort. The flowers of the F_1 hybrids (made either way) are cream-colored, but appear to be variable because the old flowers are so light as to be sometimes mistaken for whites. Further the smaller-flowered plants appear to be a darker yellow owing to a concentration of chromoplasts which show through the upper two layers of cells. There is no question but that the inheritance of these differences is Mendelian, but it is not certain that only one factor is involved. Three F_2 populations gave ratios of 196 yellows to 61 whites, 50 yellows to 15 whites, and 57 yellows to 15 whites respectively. A heterozygous F_3 family also gave a ratio of 112 yellows to 29 whites, but one of our F_2 families produced 70 yellows to 6 whites. This constant excess of yellows leads one to suspect complications, but it can be said that no white ever produced yellows after self-pollination, though a number of such families were grown.

It is possible that there is a correlation between small flowers and yellow color though this could not be established.

FERTILITY OF THE HYBRIDS

These slightly distorted ratios give some cause for the surmise that differential fertility exists among the gametes and the zygotes. That all the possible gametic constitutions mature at spermatogenesis cannot be asserted without a cytological study of the early stages. The capsules on the F_1 plants were well filled, however, and the germination of the seeds was between 90 percent and 100 percent.[1] This seems a fair proof that the ovules were all functional and that there was no selective elimination of zygotes.

On the other hand, all of the pollen produced by the F_1 plants and of the plants of later generations was not well formed. An examination of the pollen of 20 F_1 plants after having simply shaken it out on slides showed both when dry and in glycerin or in sugar solutions that apparently functional pollen grains existed in percentages varying from 70 to 96. Of course one cannot say that all of these seemingly well-formed pollen grains are functional, as DORSEY (1915) has shown that in certain Vitis species they sometimes contain no generative nuclei; but since in nearly all the plants there are around 85-90 percent perfectly formed pollen grains one may be fairly certain that if much selective elimination of gametes occurs it occurs before the pollen grains are formed, for the parent species themselves show only from 80-90 percent of well formed grains.

HEIGHT

Nicotiana Langsdorffii (328) and *N. alata* (321) are nearly the same height,—about 132 cm and 120 cm respectively,—but they are very difficult to measure owing to their becoming so profusely branched during

---

[1] GOODSPEED (1913) has criticized a table published by EAST and HAYES (1912, p. 28) entitled "Condition of hybrids in crosses between species of Nicotiana" because a number of Nicotiana hybrids were tabled as showing 100 percent germination. This table was published to indicate the general type of certain hybrids with regard to vigor, and I think served its purpose. It was distinctly stated, however, (p. 29) that "the voluminous data that have been collected on these hybrids have been condensed and approximated so that they include only facts germane to the matter in hand." It would seem that it might have been clear to GOODSPEED from this statement that these germinations were only classes. Possibly it would have been better to have said germination "high, medium, low and failing," but it does not seem to me that the readers were led far astray. As a matter of fact the germinations tabled as 100 percent, included all hybrids that tested over 90 percent.

the latter part of the season. The F_1 generation was as uniform as either parent and showed distinct evidence of hybrid vigor. The plants varied from 140 cm to 160 cm. In the second hybrid generation there was no evidence of segregation into distinct types, either as regards height or general habits of growth but plants varied from below the height of No. 321 (extremes about 100 cm) to that of the F_1 generation.

RAPIDITY OF GROWTH

Though both of these species continue flowering until frost, *N. Langsdorffii* commences flowering earlier than *N. alata*, when planted at the same time, and owing to the multitude of ripe capsules formed, takes on a more mature appearance in September. The variation in time of flowering within each species is very slight. In seasons with normal rainfall, sunlight and heat, plants of *N. Langsdorffii* planted in the greenhouse at the same time and set in the field on the same day, come into blossom within three days of each other. Plants of *N. alata* treated in the same manner, show greater variation, sometimes a week elapsing between the time that extremes begin blossoming. The F_1 plants are as uniform in this respect as *N. Langsdorffii* and are slightly earlier. The F_2 plants, on the other hand, are more variable than those of *N. alata,* and this variability is not wholly an effect of environment as is beautifully demonstrated by the F_3 cultures. Ten progeny rows from different F_2 plants showed a difference of 25 days in the time the plants began to flower. Four of the families were variable like the F_2 population, but the remainder were very uniform within the family. On the fifteenth of July two families were in full blossom without an exception, one family had just begun to bloom, one family had the central stalks well advanced and two families were in the rosette stage.

LEAVES

In general the shape of the leaves of both of these species is the same. The basal leaves of *N. alata*, however, are acute, with redundant, folded margins, while those of *N. Langsdorffii* are obtuse and not redundant at the margins. *N. Langsdorffii* is much more rugose than *N. alata*. Both species are decurrent. The tips of the leaves of the F_1 plants are intermediate, but in other qualities the leaves are like those of *N. alata*. The F_2 plants run the whole gamut of these variations. There are plants, the rugosity of whose leaves is like *N. Langsdorffii,* that are like *N. alata* in other respects (except that the flowers are smaller).

TABLE 1

Frequency distribution of corolla length in the families of cross 328 × 321.

Pedigree Number	Size in parent	Class Centers in millimeters																										No.
		19	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	
328, (1914)		10	41																									51
328, (1911+1914)		13	56																									69
321, (1911)																				3	8	10	11	8	5	3	1	49
(328×321) F_1							1	4	24	16	1																	46
(328×321)—1 F_2	41		1	1	5	35	52	58	45	35	13	6	2	1	0	1	1											256
(328×321) total F_2			2	3	13	65	110	132	107	82	33	15	6	7	0	4	2											581
(328×321) 1—1 F_3	23		40	10																								51
(328×321) 1—2 F_3	37					1	24	25																				50
(328×321) 1—3 F_3	40						4	11	26	6	1																	48
(328×321) 1—4 F_3	63								1	3	14	10	17	11	7	5	3											71
(328×321) 1—41 F_3	60							1	1	5	12	17	9	11	7	2	1	0	0	0	1							67
(328×321) 1—5 F_3	54							2	0	7	5	2	1	3	1	2	1	1										25
(328×321) 1—6 F_3	60							2	2	9	27	29	29	17	28	15	3	3	1	3								168
(328×321) 1—7 F_3	21	11	39																									50

Those plants that have returned to the *N. Langsdorffii* habit and size of flower, however, always have rugose leaves though they may be acute.

In all of these respects the reciprocal crosses are so nearly alike that it is impossible to distinguish between them.

COROLLA LENGTH

As I have explained in other papers (EAST 1916 a, b), corolla length is an excellent character upon which to make genetic studies because of the very slight effect produced by environmental differences. Corolla measurements of single flowers when taken with due precautions as to uniformity of age of plant, age of flower, position of flower, etc., well represent the phenotypes of the plants concerned.

Table 1 gives the frequency distributions of such measurements upon populations of the pure species, the cross when *N. Langsdorffii* was used as the female, a single F_2 population, the total of several F_2 populations and eight F_3 families. Only three of these distributions contain as many individual measurements as I should like, and one—(328 × 321)1-5—must be discarded entirely on account of the small number of plants.

The statistical constants for these distributions are shown in table 2.

TABLE 2

Statistical constants for the frequency distributions of corolla length shown in table 1.

Pedigree Number	Size in parent	Mean	S. D.	C. V.	No.
328, (1914)		21.41 ± .11	1.19 ± .08	5.56 ± .37	51
328, (1911 + 1914)		21.43 ± .10	1.17 ± .07	5.46 ± .31	69
321, (1911)		81.76 ± .49	5.08 ± .35	6.21 ± .42	49
(328 × 321) F_1		40.78 ± .22	2.20 ± .15	5.39 ± .38	46
(328 × 321) — 1 F_2	41	37.77 ± .24	5.63 ± .17	14.91 ± .45	256
(328 × 321) total F_2		38.30 ± .17	5.99 ± .12	15.64 ± .32	581
(328 × 321) 1 — 1 F_3	23	22.65 ± .12	1.24 ± .08	5.47 ± .37	51
(328 × 321) 1 — 2 F_3	37	35.44 ± .15	1.62 ± .11	4.57 ± .31	50
(328 × 321) 1 — 3 F_3	40	39.31 ± .25	2.54 ± .17	6.46 ± .44	48
(328 × 321) 1 — 4 F_3	63	52.04 ± .44	5.52 ± .31	10.61 ± .61	71
(328 × 321) 1 — 41 F_3	60	51.02 ± .51	6.16 ± .36	12.07 ± .71	67
(328 × 321) 1 — 5 F_3	54	49.24 ± 1.09	8.05 ± .77	16.35 ± 1.60	25
(328 × 321) 1 — 6 F_3	60	52.79 ± .35	6.79 ± .25	12.86 ± .48	168
(328 × 321) 1 — 7 F_3	21	21.34 ± .12	1.24 ± .08	5.81 ± .39	50

As may be seen, *N. Langsdorffii* (No. 328) has a very low variability. This is to be expected, for *N. Langsdorffii* is practically always self-fertilized naturally. *N. alata* is often self-fertilized, but evidence of considerable cross-fertilization has been found by observing the actions of Sphingidae in the evening, by isolating plants, and by self-sterility studies. Though the coefficient of variability (6.21 ± .42 percent) is almost as low as that of No. 328, therefore, it is probable that No. 321 is not so nearly homozygous. Furthermore, the number of individuals measured is small. On the other hand, since a single plant of No. 321 was used in the cross, it is possible that the true variability of this "blood" introduced, is somewhat smaller than that represented by the frequency distribution.

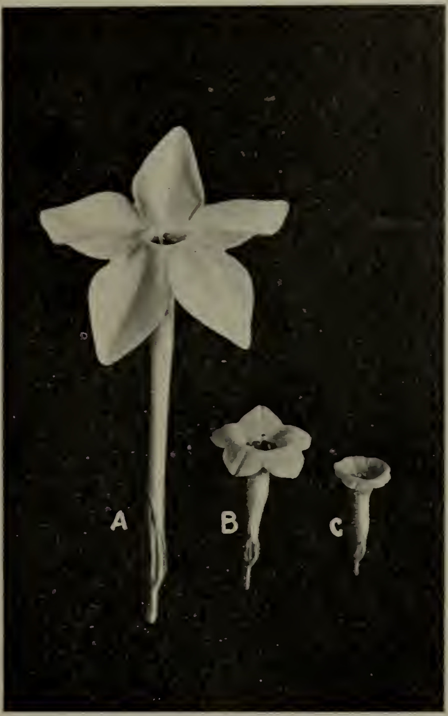


FIGURE 3

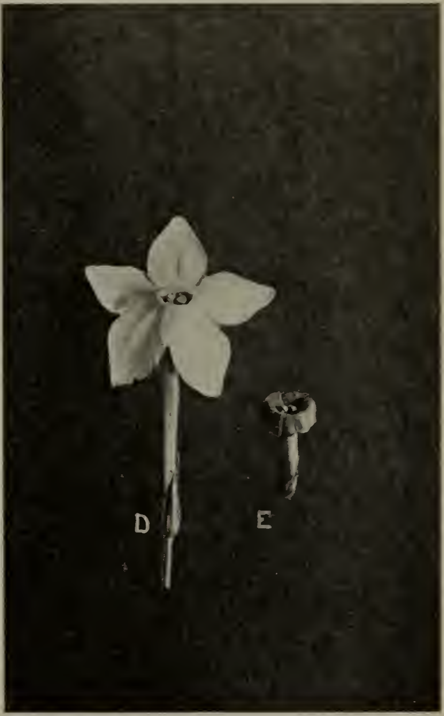


FIGURE 4

FIGURE 3. A, *N. alata grandiflora;* B, F_1 of *N. Langsdorffii* × *N. alata grandiflora;* C, *N. Langsdorffii* (1911) × ½.

FIGURE 4. D and E, extremes of the F_2 generation (1912) × ½.

Curiously enough the mean of the F_1 population is smaller than the average of the two parents. Thus there apparently is no effect of heterosis on the flowers. The square root of the F_1 mean is more nearly that of the average of the square roots of the means of the two parents, but I do not feel justified in attaching any significance to the fact.

The coefficient of variation of the F_2 generation is nearly three times that of the F_1 generation. Though extremes like each parent were not produced, it is hardly possible to see any other cause for this great difference in variability than segregation and recombination of Mendelian factors. From the theory of probability one might expect to recover both parents with a comparatively small number of F_2 plants, but the variability of F_1 is so small that even the plants obtained in F_2 could not be expected in the F_1 if the whole of New England were planted with them.

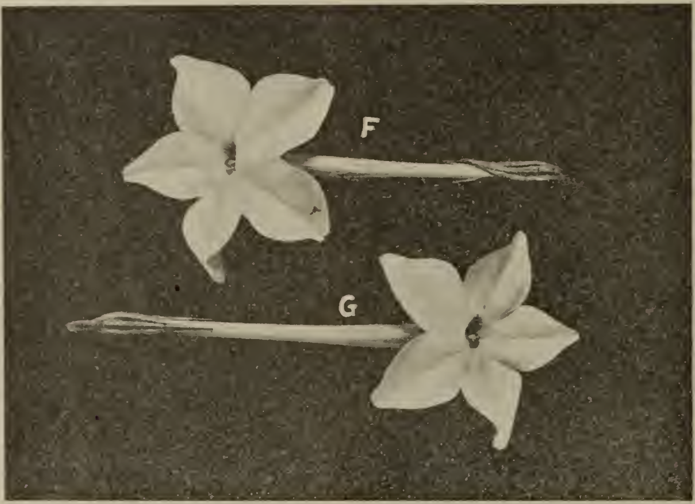


FIGURE 5. F, extreme of the F_3 generation, and G, pure N. *alata grandiflora* (1913) × ½.

In the F_3 generation there was regression toward the mean of the F_2 population in six out of seven cases (excluding No. 1-5 on account of the small number of plants), *but the greatest extremes gave the least regression.* The coefficients of variability were lower than that of F_2 in every family, and three of them bred as true as the parental species. F_3 family No. 1-7 reproduced N. *Langsdorffii* exactly.

The Mendelian theory calls for the production of the same type of F_2 population no matter what F_1 parent is selected, when the original individuals entering the cross are homozygous. Critics of the use of the Mendelian terminology in crosses involving size characters have maintained, however, that small F_1 individuals will give F_2 populations

FIGURE 6

FIGURE 7

FIGURE 6. Individual plant produced by an F_2 segregate that was like *N. Langsdorffii* in every detail (E of figure 4).

FIGURE 7. Progeny row showing uniformity of F_3 family to which the plant shown in figure 6 belonged.

with lower means than will large individuals. As there are many indications that the plants entering into this cross were very nearly true homozygotes I have endeavored to test this proposition. Of course, as might be expected by pro-Mendelians, in such a cross the variability of the F_1 population is so low that the extremes selected differed by only 8 mm. Nevertheless five F_2 frequency distributions from different F_1 parents are presented in table 3. The statistical constants shown in table 4 emphasize the fact that the means and the standard deviations

Table 3

Frequency distributions of corolla length in five F_2 families of cross 321 × 328 — 1.

Pedigree Number	Size in parent	Class centers in millimeters															No.
		22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	
(328 × 321) — 1	41	1	1	5	35	52	58	45	35	13	6	2	1	0	1	1	256
(328 × 321) — A	44	1	1	3	9	27	25	24	11	2	3	1	1	0	1		109
(328 × 321) — 2	40			1	6	8	18	11	11	7	1	2	0	0	2		67
(328 × 321) — 3	36		1	2	7	13	18	16	12	6	1	0	1				77
(328 × 321) — 4	39			2	8	10	13	11	13	5	4	1	4	0	0	1	72

TABLE 4

Statistical constants of the corolla length in the five F_2 families reported in table 3

Number	Size in parent	Mean	S. D.	C. V.	No.
(328 × 321) — 1	41	37.77 ± .24	5.63 ± .17	14.91 ± .45	256
(328 × 321) — A	44	37.55 ± .36	5.65 ± .26	15.05 ± .70	109
(328 × 321) — 2	40	39.73 ± .52	6.32 ± .37	15.91 ± .95	67
(328 × 321) — 3	36	38.21 ± .40	5.21 ± .28	13.63 ± .75	77
(328 × 321) — 4	39	40.08 ± .56	7.11 ± .40	17.24 ± 1.00	72

very nearly overlap. In other words the curves are very nearly identical, and it can be shown mathematically that the probability is very high that they are all samples of the same population. The similarity of the curves is shown graphically in figure 9. The points of the theoretical curves of these five F_2 populations were calculated and are shown in comparison with the theoretical curve of the total distribution of all F_2 observations. The extreme classes are so nearly identical that curves could not be distinguished when drawn super-imposed, so that only the points are indicated. Where no points for a particular curve are given it is understood that they lie on the single curve of total observations which is drawn.

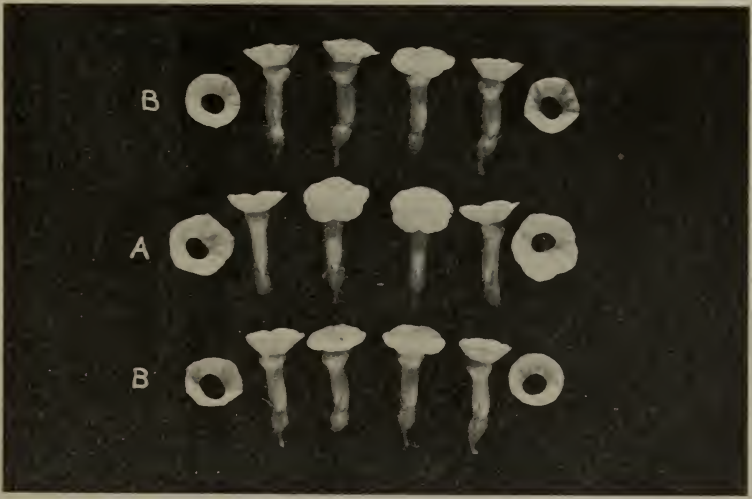


FIGURE 8. A, a random sample of *N. Langsdorffii* flowers from six different plants; B, a random sample of flowers from twelve different plants from the progeny row shown in figure 7 (× ½).

Certainly no one can well maintain that these curves show any decided difference when the probable errors are taken into consideration. There is no dissimilarity in variability like that shown by F_3 populations from different points on the F_2 curve. The mean of the population from the 36-mm parent is higher than that from the 44-mm parent. This fact is not to be taken as significant; it is merely a coincidence. It is very evident that the only just conclusion is that selection has no effect.

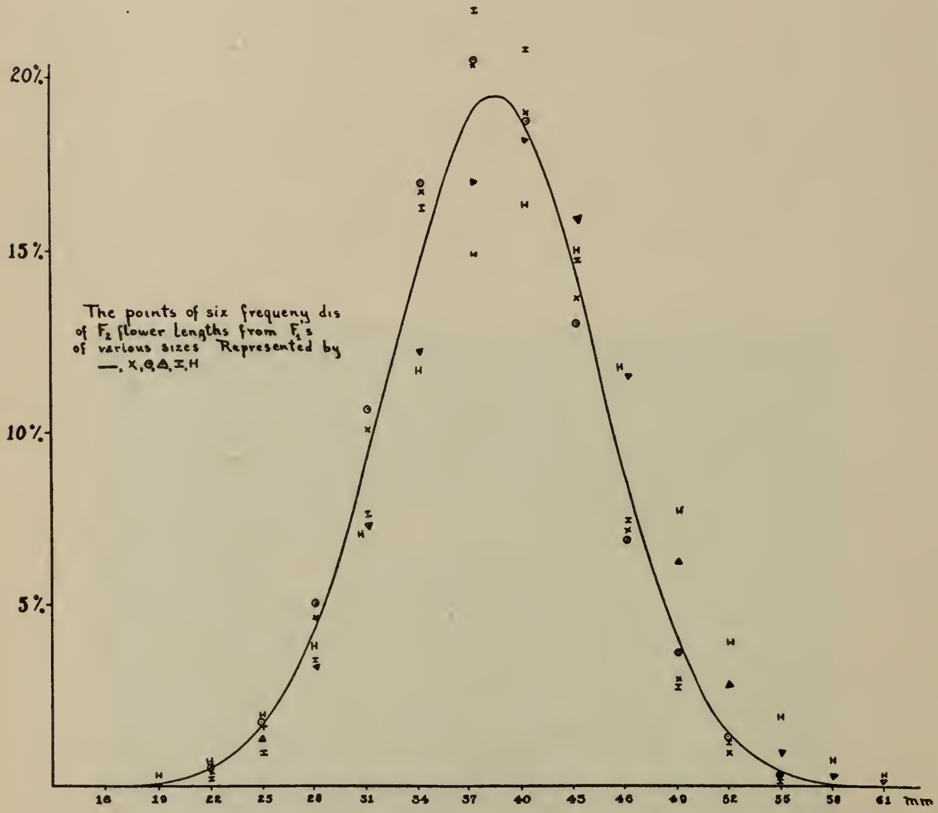


FIGURE 9. The points of the theoretical curves for flower length, calculated from the data obtained from growing F_2 populations from F_1 individuals of various sizes in cross 328 × 321. The curve drawn in full is that calculated from the combined observations.

In tables 1 and 2 one may notice an F_3 family, No. (328 × 321)1—7, that seems to have repeated the small parent, *N. Langsdorffii.* This was indeed the case. Several F_2 plants duplicated *N. Langsdorffii* in every feature and two of them were selfed and their progeny grown. Family No. (328 × 321)1—1 from the larger of these two plants as regards flower size was very uniform, but the flowers were slightly larger than those of the *N. Langsdorffii* strain used, and the plants differed from it slightly in other ways. In short, it could hardly be maintained that the great-grandparent had been duplicated. On the other hand family (328 × 321) 1—7 was exactly like a family from a selfed plant of No. 328. I could not find a distinguishing trait by the most minute examination. Figures 6, 7 and 8 show this fact plainly, but since photographs of the other small family would appear to show the same thing, so small are the differences between it and our strain of No. 328, a table of corolla measurements has been introduced in order to demonstrate the matter quantitatively.

Since it is obvious that the use of 3-mm classes in table 1—classes as small as can be treated conveniently in connection with such great size difference—obscures somewhat the true distribution of the corolla length of No. 328, table 5 gives the distribution of the corolla lengths of the same plants in 1-mm classes. This brings out the wonderful uniformity of the populations of both No. 328 and No. (328 × 321) 1—7 and the marvelous similarity between the two families. Furthermore, it shows how similar are two populations of No. 328 grown from the same seed but in different years.

TABLE 5

Frequency distribution of No. 328 and of an F_3 family that bred true to the characters of this species.

Pedigree Number	Class centers in millimeters					Mean	S. D.	C. V.	No.
	19	20	21	22	23				
328, (1911)		3	12	1	2				
328, (1914)	1	9	33	7	1	20.96 ± .06	0.69 ± .05	3.27 ± .21	51
328, total	1	12	45	8	3	21.00 ± .06	0.72 ± .04	3.43 ± .20	69
(328 × 321) 1 — 7 F_3		11	33	6		20.90 ± .05	0.57 ± .04	2.75 ± .19	50

THE RECIPROCAL CROSS

The cross in which No. 321 was used as the mother, was not a true reciprocal of the other in that the same individuals were not used. In fact a different strain of *N. Langsdorffii* known as No. 328—1 was used, which had flowers slightly smaller than No. 328. For this reason as well as that each generation of this cross was grown a year later than the

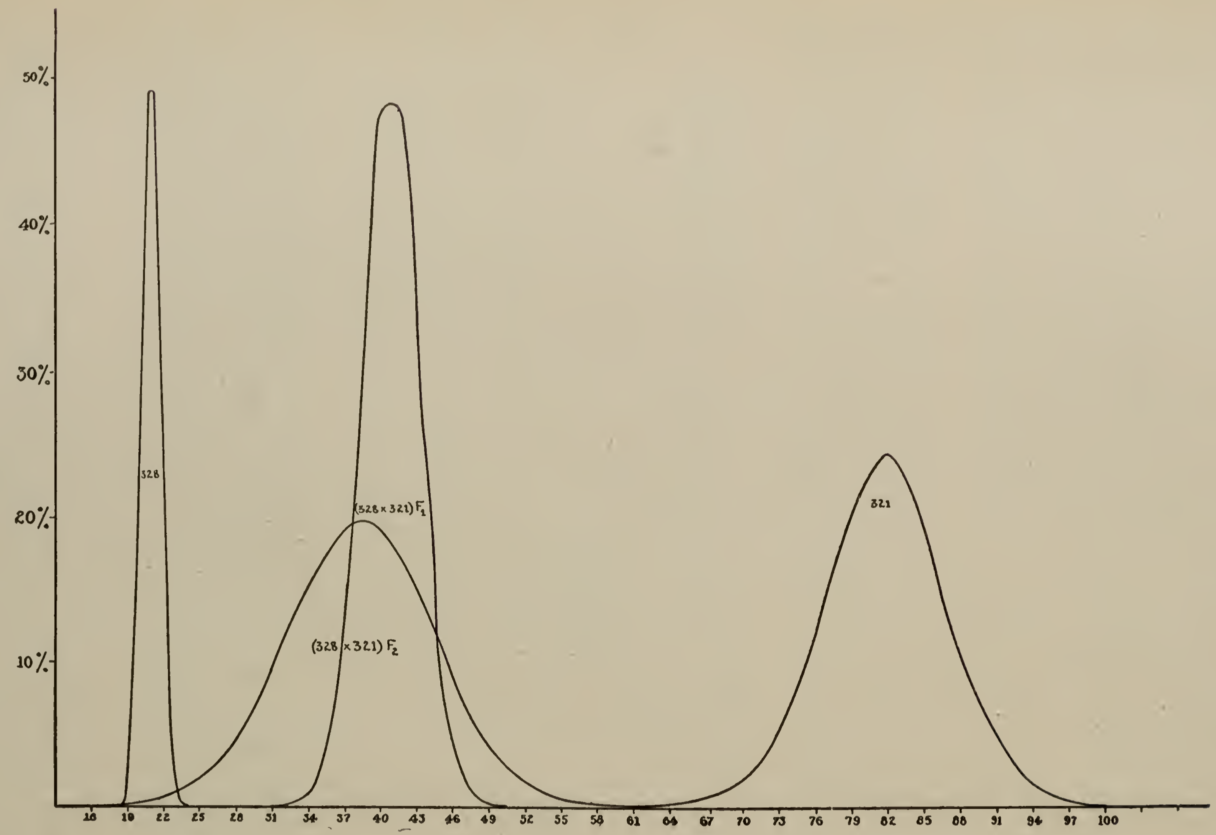


FIGURE 10. The theoretical curves of flower length for population of *N. Langsdorffii* (328), of *N. alata grandiflora* (321), and of the F_1 and F_2 of the cross 328 × 321. The curve of 328 cannot be compared with the others because it is shown in classes of one millimeter instead of classes of three millimeters.

TABLE 6

Frequency distribution of corolla length in the families of cross 321 × 328.

Pedigree Number	Size in parent	Class centers in millimeters																											No.
		16	19	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	
328—1, (1910)			26	4																									30
328—1, (1912)		2	20	4																									26
328 – 1, total		2	46	8																									56
321, (1911)																					3	8	10	11	8	5	3	1	49
(321 × 328—1) F_1										8	21	2																	31
(321 × 328—1) F_2				1	0	9	16	21	53	25	23	6	6	3															163
(321 × 328—1)1—1 F_3	22	8	75	18																									101
(321 × 328—1)1—2 F_3	49								7	17	25	18	12	2															81
(321 × 328—1)1—3 F_3	51						1	2	4	8	30	31	19	6	1	2	0	1											105
(321 × 328—1)1—4 F_3	49								6	8	19	15	18	1															67

other, the slight differences between the two can not be attributed to the different way of making the cross. The cross with No. 321 as the mother was more difficult to make but this is probably due to the greater length of the style of No. 321.

Cross 321 × 328 is notable for the extreme uniformity of the first hybrid generation and the great increase in variability in the second hybrid generation, as is shown in tables 6 and 7. *N. Langsdorffii* was again reproduced in F_2 and plant (321 × 328) 1—1 bred true to its characters. There was no nearer approach to No. 321, however, than there was in cross 328 × 321. The cross appeared to be fully fertile and the seeds germinated well though in general not so perfectly as those of the reverse cross. It does not seem as if the slight infertility shown, however, could be the explanation of the failure to reproduce the larger parent.

TABLE 7

Statistical constants for the frequency distributions of corolla length shown in table 6.

Pedigree Number	Size in parent	Mean	S. D.	C. V.	No
328 — 1, (1910)		19.40 ± .13	1.02 ± .09	5.26 ± .46	30
328 — 1, (1912)		19.23 ± .19	1.42 ± .13	7.38 ± .69	26
328 — 1, total		19.32 ± .11	1.23 ± .08	6.37 ± .41	56
321, (1911)		81.76 ± .49	5.08 ± .35	6.21 ± .42	49
(321 × 328 — 1) F_1		42.42 ± .19	1.60 ± .14	3.77 ± .32	31
(321 × 328 — 1) F_2		37.79 ± .28	5.36 ± .20	14.18 ± .54	163
(321 × 328 — 1) 1 — 1 F_3	22	19.30 ± .10	1.50 ± .07	7.77 ± .37	101
(321 × 328 — 1) 1 — 2 F_3	49	43.63 ± .28	3.73 ± .20	8.55 ± .45	81
(321 × 328 — 1) 1 — 3 F_3	51	45.34 ± .32	4.80 ± .22	10.59 ± .50	105
(321 × 328 — 1) 1 — 4 F_3	49	44.52 ± .32	3.85 ± .22	8.65 ± .50	67

Again the coefficients of variability of the four F_3 families grown are below that of the F_2 generation. Considering them together with the other later generations previously reported it would seem as if the case for Mendelian inheritance were pretty clearly proven.

CONCLUSION

A fertile cross between two distinct species, *Nicotiana Langsdorffii* and *Nicotiana alata grandiflora,* each uniform in its characters, has been reported here with the following results, no matter which way the cross was made.

1. The F_1 populations are as uniform as the parents.
2. The F_2 generations are nearly three times as variable as the F_1 generations.
3. Individuals reproducing the smaller species were found in the F_2 generation.
4. Certain of these F_2 individuals reproduced *N. Langsdorffii* populations in the F_3 generation.
5. No F_2 individuals reproducing *N. alata grandiflora* were found, but F_3 plants approaching such a type were produced.
6. Galtonian regression occurred, but selected extremes regressed no more than those deviating moderately from the parental mean.
7. Individuals from the same point on the F_2 curve showed different variabilities in F_3.
8. The variabilities of F_3 families were invariably smaller than those of F_2 families.
9. The above conclusions are based upon corolla length measurements but apparently are true for other characters, except that in other characters, *N. alata grandiflora* types were reproduced.
10. Mendelian inheritance of corolla color and pollen color is shown.
11. Mendelian inheritance seems to be the *only* logical interpretation of the other phenomena.

LITERATURE CITED

COMES, O., 1899 Monographie du genre Nicotiana. Naples: Typographie Coöpérative.

DORSEY, M. J., 1915 Pollen sterility in grapes. Jour. Heredity **6**: 243-249.

EAST, E. M., 1916 a Significant accuracy in recording genetic data. Amer. Jour. Bot. **5**: 211-222.

1916 b Studies on size inheritance in Nicotiana. Genetics **1**: 164-176.

EAST, E. M., and HAYES, H. K., 1912 Heterozygosis in evolution and in plant breeding. U. S. D. A. Bur. Plant Ind. Bull. 243, pp. 58.

FOCKE, W. O., 1881 Die Pflanzenmischlinge. 569 pp. Berlin: Borntraeger.

GODRON, D. A., 1863 Des hybrides végétaux considérés au point de vue de leur fécondité et de la perpétuité ou non-perpétuité de leurs caractères. Ann. sci. nat., Bot. Ser. IV, **19**: 135-179.

GOODSPEED, T. H., 1913 On the partial sterility of Nicotiana hybrids made with *N. sylvestris* as a parent. Univ. Cal. Pub. Bot. **5**: 189-198.

LOCK, R. H., 1909 A preliminary survey of species crosses in the genus Nicotiana from the Mendelian standpoint. Ann. Roy. Bot. Gar. Peradeniya **4**: 195-227. Pl. 18-29.

NAUDIN, Ch., 1865 Nouvelles recherches sur l'hybridité dans les végétaux. Nouv. Arch. Mus. Paris **1**: 25-176. Pl. 9.

Hidden Feeblemindedness

E. M. EAST

Reprinted, without change of paging, from the Journal of Heredity (Organ of the American Genetic Association), Vol. VIII, No. 5, Washington, D. C. May, 1917.

HIDDEN FEEBLEMINDEDNESS

One Person in Fourteen of the American Population Probably Carries the Trait in a Recessive Form, Although Normal to all Appearances—One-Fourth of Offspring will be Feebleminded if Mating is Made with Another Carrier

E. M. East
Bussey Institution, Forest Hills, Mass.

THE increase in the number of feebleminded in the United States during the past few years has been such that the heredity of the trait, and the classification and treatment of those so afflicted, have been the subject of much careful study. The result of this activity has been very creditable. Thanks to the researches of Goddard, the method of inheritance of feeblemindedness is as clear as that of any other heritable variation in the human race. Owing to the ingenious psychological methods of Binet and Simon, the grade of mentality can be determined reasonably well. Even our slowly moving legislative bodies have been somewhat disturbed by the facts and have passed a considerable number of laws designed to cut off this defective germplasm, either through segregation of the sexes during the reproductive period or by sterilization.

One can have only words of commendation for the serious efforts to face the problem; nevertheless, in the numerous papers on feeblemindedness that have been published during the last decade, not a single author appears to have appreciated the real menace. Our modern Red Cross Knights have glimpsed but the face of the dragon.

Goddard has shown that feeblemindedness is transmitted as a Mendelian recessive. In other words feebleminded individuals may be produced in three ways. If feebleminded mates with feebleminded all of the offspring will be feebleminded. If a feebleminded individual mates with one carrying the trait in his or her germcells, on the average one-half of the offspring will be feebleminded. It is these two types that segregation or sterilization will affect. But these are not the only sources of feeblemindedness, and perhaps they are not the most dangerous. If two carriers of feeblemindedness mate, one-quarter of their offspring will exhibit the trait and one-half of them will transmit it. Let us endeavor to see what this means.

THE NUMBER AFFECTED

It appears that in our present population of 100,000,000 or thereabouts, there are 300,000 persons who are feebleminded through an hereditary defect, a ratio of 3 per 1,000. This is an estimate to be sure, but it is so conservative that it probably veils the true state of affairs.

Now how many of these defectives have been the result of a mating wherein at least one of the parents was feebleminded? This question is a difficult one and can only be answered with a rough approximation. The best estimate that I can make from a careful examination of the meagre statistics at present available is 100,000. The dose must not be too bitter, however, so let us double this estimate. This leaves 100,000 feebleminded persons that must have been produced by the mating of two transmitters of feeblemindedness who did not show defective mentality themselves, unless an unprecedented percentage of origin *de novo* be assumed.

These 100,000 defectives were produced during a period in which there were rather less than 20,000,000 married couples of reproductive age. They were produced by parents both of which carried feeblemindedness. But only one-fourth of the progeny of such matings show feeblemindedness. Therefore, at least 100,000 couples of this type were reproducing during this generation. This would presuppose the survival of four children per couple long enough to have their mental status determined, an assumption that would probably require a total reproductivity of seven children per married pair. Among the children from these matings would be some 200,000 carriers of defective germ-cells, but we will omit them from our considerations. The important point is that out of 20,000,000 pairs of married persons, if we treat the problem as static, 100,000 were transmitting feeblemindedness. What then is the number of such persons in the population?

Let us state the question in another way. A certain number of persons out of a population of 40,000,000 of a marriageable age have defective germ-cells. If two of them marry, one-quarter of their children will be feebleminded. If 100,000 of such marriages did occur, what is the ratio of carriers of feeblemindedness to normals in the general population? The correct answer will depend of course upon how much selective mating takes place. There is unquestionably a general tendency for carriers of feeblemindedness to be brought together and a marriage to result. But this cannot be taken into account very accurately and had best be left out of our calculations.

Pairing among carriers of feeblemindedness has occurred in the ratio of 1 to 200 marriages; then, if no selective mating has taken place, carriers of feeblemindedness must occur in the general population in the ratio of 1 to 14.

One-fourteenth is approximately the square root of 1/200. If 1/14 of the population carry feeblemindedness and 13/14 are normal, then the probability of normal mating with normal is $13/14 \times 13/14 = 169/196$, the probability of normal mating with carriers of feeblemindedness is $1/14 \times 13/14 + 13/14 \times 1/14 = 26/196$, and the probability of two carriers of feeblemindedness mating is $1/14 \times 1/14 = 1/196$.

Possibly this figure is somewhat too high for the single trait feeblemindedness. We have not corrected for changes in the population during the length of the period considered or for selective mating. But, to balance this we have used a low estimate of the number of feebleminded, a high estimate of the number of defectives produced by parents of which at least one exhibited defects, and a high birth-rate in families of those transmitting the defect. Further, no mention has been made of epilepsy and of certain types of insanity, which are inherited in the same way, and to which the same line of reasoning applies. In view of these facts it is probable that the conclusion that 1 person out of every 14 carries the basis of serious mental defectiveness in one-half of his or her reproductive cells understates rather than overstates the facts.

The problem of cutting off defective germ-plasm, therefore, is not the comparatively simple one of preventing the multiplication of those so affected. This task, though sufficiently difficult in practice, is possible: the way has been pointed out; something has been accomplished. It is rather the almost hopeless task of reducing the birth-rate among transmitters of serious defects.

NEED FOR RESEARCH

A stupendous task necessitates prodigious efforts. Already there is a tremendous selective birth-rate in favor of lesser civic worth, and it is extremely doubtful whether, under our present economic system, much can be accomplished by recommending early marriages and large families among those whose accomplishments have proved their social value. Whether family limitation among those carrying defective germ-plasms can be effected must be decided in the future. It will be a distant future if a stupid government persists in refusing to countenance rational parenthood among those least fitted to reproduce the race, the while shutting one eye and winking the other at what has become a national practice among those best fitted to build a greater America. There is one suggestion, however, at which no one will cavil. We have assumed that a normal mentality is completely dominant over a defective one. Is this true? Complete dominance is rare among those characters commonly studied by animal and plant geneticists. Is it not likely that the Binet-Simon or other proper tests would show that carriers of mental defects exhibit a lower mentality than pure normals? Would it not be wise to start some investigations along this line?

The Explanation of Self-sterility

E. M. EAST

Reprinted, without change of paging, from the Journal of Heredity (Organ of the American Genetic Association), Vol. VIII, No. 8, Washington, D. C., August, 1917.

THE EXPLANATION OF SELF-STERILITY

E. M. EAST, *Bussey Institution, Forest Hills, Mass.*

IN a recent paper by C. W. Moore[1] on the subject of self-sterility, several ill-advised statements were made to which attention should be called.

The paper begins with the sentence:

> Several who have made a study of the problem of the inheritance of self-sterility of plants have obtained results which did not point to any one definite manner in which flowers act when self-pollinated.

One might read into the meaning of this statement either that there was great difference of opinion regarding the behavior of self-sterile plants or that little was known regarding self-sterility before the appearance of the paper under discussion. As a matter of fact a great many details regarding self-sterile plants are known. Darwin dealt with the matter at some length, and more recently extended researches by Jost, Correns, Compton and Stout have appeared. The present writer has also investigated the subject rather minutely although only preliminary reports of the work have been published. As to the gross facts, there is not a great difference of opinion among the later writers. Each has found that pollen grains germinate after self-pollination as readily as they do after cross-pollination, but that they grow more slowly, and the present writer has determined that the growth curves of self-pollen tubes are approximately straight lines, while growth curves of cross-pollen tubes are similar to those of autocatalytic reactions. Each has found that there is cross-sterility of the same nature as self-sterility. In other words, the plants of a self-sterile race are not only self-incompatible, but some combinations are cross-incompatible. The differences of opinion come in interpretation of these results, and these differences are due largely, we believe, to the fragmentary character of the evidence.

Moore founds an hypothesis by which to explain self-sterility on the supposed fact that self-tubes are greater in diameter than cross-tubes. In fact this seems to be the main thesis of his paper. He says:

> . . . the greater width of the self-pollinated pollen tubes of Tradescantia is due to the fact that the food supply is more favorable to the nourishment of a self-pollen tube than it is to a cross-pollen tube. On account of the abundant food supply the pollen tubes did not lengthen, but grew wider since they were in a very favorable medium. By this hypothesis it is possible to explain most of the data here presented. . . .

What Moore did was to measure *short* self-pollen tubes and *long* cross-pollen tubes as he distinctly states on page 204. Now if he had measured self-pollen tubes and cross-pollen tubes of the same length, as he should have done, it is almost certain that he would have found them to be of the same width. At least this is the observation of the writer on numerous pistils of three different self-sterile species of Nicotiana. Moore's main thesis, therefore, seems to be based upon an improper observation.

The second point made in the paper, involving a criticism of the present writer, is similarly without foundation He says:

> He [East] states that "all gametes having in their hereditary constitution something different from that of the cells of the mother plant, however, can provoke the proper secretion to stimulate the pollen tube growth, reach the ovary before the flower wilts, and produce seeds." From this it may be inferred that there may be an enzyme in the pollen grain that in a cross-pollination is able to induce the stigma to excrete a stimulating substance so that the pollen tube is able to grow. In a self-pollination this enzyme is not able to act. However, if this were the case, when a few cross-pollen grains were placed on a self-pollinated stigma, they would be expected to germinate and cause the stigma to produce the stimulating substance. Thus the pollen tubes from the self-pollination would also benefit by the stimulating influence and should be

---

[1] JOURNAL OF HEREDITY, viii, 203–207, 1917.

[Reprinted from THE AMERICAN NATURALIST, Vol. LI., March, 1917.]

THE BEARING OF SOME GENERAL BIOLOGICAL FACTS ON BUD-VARIATION[1]

PROFESSOR E. M. EAST
BUSSEY INSTITUTION, HARVARD UNIVERSITY

I TAKE it no one denies that in the Angiosperms variations may be produced in connection with reproduction by means of buds and that these variations may be perpetuated by the same method. Practically, as horticulturists and plant breeders, we care little about the occurrence of bud-variations elsewhere in the organic world. Nevertheless, it may help in the orientation of our ideas if we remember that budding is not a rare or unconventional method of reproduction. In a generalized form, the earliest method, it has persisted throughout the plant kingdom from the most primitive to the highest and most specialized types. Sexual reproduction has not replaced it, but has been added to it. Even in the animal kingdom, though eliminated among the higher forms, it still exists as an occasional alternate method in three fourths of the phyla. Such being the case, it would seem logically to follow that variation must have been within its possibilities.

The cause, the frequency, the type, the constancy, the mechanism, of these variations are more debatable, however, and on these questions many biological facts which superficially seem unconnected, have a direct bearing. In

---

[1] Read before the meeting of the Society for Horticultural Science, December 28, 1916.

fact, on certain phases circumstantial evidence is the only evidence at hand.

The exact nature of the cause or causes of bud-variation can hardly be discussed profitably. We may imagine irregularities of cell division directed by combinations of unknown factors, but to describe these factors in concrete terms is at present impossible. At the same time, cause can not be neglected entirely even at present, for cause in a generalized sense is intimately connected with frequency in that vigorous perennial the question of the inheritance of acquired characters. The data on this subject are so voluminous that each for himself must give them careful conscientious consideration. Here no more can be done than to point out some of the conclusions to which I, personally, have been driven, and their connection with the subject in hand. These conclusions are:

1. Broad and varied circumstantial evidence indicates unmistakably that the inheritance of acquired characters has played an extremely important rôle in evolution.

2. Numerous experimental investigations designed to test the possibility of such inheritance directly have either failed utterly or have been open to serious destructive criticism. Direct proof of the inheritance of acquired characters is therefore lacking.

3. If conclusions 1 and 2 are to be harmonized, either modifications are fully inherited so rarely that proof that they do not belong to the general category of chance changes in constitution of the germ-plasm is impossible, or the imprint of the environment is so weak that extremely long periods of time—perhaps geological epochs—are necessary for its manifestation.

Diametrically opposed views on the inheritance of acquired characters are held tenaciously and unequivocally by equally eminent biologists. Those who concur with the Lamarckian position are nearly always the students of evolution who approach the subject from the historical or the philosophical side and who rely almost entirely on circumstantial evidence; those who adhere to the side of Weismann are usually experimentalists whose evidence is indeed direct, but often questionable, usually capable of various interpretations, and always fragmentary. I have been bold enough to grasp both horns of the dilemma, and to plead that each is right from his point of view. My confession of faith is, the environment has been an immense factor in organic evolution, but its effects are shown either so infrequently or after the elapse of so great a time, that for the practical purposes of plant breeding we can neglect it as we would neglect an infinitesimal in a calculation. As Bergson, I think, said:

> We have been trying to prove that the hour hand moves, in a second of time.

A few words will make clear the general arguments in favor of this position, although adequate support to the thesis would require considerable time.

In the first place, it seems to me the possibility of the inheritance of acquirements must be admitted. Weismann's general contention that the chromatin of the germ-cells is the actual hereditary substance, and that the germ-cells themselves may be regarded as one-celled organisms reproducing by fission and conjugating at certain times, while the body must be considered simply an appendage thrown off from and independent of the germ-cells, is not supported merely by the embryological researches of Boveri, Kahle and Hegner on two or three animal forms, or by the ingenious ovarian transplantations made by Castle and Phillips on guinea pigs, but by all of the recent pedigree culture and cytological genetic work, botanical as well as zoological. Nevertheless it has not been and logically can not be proven that there is no way for environmental forces to produce germ-plasmic changes. Memory is just as strange a phenomenon and Semon has done biology a service by pointing out the analogy between the mechanical requirements for memory and for the inheritance of somatic modifications.

This possibility being admitted, one may well concede the plausibility of the arguments of the numerous paleontologists, taxonomists and ecologists in favor of Lamarckian principles, in spite of the fact that their evidence is circumstantial. They take a comprehensive view of the actual conditions that exist among organisms, which is impossible to the experimentalist. It will not do simply to say that the manifest convergence of analogous organs in all parts of the organic world, or the wonderful adaptations of the social insects *may be explained in some other way.* Of course there may be other explanations for these phenomena; but until more satisfactory explanations are forthcoming it is rightfully a custom in science that the adequate interpretation at hand should be accepted.

On the other hand it is equally wrong for the ardent devotees of Lamarckism to clutch at every isolated case, every inadequate and abortive experiment, when judicial consideration shows not a single *unassailable* instance of the inheritance of a somatic modification. Many of these experiments have a direct bearing on bud-variation, and I shall attempt to show where they lead us.

1. *Inheritance of Mutilations.*—The most radical Lamarckians of the present day only go so far as to suppose that mutilations are inherited on very rare occasions—and they are always zoologists. Ethnology has furnished us with so many histories of mutilations of ears, of lips, of feet, of reproductive organs, long continued in the folkways of a people, that new laboratory experiments have been deserving of the ridicule they have received. Botanists have seldom had any delusions on the subject. Plants are so continually mutilated in the buffetings they receive during life, with no result in the next generation, that the non-inheritance of the effects of such injuries is taken as a matter of course. Yet there is occasionally one whose reason fails at the critical moment, and who holds that cuttings from the chrysanthemum with the large flower resulting from the removal of lateral branches, will produce larger flowers in the next generation than will an untreated sister plant. If not this, some equally indefensible doctrine.

2. *Effects of Changed Food Supply.*—This last example was really one of changed food supply induced by mutilation. Change of food supply by other methods has been the basis of scores of experiments, particularly on insects. Many insects are so very whimsical about what they eat that it seems possible their selective appetite may be an inherited instinct impressed by the environment of countless generations. But the total result of all experiments on them is merely to prove that a second generation may be influenced in the start they get in life by the nutrition of the mother.

The same thing is true in plants. We fertilize a pop corn to get a bumper crop of good plump healthy seeds, but we don't expect a dent corn as the next year's result. We very properly endeavor to give our potatoes a balanced ration, in expectancy of a larger yield of well-matured, healthy tubers, but we should not expect these tubers to affect our next season's supply other than by their health. Similarly we take scions from well-lighted parts of the tree where growth has been good. In such twigs the graft union heals easily and properly, and a fit channel for conveying nutrients is established. In doing these things we are practising sanitation or preventive medicine, as it were, a laudable proceeding. But the horticulturist who promises a *different variety* by such means is illogical and misleading.

Yet we find Bailey so imbued with the idea of making out a perfect case for Lamarckism that he lends the weight of his authority to the following statement among others:[2]

> Whilst these ''sports'' are well known to horticulturists they are generally considered to be rare, but nothing can be farther from the truth. As a matter of fact, every branch of a tree is different from every other branch, and when the difference is sufficient to attract attention, or to have commercial value, it is propagated and called a ''sport.''

We may admit the differences between the branches of a tree without cavil. What is more serious is the impli-

---

[2] ''Survival of the Unlike,'' p. 72.

cation to the reader that all variations have the same coefficients of heredity, that a bud-variation is simply a wide fluctuation imposed by external conditions. If this were true the whole organic world would be chaos. But species and varieties do exist. They may be "judgments" in one sense, but in another they are concrete things. In fact we learn this further on in this volume when it suits Bailey's purpose to have asexually propagated varieties very constant. He says (p. 353):

> At first thought this fact—that varieties may be self-sterile—looks strange, but it is after all what we should expect, because any variety of tree fruits, being propagated by buds, is really but a multiplication of one original plant, and all the trees which spring from this original are expected to reproduce its characters.

3. *The Effects of Disease.*—The influence of disease is in many ways like that of malnutrition, in that it is wholly an effect on the physiological efficiency of the reproducing cells. This fact is fairly clear when dealing with diseases with outstanding symptoms. In many instances, however, diseases are not easily diagnosed. There may even be no suspicion that disease is present. In such cases it is rather hard to believe that selection is not accomplishing a positive and radical improvement. A good example of this is the selection of potato tubers. No one consciously selects a seed potato infected with blight. Independent of the probability of reinfection, there is the likelihood that the diseased tuber will not be able to produce a normal plant because of the effect the fungus has had on its own cells. One doesn't usually believe, however, that rejection of this tuber and selection of the healthy sister is going to lead to the formation of a new race. Yet numerous experiments on potatoes in which it is shown that successive selections have raised the average yield over that of the unselected tubers, are probably of just this type. The race is kept up by the rejection of diseased tubers, but there is no evidence whatever that it is *improved.* I am not going to argue that desirable asexual variations may not occur during this time, and be retained. I say only that any improvement

indicated by the raw data must be discounted by the amount of deterioration shown by the unselected variety under similar conditions. Such deterioration is very common, and is due to disease, I believe, rather than to any supposed disadvantage of asexual reproduction *per se*.

This category of facts has been cited under the discussion of the inheritance of acquired characters, because such phenomena have perplexed other than botanists. Belief in the transmission of disease, or the effects of disease, by sexual reproduction was current for many years. It is only since the possibility of infection in the egg itself was demonstrated for various diseases, that the true state of affairs has been known.

Many other types of experiments designed to demonstrate Lamarckism might be cited, but they have no direct bearing on bud-variation except in so far as a positive case would affect our general attitude on the frequency of their occurrence. They are all similarly negative or questionable, however, so that we must conclude with Weismann that no case of inheritance of acquirements has been proved beyond a reasonable doubt. In other words we grant such a possibility but believe it to be so rare or so gradual that practically it may be disregarded.

In reality one could hardly have expected any other conclusion from the type of experiment by which the question has been attacked. Generalized they are something like this. Species X having been grown under environment A for numerous generations is removed to environment B. An adaptive change occurs which persists during several generations. Later the descendants of the original plants are returned to environment A and the change is reversed. When the reverse change occurs more slowly than the original change, it is argued that Lamarckian inheritance is shown. The logic used to draw such a conclusion is indefensible, even if the difficulty of correcting properly for changes due to normal heredity is left out of consideration.

If acquired characters are inherited and the changes induced are reversible, the long period under environment *A* should have produced a deep impression on species *X*. Change under environment *B* should be slow. Reversal should be rapid, however, because of the slight impression environment *B* must be supposed to have made during the very few generations in which its influence was possible.

If acquired characters *are not inherited,* precisely the same changes should occur, owing to somatic adaptation, the only differences being that the total amount of change in each case would be reached in the second generation after the environment had acted during the earliest stages of the life history.

If, on the other hand, the changes induced by environment *B* are not reversible, judgment must be based on the percentage of individuals changed by *B* and not rechanged by *A*. One can readily see how a just judgment would be clouded by probable reversible somatic effects in such cases. Instances of the inheritance of acquirements, unless they were very frequent, which from our general evidence is unthinkable, would be indistinguishable from ordinary chance variations.

Such methods of attack on the subject being almost predestined to failure from the inherent difficulties of the problem, it would seem wiser to seek for a more hopeful methodology, and in the meantime to accept the only conclusion justified by the data at hand; namely, the inheritance of acquired characters is either so rare an occurrence or so slow a process, that by plant-breeders it may be assumed to be non-existent. One realizes of course that the problem of sexual transmission of somatic acquirements is not necessarily the same as that of asexual transmission, but the experimental results have been the same in both cases. Let us, admit, therefore, that one can not hope to obtain real improvement in asexually propagated varieties merely by selecting buds from plants or parts of plants which have developed under especially favorable conditions.

This does not mean that radical environmental changes may not be the direct cause of such a modification. Dr. H. J. Webber once informed the writer that immediately after the great Florida freeze of the early nineties bud-variations in the citrus fruits of that region were greatly increased. Such variations may have been induced by the freezing, but they were not adaptive variations.

The conclusions reached thus far have not involved a point of theory which practically is difficult to separate from the one just discussed. It is this. If we disregard adaptive variations, is there not still a reason for selecting fluctuations? Are there not internal factors which so act that there is a narrow but appreciable variability in an asexually produced population which may offer a basis for selection? In other words, how constant is an asexually propagated race?

We can make an effort to compute the frequency of marked bud-variations. But have we any right to assume that these represent the sum total of all bud-variations? Are not bud-variations and perhaps all inherited variations like residual errors, the small ones frequent, the large ones rare? This may be the case, but I should like to emphasize the fact that we have no true criterion for determining the size of a variation. A variation that appears large by visual criteria may be an extremely small change in the constitution of the plant, and *vice versa.* In view of this fact together with the practical consideration that commercially valuable variations must be measurable within a reasonable duration of time—say a lifetime—it is by no means certain that we are going far astray in calculating the frequency of bud-variations by the so-called marked jumps or mutations.

Furthermore the range of the fluctuations of asexually propagated varieties of most species is very small even when broadened—as it always is—by the addition of the effects of variable external conditions. It is not hard to recognize a Winesap apple, a Clapp's Favorite pear or a Concord grape, even though these varieties have been grown extensively for a considerable number of years. Certain local subvarieties of the pome fruits are said to exist, but they are so extremely rare that one may admit all cases of disputed origin and still have very little asexual variation to account for.

I have never seen a published calculation of the frequency of bud-variation, and presume it would be of little value anyway, since the general evidence indicates a different frequency for different species and even for the same species at different times. It may be mentioned, however, that in personal examination of over 100,000 hills of potatoes belonging to several hundred varieties, 12 definite bud-variations have been seen, a frequency of 1 in 10,000; while just as careful a scrutiny of about 200,000 plants belonging to the genus *Nicotiana* has brought to light but 1 case.

Probably a more practical and just as satisfactory an estimate of the frequency of bud-variations in economic plants is the record of varieties that have been produced in this manner. Naturally such a record contributes little to theory because only a portion of the variations arising are observed, and only a fraction of those observed are propagated. Further, the origin of comparatively few commercial varieties is known. Yet we may get some idea of what to expect in the future, by noting what has occurred in the past.

Data gathered in this manner will appear to give us different values depending on how we approach the matter. For example, in Cramer's wonderful monograph on bud-variation, the grape is cited as one of the species that often varies in this manner. He cites some 25 or more such varieties. Yet in the large list of American grapes in Hedrick's ''Grapes of New York'' only one doubtful case of bud-origin is reported. When one remembers that hundreds of varieties of grapes are grown and millions of vines are examined each year, improvement by this method seems rather hopeless. And examination of the list of present-day apples, pears, plums and cherries, of the bush-fruits, or of potatoes—all groups of considerable horticultural importance—is still more disappointing, for I venture to say that the varieties of these types in cultivation which have originated as bud-variations can be counted on the fingers of one hand.

At the same time it would be wrong not to attribute any importance to bud-variation as a plant breeding adjunct. Cramer lists several hundred chrysanthemums and over a hundred roses as of bud-origin, as well as a smaller number of varieties in species where bud-variation appears to be less prevalent. Further, Shamel is said to have found bud-variation in the citrus-fruits to be sufficiently common to be worthy of an extended investigation.

These species, however, with perhaps the banana and the pineapple—the origin of whose varieties is little known—are the outstanding examples of comparatively frequent bud-variation, picked from our whole long list of cultivated plants. The first two examples, moreover, are species belonging to the domain of floriculture, where rather superficial characters such as color are valuable. In very few other species have bud-variations been recorded in sufficient numbers to justify us in employing any other adjective than "rare" in describing them. And of the sum total of these varieties only an extremely small percentage are of such a nature that agriculture would suffer a material loss if they were eliminated.

Perhaps these last statements appear to imply a very limited type of bud-variations. This is not true. Bud-variations are wholly comparable to seed-variations in their nature, but they are handicapped because recombinations of variant characters are possible only in sexual reproduction. N bud-variations in a species are simply N variations, but N seed-variations may become 2^n seed-variations provided they are not linked together in heredity. An immense advantage thus accrues in favor of seminal reproduction because by far the greater number of commercially valuable characters are complex in their heredity, *i. e.,* they are represented in the germ-plasm by several factors independently inherited.

Cramer divides bud-variations into the same classes that de Vries has used for sexual mutations: progressive, where new characters arise; retrogressive, where a character becomes latent or lost; and degressive, where latent characters become active. In this important monograph practically all recorded bud-variations to the date of publication, 1907, are discussed. Yet not a single case of *progressive* variation is listed. They are all catalogued as retrogressive or degressive. Their classification is correct, however, only when a progressive variation is defined as the addition of a character wholly unknown in the previous history of the species.

As examples of what bud-variation does produce we may well study Cramer's painstaking work. There are losses of thorns, hairs and other epidermal characters, together with an occasional degressive change of the same kind. There are changes in color in vegetative parts. Green becomes red or "aurea" yellow, or a loss of anthocyan occurs. Sometimes the changes are such that the plants remain striped or otherwise variegated. Flowers and fruits exhibit the same types of color variations in considerable numbers. They are mostly losses, with the appearance of what in Mendelian terminology is called hypostatic colors, but once in a great while epistatic colors recur anew.

Monstrosities appear. Other parts of the flower take on the appearance and form of petals or of sepals. Doubling occurs in several different ways. Fasciations arise. Changes in the character of the reproductive apparatus are not uncommon, sometimes giving us seedless fruits.

Plants change their habit of growth. They become dwarf. They retain juvenile characters. They become laciniate, or develop the trait known as "weeping."

Thus we see that bud-variation is not limited in its manifestations; and what is more important, we realize that bud-variations are very comparable to seminal variations, there being hardly a type of change known in sexually reproduced plants that has not been duplicated asexually. What then is the difference, if any, between true somatic changes and true germinal changes in constitution? We can get clues which indicate a fairly satisfactory solution of this problem from three different lines of research, pedigree cultures, graft-hybrids and cell-studies.

It is a noteworthy fact that the character of the progeny produced sexually by bud-variations has been studied in a comparatively few cases, and in most of these instances self-pollinations were not made. Nevertheless Cramer believes the following conclusions are justified:

1. In a vegetative Mendelization, of the progeny of a branch with the positive character 75 per cent. have the character and 25 per cent. are without it, while the progeny of a branch without the character all lack it.

2. In a vegetative "Zwischenrasse" by which he generally means a variegated race, of the progeny of each type (original and variant), a part retain and a part lack the character, the percentage being variable.

3. In a vegetative mutation, by which he means any change not a "Zwischenrasse" and which did not appear to him to be Mendelian in type, of the progeny of a branch retaining the positive character, either all possessed it or a part were with and a part without it, while the progeny of a branch without the character were all of the same type.

If we allow for some deviation due to cross-pollination, I believe that Cramer's records support this view, and that modern genetic research suggests the interpretation.

In the first place, the "Zwischenrasse" are evidently of the type studied principally by Correns and by Baur in sexually reproducing races. They are due to chromatophore changes, and in many cases at least are not the result of nuclear activity. This being true, one would expect in neither asexual nor sexual reproduction the same type of inheritance for variegated races that obtains for other types of variation. Inheritance will parallel cytoplasmic rather than nuclear distribution; an expectation apparently realized for both types of reproduction.

Omitting the "Zwischenrassen"' therefore, we have two phenomena to explain, both of which are similar to cases of inheritance in sexual reproduction where chromatin distribution parallels the facts. In each instance the negative variant—may we call it the recessive—breeds true. In one case the positive variant breeds true, in the other case it gives a simple Mendelian ratio.

The mechanism necessary for such phenomena is not difficult to picture. Bud-variations are many times more frequent in hybrids, that is, in plants heterozygous for one or more characters, than they are in *pure* species. This is the view of Cramer, this was the view of Masters, the eminent English student of bud-variations and teratological phenomena, this was the conclusion drawn by the present writer in several articles published some years ago. Such results would be obtained either when the proper germinal change occurs in the chromosome whose mate lacks a character for which the plant is heterozygous; or, when there is a dichotomy in which the chromosomes of such a pair are not halved but pass the material basis necessary for the production of the positive character to one daughter cell and not to the other, provided the daughter cell lacking the character gives rise to a branch.

A bud-variation in a character for which the plant was homozygous would be obtained only when simultaneous like changes occur in both chromosomes of a homologous pair, or when the material basis necessary for the production of the positive character all passes to one daughter cell, as described above.

This hypothesis would account for the fact that heterozygotes give rise to bud-variations more frequently than homozygotes, since a germinal change seldom gives rise to a new positive character, and a change in one chromosome of an identical pair tending toward the production of a recessive, would not show in the latter case.

I am not certain that this hypothesis may not with reason be applied to variations that are usually considered seminal. There is no particular ground for assuming that such variations occur only at the maturation of the germ-cells. We know that progressive variations of whatever origin are extremely rare. Why then may not most variations be produced in cell divisions previous to the formation of the germ-cells? When recessive we should not note them as bud-variations unless the plant is heterozygous and the mutating cell gives rise to a branch; when dominant we should only note them in the latter eventuality. But if these mutating cells should later give rise to germ-cells, the change would become apparent in the progeny.

We have still one other hypothetical case to consider. It is said that some bud-variations are not transmitted by seed. I have not been able to trace an authentic case, but such is the general belief, fathered, I think, by Darwin. The usual citation is the nectarine, which sometimes is said to give nectarines but at other times gives only peaches. Whether trichome characters only behave thus I do not know. But if that be true, we can understand why if we refer to Winkler's work on the so-called graft-hybrids.

Winkler found that the most interesting of these peculiar phenomena are caused by the tissue of one species growing around the tissue of the other. He therefore gave them the euphonious name of periclinal chimeras. Cytological examination showed that the epidermal tissues only are from one race, the remaining tissues being from the other. It is really a symbiosis and not a union. Now as the germ-cells are formed wholly from subepidermal and never from epidermal tissues, the seeds of these plants always produced seedlings like the type forming the *inner cell-layers.*

It seems probable that the production of the nectarine may be analogous. If the change producing the nectarine occurs after the epidermal tissue has been segregated from other tissues, the cells which are ancestors of the germ-cells should not be affected and the nectarine seedlings would give peaches. If, on the other hand, the change producing the nectarine, has occurred before any such segregation, the progeny sexually produced should in part be nectarines.

DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS

DONALD F. JONES

Connecticut Agricultural Experiment Station, New Haven, Connecticut

Reprinted from GENETICS **2:** 466-479

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS

DONALD F. JONES

Connecticut Agricultural Experiment Station, New Haven, Connecticut

DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS[1]

DONALD F. JONES
Connecticut Agricultural Experiment Station, New Haven, Connecticut

[Received March 1, 1917]

A stimulation resulting from hybridization in both plants and animals has long been recognized. The increased growth as the result of crossing is so common an occurrence that it is probably familiar to everyone who has made any hybridization experiments.

This stimulation, variously spoken of as "hybrid vigor," stimulus due to heterozygosis, heterosis, etc., was clearly established as an organic phenomenon by the abundant cases cited by early investigators such as KÖLREUTER (1766), GÄRTNER (1849), DARWIN (1877) and FOCKE (1881), as well as a large number of other investigators at that time and an increasingly large number since then. The important investigations in recent times (EAST 1908, 1909; SHULL 1908, 1909, 1910, 1911; EAST and HAYES 1912) are so familiar that it is not necessary to do more than mention them.

Concrete explanations as to the cause of these results have not accompanied the accumulation of facts. Various hypotheses have attempted to account for the results, but they have been little more than outlines of the problem.

The valuable contributions of EAST (1908, 1909) and of SHULL (1908, 1909, 1910, 1911) established the fact that continued inbreeding is not a process of continuous degeneration but that the reduction in the amount of growth is due to the isolation of unlike biotypes differing in the amount of growth attained at normal maturity. Together with this isolation of biotypes there was a loss of a stimulation which was assumed to be derived in some way from crossing. This decrease of vigor becomes less after continued inbreeding and to all appearances ceases as complete homozygosis is approached. This stimulation has been shown to be correlated more or less closely with the degree of heterozygosity. The whole subject has been ably presented and discussed by EAST and

---

[1] Contribution from the CONNECTICUT AGRICULTURAL EXPERIMENT STATION and from the Bussey Institution of HARVARD UNIVERSITY.

Hayes (1912). A quotation from this paper (pp. 36 and 37) presents the matter as it stands at present:

> "The hypotheses in regard to the way by which the act of fertilization initiates development are numerous, but since they are entirely speculative it is not necessary to discuss them here. The only conclusion that seems justified is that they are not immediately psychological or vitalistic in nature. Loeb's remarkable researches prove this. But whatever may be the explanation of the means by which the process is carried out, the statement can be made unreservedly that the heterozygous condition carries with it the function of increasing this stimulus to development. It may be mechanical, chemical, or electrical. One can say that greater developmental energy is evolved when the mate to an allelomorphic pair is lacking than when both are present in the zygote. In other words, developmental stimulus is less when like genes are received from both parents. But it is clearly recognized that this is a statement and not an explanation. The explanation is awaited."

Keeble and Pellew (1910) first suggested a concrete explanation to account for the results of this nature which they obtained with peas. Two varieties of garden peas, as grown by them, each averaged from 5 to 6 feet in height. The F_1 grown from this cross averaged from 7 to 8 feet in height, 2 feet taller than either parent. A result of this kind is comparable to heterosis. The F_2 was put into four classes: one class containing plants as tall as the F_1, two classes of semi-tall plants similar in height to the two parents, and one class of dwarfs shorter than either parent. The two classes of semi-tall plants, similar in height, were differentiated in the same manner as the two parents; one had thick stems and short internodes, the other had thin stems and long internodes. Other differences helped to distinguish the two classes of equal height. The number of plants falling into these four classes agreed closely with the expectation from a di-hybrid ratio where two factors showing dominance were concerned, giving a 9:3:3:1 ratio.

The writers assumed two factors to be concerned: one producing thick stems, the other long internodes. These factors they designated T and L. One of the parental varieties was medium in height because it possessed one of these factors, e.g., that for thick stems, but lacked the other. Such a plant had the formula $TTll$. The other variety was of medium height because it lacked this T factor but possessed the factor for long internodes, and was given the formula $ttLL$. Both of these factors showed dominance over the allelomorphic condition; hence the F_1 was taller than either parent because both factors were present together. Whether or not later investigations have justified the interpretation that Keeble and Pellew have placed on the data as explaining height of their peas makes no material difference to the discussion here. Taken as it stands, it is a beautiful illustration of the way in which dominance may increase a character in F_1 over the condition of either parent.

Curiously enough, this explanation has never been considered an adequate one or in any way essentially related to the universal phenomenon of heterosis. This hypothesis of dominance accounting for heterosis, as outlined by KEEBLE and PELLEW, has two objections which have up to the present been considered insurmountable.

The chief objection has been that, if heterosis were due to the dominance of a greater or less number of factors governing the amount of development, it would be possible in generations subsequent to the F_2 to recombine in one homozygous race all of the factors resulting in large growth and, conversely, the negative condition in another homozygous race. In other words, it would be possible to obtain one strain having all of the dominant factors, and another with all of these dominant factors lacking. Both of these races should be homozygous, hence self-fertilization should not result in less vigorous progeny. The completely recessive race should be below the parents in its power for development, as the F_1 and the complete dominant were above the parents. That all of these supposedly necessary corollaries are not supported by the facts is well known.

Both SHULL (1911) and EAST and HAYES (1912) have considered this objection to be valid. A quotation (p. 39) from the latter makes their position on this point clear.

> "KEEBLE and PELLEW (1910) have recently suggested that 'the greater height and vigor which the F_1 generation of hybrids commonly exhibit may be due to the meeting in the zygote of dominant growth factors of more than one allelomorphic pair, one (or more) provided by the gametes of one parent, the other (or others) by the gametes of the other parent.' We do not believe this theory is correct. The 'tallness' and 'dwarfness' in peas which KEEBLE was investigating is a phenomenon apparently quite different from the ordinary transmissible size differences among plant varieties. Dwarf varieties exist among many cultivated plants, and in many known cases dwarfness is recessive to tallness. It acts as a monohybrid or possibly a dihybrid in inheritance, and tallness is fully dominant. Varietal size differences generally show no dominance, however, and are caused by several factors. Transmissible size differences are undoubtedly caused by certain genetic combinations (EAST 1911), but this has nothing to do with the increase of vigor which we are discussing. The latter is too universal a phenomenon among crosses to have any such explanation. Furthermore, such interpretation would not fitly explain the fact that all maize varieties lose vigor when inbred."

Another objection to the hypothesis of dominance has been raised by

EMERSON and EAST (1913). In this publication it is said that, if the effect of heterosis were due to dominance, the distribution of the F_2 individuals would be unsymmetrical in respect to characters in which heterosis was shown in F_1. This follows from the familiar Mendelian expectations where there is dominance and any number of factors is concerned. For the purpose of illustrating this point let us take the case of height of peas already cited. In the F_2 population a distribution of the individuals in respect to height is, theoretically, 9 tall plants (with both factors present), 6 medium-tall plants (3 with one factor + 3 with the other), and one short plant (with both factors lacking).

Similar asymmetrical distributions in F_2 would occur with any number of factors (if there were no other facts to be taken into consideration), as seen from the figures given in table 1 modified somewhat from those given by BAUR (1911, p. 63).

In any case of a size character similar to height of peas with any number of factors, the plotting of the number of individuals in F_2 occurring in the classes given in row B in table 1 would give an asymmetrical distribution. This is on the assumption that the individual having the greatest number of dominant factors present (whether in the simplex or duplex state) would attain the greatest development of the size character.

In the vast amount of data accumulated upon the inheritance of quantitative characters no such tendencies toward an asymmetrical distribution is evident in the majority of cases recorded. In EMERSON and EAST's paper, referred to, dealing with quantitative characters in maize, and in HAYES's publication (1912) dealing with the same type of characters in tobacco, the distributions in F_2, where heterosis is shown in F_1, are all considered to be of the type of normal frequency distributions. If any skewness is shown by any of these it is too slight to suggest the types of curves obtained by plotting the figures in table 1, B.

It is perfectly evident that the two objections raised against the hypothesis of dominance as a means of accounting for heterosis, as outlined by KEEBLE and PELLEW, and as it has been considered up to the present, are valid. But both these objections to dominance as an interpretation of heterosis have failed to take into consideration the fact of linkage.

Abundant evidence is fast being accumulated[2] to show that characters are inherited in groups. The different theories accounting for this link-

---

[2] It is unnecessary to give references to the convincing results obtained by MORGAN, BATESON, and their collaborators, as well as to those obtained by many others whose work is of great importance if not so extensive.

TABLE 1

Distribution of F_2 individuals when each character shows complete dominance and each has a visible effect.

Number of factors in which the F_1 is heterozygous	Distribution of the individuals	Total number in the population
1	A 3 : 1	4
	B 3 : 1	
	C 1 : 0	
	D 1 : 1	
2	A 9 : 3 : 3 : 1	16
	B 9 : 6 : 1	
	C 2 : 1 : 0	
	D 1 : 2 : 1	
3	A 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1	64
	B 27 : 27 : 9 : 1	
	C 3 : 2 : 1 : 0	
	D 1 : 3 : 3 : 1	
4	A 81 : 27 : 27 : 27 : 27 : 9 : 9 : 9 : 9 : 9 : 9 : 3 : 3 : 3 : 3 : 1	256
	B 81 : 108 : 54 : 12 : 1	
	C 4 : 3 : 2 : 1 : 0	
	D 1 : 4 : 6 : 4 : 1	
n	A $3^n : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-1} : 3^{n-2} : 3^{n-2}$: etc. .... : 1	$(2^n)^2$
	B $1(3^n) : D(3^{n-1}) : D(3^{n-2})$: .... etc. .... : 1	
	C $n : n-1 : n-2$: .... etc. ... $n-n$	
	D 1 : ... etc. = coefficients of the expanded binomial $(a+a)^n$ .... : 1	

A, The distribution into the visibly different categories. B, The distribution into categories with different numbers of dominant factors present (either in a homozygous or heterozygous condition). C, The number of dominant factors in which the categories differ. D, The number of visibly different categories with the same number of dominant factors present.

age of characters make no essential difference in the use to which these facts will be put here. It is only necessary to accept as an established fact that characters are inherited in groups and that it is these groups of factors which Mendelize. The chromosome view of heredity, as developed by MORGAN and others (1915), will be used because it gives a means of representation in a simple, graphical manner.

The increasing complexity of Mendelism points very strongly to the probability that the important characters of an organism are determined by factors represented in all or most of the chromosomes or linkage groups. This idea has been proposed by EAST (1915) and seems to be in accord with the facts. If this view is approximately correct, and if it may also be assumed that, in addition to the factors which differentiate varieties, many different factors may bring about the same visible effect, then it is possible to meet the two objections raised against dominance as a means of accounting for heterosis.

As an illustration of what is meant by different factors bringing about the same visible effect, an example may be taken in which one variety of plants grows to an average height of six feet because of one set of factors, and another variety grows to approximately the same average height but attains this height through the operation of a different set of factors. This is comprehensible when it is remembered that height is only an expression of a plant's power to develop. Hereditary factors which affect any part of the plant may indirectly determine height. Direct proof as to the essential correctness of this assumption, i.e., of different factors producing the same somatic effect, is at hand in the cases of duplicate genes producing the same morphological result in *Avena sativa* (NILSSON-EHLE 1909) and *Bursa bursa-pastoris* (SHULL 1914), as well as the other cases of duplicate genes reported by NILSSON-EHLE (1908) and EAST (1910).

The widespread occurrence of abnormalities and other characters detrimental to the organism's best development is well known in both the plant and animal kingdoms. This is especially true in naturally cross-pollinated species of plants. It may be taken for granted that no one variety has all of these unfavorable characters nor, on the other hand, has it all the favorable characters. For the most part each variety possesses a random sample of the favorable and unfavorable characters. There are differences between varieties in their power for development, however, just as there are differences in superficial characters. Some varieties of plants grow taller than others; some grow faster; some produce more seed. But, on the average, most of the varieties of a species tend to grow to about the same extent, however much they may differ in superficial characters.

If, for the most part, these favorable characters are dominant over the unfavorable (if normalities are dominant over abnormalities) it is not necessary to assume complete dominance in order to have a reasonable explanation of the increased development in F_1 over the average of the parents or any subsequent generation. It is in F_1, and in F_1 only, that the maximum number of different factors can be accumulated in any one individual.

Because of linkage it is impossible to recombine in any one individual in later generations any greater number of characters in the homozygous condition than were present in the parents if the factors were distributed uniformly in all of the chromosome pairs. Possible exceptions to this statement will be discussed later. This view of the situation explains why the effects of heterozygosis result in a greater development in F_1 than in the parents, and not less. Why should crossing not have resulted in a depressing or indifferent effect instead of a stimulating one, according to previous views?[3] It also makes it seem probable that the effects of heterozygosis remain throughout the life of the sporophyte, even through innumerable asexual generations. Furthermore, it will be shown that no skewness in the distribution of F_2 is expected.

Let me submit in the form of a concrete illustration the abstract view that I have tried to present in the preceding paragraphs. A purely hypothetical case will be assumed, in which two homozygous varieties of plants, having three pairs of chromosomes, both attain approximately the same development as represented by any measurable character. This development will be considered to amount to 6 units, 2 of which are contributed by each chromosome pair. One of these varieties, which will be called "X," attains this development because of factors distributed in the three pairs of chromosomes. Any number of factors may be chosen, but, for the sake of simplicity, only three in each chromosome will be employed. These are numbered 1, 3, 5; 7, 9, 11; and 13, 15, 17; in the following diagram, each different in its contribution to the plant's development. The other variety, "Y", develops to an equal extent in the character measured, and this development will also be considered to amount to 6 units. It attains this same development, however, by a different set of factors distributed in the three chromosomes, numbered 2, 4, 6; 8, 10, 12; and 14, 16, 18. It is also assumed that these 6 factors are fully as effective in the $1n$ condition as in the $2n$ condition, i.e., show perfect dominance. It will be seen from the diagram that the F_1 develops to twice the extent of either parent, because there are present here 18 different factors (in the $1n$ condition), whereas the parents have only 9 (in the $2n$ condition). In the diagram, any other factorial complex common to both varieties is ignored. The development of the parents of 6 units and of the F_1 of 12 units is additional to that afforded by this common factorial complex.

Following this hypothetical case into the F_2 generation by selfing or

---

[3] Crosses between plants not closely related do result in no greater development than the parents and in many cases much less than the parents. This is because characters which are widely dissimilar are unfavorable to the organism's best development when acting together.

breeding together these F_1 plants, the theoretical results given in table 2 are obtained.

Summing up the results of this tabulation, it will be found that eight plants are homozygous and have the same development as either parent, i.e., of six units. Eight plants are heterozygous in all three chromosome pairs and have the same amount of growth as F_1, i.e., of twelve units. The remaining 48 plants fall into two equal-sized groups developing to eight and ten units respectively. In other words, the distribution is symmetrical, and this symmetry remains, however many chromosomes are concerned.

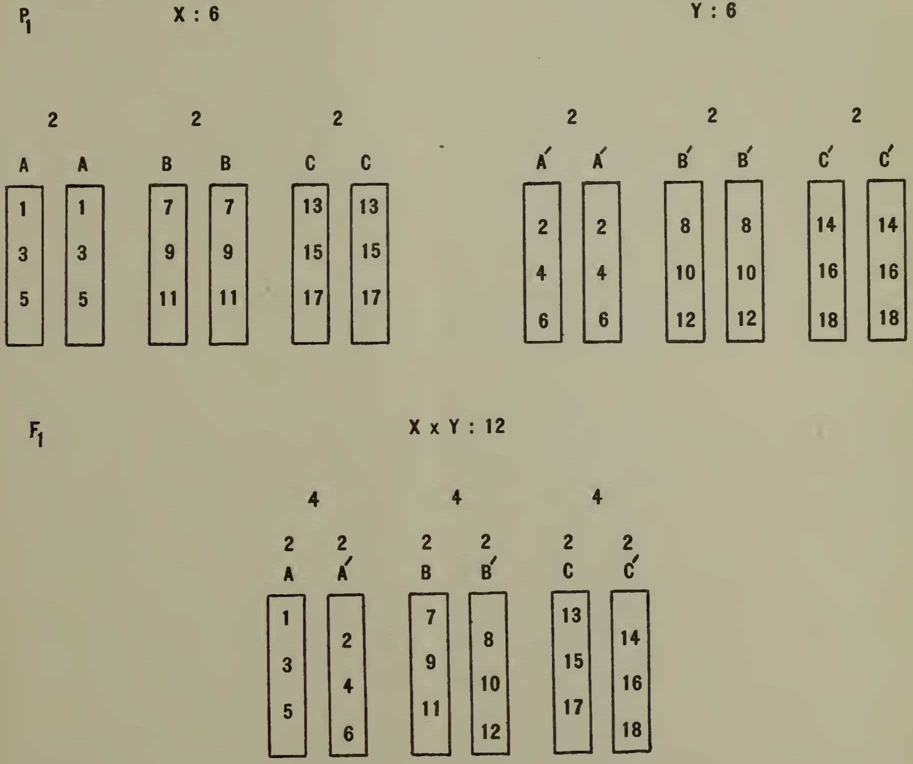


DIAGRAM 1.—To show how factors contributed by each parent may enable the first generation of a cross to obtain a greater development than either parent.

Furthermore, it should be noted that the mean development of F_2 is nine units, which is an excess above the parents of just half of the excess of the F_1 over the parents. In other words, the extra growth derived by crossing the two varieties has diminished 50 percent. In F_3 from a random sample of F_2, it can be shown that this excess again diminishes 50 percent, so that the effect is only 25 percent as great in F_3 as in F_1,

TABLE 2

Composition of a tri-hybrid in F_2 according to Mendelism, and the development which each individual attains depending upon the number of heterozygous chromosomes contained and thereby the total number of different factors present.

Number of individuals in each category	Categories	Contribution of each chromosome pair	Total development
1	A A B B C C	2 + 2 + 2	6
2	A A′ B B C C	4 + 2 + 2	8
2	A A B B′ C C	2 + 4 + 2	8
2	A A B B C C′	2 + 2 + 4	8
4	A A′ B B′ C C	4 + 4 + 2	10
4	A A B B′ C C′	2 + 4 + 4	10
4	A A′ B B C C′	4 + 2 + 4	10
8	A A′ B B′ C C′	4 + 4 + 4	12
1	A A B B C′C′	2 + 2 + 2	6
2	A A B B′ C′C′	2 + 4 + 2	8
2	A A′ B B C′C′	4 + 2 + 2	8
4	A A′ B B′ C′C′	4 + 4 + 2	10
1	A A B′B′ C C	2 + 2 + 2	6
2	A A B′B′ C C′	2 + 2 + 4	8
2	A A′ B′B′ C C	4 + 2 + 2	8
4	A A′ B′B′ C C′	4 + 2 + 4	10
1	A′A′ B B C C	2 + 2 + 2	6
2	A′A′ B B′ C C	2 + 4 + 2	8
2	A′A′ B B C C′	2 + 2 + 4	8
4	A′A′ B B′ C C′	2 + 4 + 4	10
1	A′A′ B′B′ C C	2 + 2 + 2	6
2	A′A′ B′B′ C C′	2 + 2 + 4	8
1	A′A′ B B C′C′	2 + 2 + 2	6
2	A′A′ B B′ C′C′	2 + 4 + 2	8
1	A A B′B′ C′C′	2 + 2 + 2	6
2	A A′ B′B′ C′C′	4 + 2 + 2	8
1	A′A′ B′B′ C′C′	2 + 2 + 2	6
64 Total			

Distribution of the F_2 individuals according to the development attained.

Classes	6	8	10	12	= 4	Number of classes
Frequency	8	24	24	8	=64	Total population

and so on in subsequent generations. This is in accord with the mathematical prediction made by EAST and HAYES (1912), to which actual data obtained from maize roughly approximate, as shown by JONES (1916).

The development attained by any individual in table 2 is correlated with the number of heterozygous factors present. This has been maintained by all recent writers on the subject as a rough description of the facts as obtained in actual experiments.

When different numbers of chromosomes are concerned, according to this scheme, the number of individuals in the different classes making up the whole F_2 population is given in table 3.

In any F_2 distribution there are as many individuals heterozygous for all factors (duplicating F_1 individuals) as there are individuals homozygous for all factors concerned in the original cross (two duplicating the parents; the remaining forming new homozygous combinations). The remaining individuals fall into a symmetrical distribution between these two end classes. The theoretical figures for any F_2 distribution in which n Mendelizing units are concerned can be obtained by taking the coefficients of the expanded binomial $(a + a)^n$ and multiplying these by 2^n, as shown in table 3. Since the expanded binomial is used to illustrate a normal frequency distribution, there can be no question as to the symmetry of the F_2 distributions if the diagrammatic scheme outlined is, in this respect, a description of the actual facts.

TABLE 3

Distribution of the individuals in F_2 according to the number of heterozygous chromsomes pairs they contain.

Number of chromosome pairs in which the F_1 is heterozygous	Classes with different number of heterozygous chromosome pairs and the number and ratio of individuals in these classes						Total number of individuals in the population
	0	1	2	3	4	5	
1	2 1	2 1					4
2	4 1	8 2	4 1				16
3	8 1	24 3	24 3	8 1			64
4	16 1	64 4	96 6	64 4	16 1		256
5	32 1	160 5	320 10	320 10	160 5	32 1	1024
n	2^n 1	...... etc. ......$2^n \times$ (coefficients) ....2^n ...... etc. ...... coefficients of the expanded binomial $(a + a)^n$...........1					$(2^n)^2$

In the preceding purely diagrammatic representation of the way in which dominance may account for the effects of heterozygosis, perfect dominance was assumed. Such an assumption is neither justified nor desirable. Many theoretical explanations of the inheritance of quantitative characters are based on exactly the converse assumption, i.e., that factors in the 1*n* condition have just half the effect that they have in the 2*n* condition.

In the development of an organism, however, all types of factors are concerned, both qualitative and quantitative. Partial dominance in qualitative characters is a normal occurrence. The concensus of opinion at the present time is that there may be, in reality, no cases of perfect dominance. In those cases in which the heterozygote cannot be distinguished from the pure dominant, it is assumed that the similarity is only apparent and not real. The heterozygote merely approaches the condition of the dominant type more or less closely. However much it may be true that perfect dominance rarely or never occurs, the fact and universality of partial dominance can hardly be denied.

In this connection it should be realized that the difference between the heterozygote and the recessive type in many cases is one of *kind,* while the difference between the heterozygote and the dominant type is one of *degree.* A good illustration of this point is found in the case of albinism in maize. Plants heterozygous for the factor (or factors) determining the production of chlorophyll cannot be distinguished from normal green plants—a case of apparently complete dominance. If there is in reality a difference between these heterozygous and homozygous normal green plants, although not apparent, that difference is very slight as compared with the difference between the heterozygote and the abnormal recessive. In the former case the difference, if there is any, is quantitative. The heterozygote may not have as much chlorophyll as the normal homozygote. In the second case the difference is qualitative. The heterozygote has chlorophyll; the recessive has none. This is a difference which determines the life or death of the organism.

All the evidence at hand leads to a seemingly logical conclusion, one necessary to the conception of dominance as an explanation of heterosis, which is, that *many factors in the 1n condition have more than one-half the effect that they have in the 2n condition.* Whether or not this is a logical conclusion and one that is justified by the facts remains to be seen. It certainly has the advantage of being more definite and comprehensible than the assumptions previously made (SHULL 1911; EAST and HAYES 1912), that factors in the heterozygous condition stimulate development by virtue of their being in that condition, without showing in any way why this should be so.

There is abundant evidence to show that many abnormal characters exist in a naturally cross-pollinated species and that they are recessive to the normal condition. In maize innumerable examples can be cited. In addition to the complete lack of chlorophyll already mentioned, there are also other chlorophyll factors which distinguish yellowish-green plants from normal green plants, just as there are cases of both conditions in other plants, e.g., Pelargonium (BAUR 1911). By inbreeding, strains of maize are isolated which are dwarf; some are sterile; some have contorted stems; some fasciated ears. Some are more susceptible to the bacterial wilt disease, and still others have brace roots so poorly developed that they cannot stand upright when the plants become heavy. It is unnecessary to mention more examples, because their occurrence in many kinds of material is familiar to everyone. All the characters cited are recessive, either completely or to a large degree, to the normal condition. More than one of these unfavorable characters may be present together in one inbred strain. No one strain so far known has them all.

Crossing many of these strains of maize together produces perfectly normal F_1 plants. They are normal because the factors which one strain lacks are supplied by the other, and conversely. Because more of the favorable characters are present when the strains are united in F_1 than in either parent, the F_1 is naturally able to attain a greater development. This effect is heterosis.

In the preceding diagrammatic illustration of the way in which heterosis may be brought about it was assumed that all factors had equal effects, that they were evenly distributed in the chromosomes, and that there were no crossovers. This is probably far from describing all the actual conditions. All deviations from this uniformity add to the complexity of the problem. It remains to be seen whether or not the assumption of dominance as an explanation of heterosis will not meet all or most of the requirements raised by all these complicating factors. It is only necessary to consider that a large number of factors is concerned, and that those factors are in most cases fairly evenly distributed among all the chromosomes, and that, in the main, crossovers in some places are balanced by crossovers in others.

Crossing over also provides a means of understanding why certain homozygous individuals (and varieties) may possess a greater number of desirable characters than others. Exceptionally good individuals might be formed by crossing over in heterozygotes occurring in such a manner that all, or a large number of, desirable characters would be combined together eventually in one individual. Such a condition, according to the laws of chance, would be exceedingly rare, which is well in accord with the facts.

Without going into all the possibilities which this viewpoint opens up, it is only necessary to say that a way is offered to meet the objections which have been raised against the conception of dominance as a means of accounting for the facts of heterosis as so far known.

There is still the possibility that there may be a stimulus derived from crossing quite apart from hereditary factors. The view presented here simply coördinates the existing knowledge of heredity so as to give a comprehensible view of the way in which heterosis may be brought about.

SUMMARY

1. The phenomenon of increased growth derived from crossing both plants and animals has long been known but never accounted for in a comprehensible manner by any hypothesis free from serious objections.

2. The conception of dominance, as outlined by KEEBLE and PELLEW in 1910 and illustrated by them in height of peas, has had two objections which were: *a*. If heterosis were due to dominance of factors it was thought possible to recombine in generations subsequent to the F_2 all of the dominant characters in some individuals and all of the recessive characters in others in a homozygous condition. These individuals could not be changed by inbreeding. *b*. If dominance were concerned it was considered that the F_2 population would show an asymmetrical distribution.

3. All hypotheses attempting to account for heterosis have failed to take into consideration the fact of linkage.

4. It is shown that, on account of linked factors, the complete dominant or complete recessive can never or rarely be obtained, and why the distributions in F_2 are symmetrical.

5. From the fact that partial dominance of qualitative characters is a universal phenomenon and that abnormalities are nearly always recessive to the normal conditions, it is possible to account for the increased growth in F_1 because the greatest number of different factors are combined at that time.

6. It is not necessary to assume perfect dominance. It is only necessary to accept the conclusion that many factors in the $1n$ condition have more than one-half the effect that they have in the $2n$ condition.

7. This view of dominance of linked factors as a means of accounting for heterosis makes it easier to understand: *a*, why heterozygosis should have a stimulating rather than a depressing or neutral effect; and *b*, why

the effects of heterozygosis should operate throughout the lifetime of the individual, even through many generations of asexual propagation.

LITERATURE CITED

Baur, E., 1911 Einführung in die experimentelle Vererbungslehre. pp. vi + 293. Berlin: Borntraeger.

Darwin, C., 1877 The effects of cross and self-fertilisation in the vegetable kingdom. pp. viii + 482. London: D. Appleton & Co.

East, E. M., 1908 Inbreeding in corn. Connecticut Agr. Exp. Sta. Report for 1907, pp. 419-428.

1909 The distinction between development and heredity in inbreeding. Amer. Nat. **43**: 173-181.

1910 A Mendelian interpretation of variation that is apparently continuous. Amer. Nat. **44**: 65-82.

1915 The chromosome view of heredity and its meaning to plant breeders. Amer. Nat. **49**: 457-494.

East, E. M., and Hayes, H. K., 1912 Heterozygosis in evolution and in plant breeding. U. S. Dept. of Agric., Bureau of Plant Industry Bull. 243. pp. 58.

Emerson, R. A., and East, E. M., 1913 The inheritance of quantitative characters in maize. Nebraska Agr. Exp. Sta. Research Bull. 2. pp. 120.

Focke, W. O., 1881 Die Pflanzen-Mischlinge. pp. 569. Berlin: Borntraeger.

Gärtner, C. F., 1849 Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. pp. xvi + 791. Stuttgart: C. F. Gärtner.

Hayes, H. K., 1912 Correlation and inheritance in *Nicotiana tabacum*. Connecticut Agr. Exp. Sta. Bull. 171. pp. 45.

Jones, D. F., 1916 Inbreeding in maize. Paper read before the Annual Meeting of the Botanical Society of America, at Columbus, Ohio, Dec. 1915. Abstract in Science N. S. **63**: 290, 25 F 1916.

Keeble, F., and Pellew, C., 1910 The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*). Jour. Genetics **1**: 47-56.

Kölreuter, J. G., 1766 Dritte Fortsetzung der Vorläufigen Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig: Gleditschen Handlung. Reprinted 1893 in Ostwald's Klassiker der exakten Wissenschaften, No. 41. Leipzig.

Morgan, T. H., Sturtevant, A. H., Muller, H. J., and Bridges, C. B., 1915 Mechanism of Mendelian heredity. pp. xiii + 262. New York: Henry Holt & Co.

Nilsson-Ehle, H., 1908 Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Botaniska Notiser pp. 257-294.

1909 Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Universitets Arsskrift, N. F., Afd. 2, Bd. 5, Nr. 2, 122 pp.

Shull, G. H., 1908 The composition of a field of maize. Rep. Amer. Breeders' Ass. **4**: 296-301.

1909 A pure line method of corn breeding. Rep. Amer. Breeders' Ass. **5**: 51-59.

1910 Hybridization methods in corn breeding. Amer. Breeders' Mag. **1**: 98-107.

1911 The genotypes of maize. Amer. Nat. **45**: 234-252.

1914 Duplicate genes for capsule form in *Bursa bursa-pastoris*. Zeitschr. f. ind. Abst. u. Vererb. **12**: 97-149.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

STATEMENT OF THE OWNERSHIP, MANAGEMENT, CIRCULATION, ETC., REQUIRED BY THE ACT OF CONGRESS OF AUGUST 24, 1912,

Of GENETICS, published bi-monthly at Princeton, N. J., for April 1, 1917.

State of New Jersey, County of Mercer, ss.

Before me, a notary in and for the State and county aforesaid, personally appeared C. Whitney Darrow, who, having been duly sworn according to law, deposes and says that he is the Business Manager of GENETICS, and the following is, to the best of his knowledge and belief, a true statement of the ownership, management, etc., of the aforesaid publication for the date shown in the above caption, required by the Act of August 24, 1912, embodied in section 443, Postal Laws and Regulations, to wit:

1. That the names and addresses of the publisher, editor, managing editor, and business managers are: Publisher, Princeton University Press, Princeton, N. J.; Managing Editor, George H. Shull, Princeton, N. J.; Business Managers, Princeton University Press, Princeton, N. J.

2. That the owners are: Princeton University Press, Princeton, New Jersey.

3. That the known bondholders, mortgagees, and other security holders owning or holding 1 percent or more of total amount of bonds, mortgages, or other securities are: None. C. W. Darrow, Mgr. Princeton University Press. Sworn to and subscribed before me this 4th day of June, 1917.

[SEAL] ELMER C. NELSON.

(My commission expires Feb. 8th, 1922.)

GENETICS, SEPTEMBER 1917

TABLE OF CONTENTS

[Reprinted from THE AMERICAN NATURALIST, Vol. LI., November, 1917.]

ON REVERSIBLE TRANSFORMABILITY OF ALLELOMORPHS

H. TERAO

THE IMPERIAL AGRICULTURAL EXPERIMENT STATION, TOKYO, JAPAN

IN genetical studies of variegation in plants, the fact has been observed occasionally that with a certain frequency a dominant allelomorph occurs in the corresponding recessive homozygote (De Vries,[1] Correns,[2] and Emerson[3]). In this paper the author presents a new instance of a similar phenomenon, which it is hoped may throw additional light on the subject.

In certain pedigree cultures of the rice plant, *Oryza sativa* L., there happened to occur in 1912 families containing besides ordinary fertile plants a number of sterile plants. These sterile plants were normal in their growth, but showed a considerable barrenness at the ripening season. Some of them yielded no seed whatsoever, others bore a small number of normal seeds, and very few were mosaic forms with higher fertility. These families, two in number, each belonging to a different variety, were derived from single plants of the former generation, and were very uniform in other characters. From them the experiment was started.

The rice plant, being a self-pollinated species, is convenient material for breeding experiments. Although the experiments in this investigation were made largely from open-pollinations, the results obtained were always similar to those from experiments in which plants were artificially protected against accidental natural crossing.

The observations of 1912 and 1913 are shown in summarized form in Tables I and II, *a* and *b*, and point to the following conclusions. Sterility behaves as a simple re-

---

[1] De Vries, H., "Die Mutationstheorie," Bd. I, 1901, pp. 489–511; "Species and Varieties, their Origin by Mutation," 1905, pp. 309–339.

[2] Correns, C., *Berichte der Deutschen Botanischen Gesellschaft*, Bd. 28, 1910, pp. 418–434.

[3] Emerson, R. A., AMERICAN NATURALIST, Vol. 48, 1914, pp. 87–115; *Genetics*, Vol. 2, 1917, pp. 1–35.

cessive to fertility, and the seeds resulting from partial fertility of sterile plants again give segregating families. In Family *A*, which shows an exceedingly slight fertility of sterile plants, the segregation ratio in the offspring derived from fertile individuals is quite close to expectation, but in Family *B* which shows a considerably higher grade of partial fertility of sterile plants, the progeny of fertile individuals exhibit considerable deviations from the expected segregation ratio.

TABLE I

THE SEGREGATING FAMILIES, *A* AND *B*, IN 1912

Fam.	Segregation						Partial Fertility of Sterile Plants		
	Fertile Plants	Sterile Plants	Total No. of Ind.	Steriles %	Ratio per 4		Total No. of Spikelets	Fertile Spikelets	
					D	R		No.	%
A....	36	13	49	26.53	2.94	1.06	*ca.* 9,000	2	0.02
B....	105	25	130	19.23	3.23	0.77	14,941	434	2.90

TABLE II

THE FAMILIES DERIVED FROM FAMILIES *A* AND *B*

(*a*) *The Progeny of the Fertile Plants*

Family in 1912	No. of Families			Ratio per 3		Segregating Families			
	Uniformly Fertile	Segregating	Total	Uniformly Fertile Families	Segregating Families	Fertile Plants	Sterile Plants	Total Number Individuals	Steriles %
A....	10	22	32	0.94	2.06	1,068	346	1,414	24.46
B....	41	64	105	1.17	1.83	4,874	1,301	6,175	21.06

(*b*) *The Progeny of the Seeds on the Sterile Plants*

Family in 1912	Number of Families	Fertile Plants	Sterile Plants	Total Number of Individuals	Steriles %
A........	2	2	0	2	0.00
B........	24	401	115	516	22.29

These facts may be interpreted by the following hypothesis. The dominant and the recessive types concerned are assumed to be transformed by certain unknown causes into the other allelomorph. The recessive allelomorph which has made its appearance in Families *A* and *B* is assumed to have originated in the preceding generation by the transformation of the dominant allelomorph. This recessive state of the hereditary substance, however, has a tendency to revert into the original dominant state. Such reversion is especially likely to occur in vegetative cells, where each recessive allelomorph seems to be able to revert independently. Consequently, in recessive homozygotes the reversion generally will produce heterozygotic cells, either one of the two recessive allelomorphs being changed into the dominant. The heterozygotic cells thus formed will give rise to partial fertility in otherwise sterile plants. Again, the recessive allelomorph in heterozygotic cells may be subject to similar reversion, and such reversion may occur both in the heterozygotic cells of sterile plants and in normal heterozygotes. Here, however, heterozygotic cells will be transformed into dominant homozygotic cells without visible effect on the plant concerned. The consequence of this reversion in the next generation will be that the proportion of the dominant segregates may exceed the theoretically expected figure. Finally, it may be assumed that between Families *A* and *B* there exists a difference in the reverting tendency of the recessive allelomorph, which necessarily will effect the differences in both the intensity of partial fertility of sterile plants and the deviations in the segregation ratio.

In Table III the segregating families derived from the fertile plants of Family *B* are classified according to the magnitudes of the deviations in terms of probable errors. The true percentage for the recessive is assumed, in the one case as 25 per cent. (the Mendelian ratio), and in the other case as 21 per cent. (an arbitrary number). In comparing the two different frequency distributions made in this manner with the theoretical frequency distribution, it is observed that while the frequency distribution of the deviations from 25 per cent. shows a considerable discrepancy from the theoretical, the latter fits the frequency distribution of the deviations from 21 per cent. rather closely, the goodness of fit being $P = 0.915$. Consequently, the *ca.* 4 per cent. deficiency of recessive segregates is a normal expectation and not an experimental error.

TABLE III

The Frequency Distribution of the Deviations in the Segregation Ratios in the Group of 64 Segregating Families Descended from Family *B* of the Year 1912

Dev. /P.E.	−5	−4	−3	−2	−1	0	+1	+2	+3	+4	+5	Total
Experimental frequency (I)....		1	7	14	17	15	6	4				64
Experimental frequency (II)...			1	2	11	19	14	10	5	2		64
Expectation..................		0.2	1.2	4.3	10.3	16.0	16.0	10.3	4.3	1.2	0.2	64.0

Note: In the experimental frequency (I) the true percentage for recessives is taken as 25 per cent., and in (II) as 21 per cent.

Such an aberrant segregation ratio seems to be a constant tendency all through the generations descended from Family *B*. This is shown in Table IV in which the experiments in the years from 1912 to 1915 are summarized.

TABLE IV

The Aberrant Segregation-Ratios Obtained in the Years 1912–1915

Years	No. of Fams.	Parent-plants	No. of Inds.	Fertiles	Steriles	Ster. %	Dev. %	P.E. %	D./P.E.
1912......	1	Fertile	130	105	25	19.23	5.77	2.55	2.3
1913......	64	"	6,175	4,874	1,301	21.06	3.94	0.37	10.6
1914......	10	"	1,560	1,207	353	22.63	2.43	0.74	3.3
1915......	53	"	4,696	3,732	964	20.52	4.48	0.47	9.5
Total....	128		12,561	9,918	2,643	21.04	3.96	0.26	15.2
1913......	24	Sterile	516	401	115	22.29	2.71	1.21	2.2
1914......	34	"	994	779	215	21.63	3.37	0.93	3.6
1915......	19	"	684	522	162	23.68	1.32	1.12	1.2
Total....	77		2,194	1,702	492	22.43	2.57	0.62	4.1

Again, in regard to the intensity of partial fertility of sterile plants, the descendants of Families *A* and *B* exhibited respectively relations similar to those seen in 1912. (Family *A* was not traced after 1913.) A count of fertile spikelets on sterile plants descending from Family *B* was made in 1914 on 281 plants bearing a total of 101,412 spikelets. In this count the number of fertile spikelets was 3,857, corresponding to 3.78 per cent. of the total number of spikelets. The latter figure may be regarded as the average fertility of sterile plants in the progeny of Family *B*.

The fertile spikelets of sterile plants are generally scattered at random over the panicle, and each fertile spikelet may be regarded as representing a separate case of reversion; but in mosaic forms which show higher fertility and are of rarer occurrence, the reversion may have taken place in earlier stages of plant development, resulting in larger fertile sections. Consequently, when the count of fertile spikelets is made with only the first type of sterile plants, a more correct value for the frequency of reversion may be obtained. The result of such a count on 902 panicles containing 93,635 spikelets is 1,858 fertile spikelets, *i. e.,* 1.98 per cent. of the total number of spikelets.

The mosaic forms appear in several different grades of partial fertility. In a panicle either one or more branches or even one half of the panicle can be highly or entirely fertile, the remaining part being absolutely or nearly absolutely sterile. Similarly, in a single plant some whole panicles can be entirely or highly fertile while others are of the ordinary grade of partial fertility. Furthermore, similar mosaic conditions were also observed in single flowers of sterile spikelets. While all six anthers of a sterile spikelet generally bear none or but few pollen grains, occasionally flowers appear in which certain anthers contain a considerable number of pollen grains of normal appearance and others show the ordinary state of sterility. Hence it may be assumed that the reversion can take place at any stage of plant development.

The partial homozygosity of heterozygotes, corresponding to the partial fertility of sterile plants, may be estimated in the following way. Assuming that the possibility of reversion at any stage of a plant's life, similar to that observed above, may also occur in heterozygotic cells, then we may distinguish for convenience two different types of reversions; there is the reversion which will cause partial homozygosity within a single flower, and the reversion which will produce an entirely homozygotic spikelet or larger homozygotic sectant. Suppose then that the latter reversion will give to the heterozygote homozygotic (AA) spikelets in any part "x" of the total number of spikelets which is taken as a unit, and again that in the remaining (1 — x) part of the total number of spikelets, the other type of reversion will occur, turning some part "y" of the whole generative tissue taken as a unit from the Aa state to the AA state. For simplicity, however, we may substitute "x" for "y" in the above relation, because it seems presumable that a similar probability of reversion may exist constantly all through the plant life. Such a plant will have the following constitution in regard to the generative tissue:

$$x(AA) + (1 - x)[x(AA) + (1 - x)(Aa)].$$

As the result of self-pollination, the progeny of such a parent plant will show the constitution:

$$x(AA) + (1 - x)[\tfrac{1}{4}(1 + x)^2(AA) + \tfrac{1}{2}(1 - x^2)(Aa) + \tfrac{1}{4}(1 - x)^2(aa)].$$

Applying arbitrary values to "x" in this formula, we shall get numerical relations among segregates. In Table V the results of such calculation are compared with results obtained by the experiments in 1913–1915. Thus we may find the average partial homozygosity of heterozygotes around 4 to 6 per cent., the average partial fertility of sterile plants being, as was already shown, *ca.* 4 per cent.

TABLE V

CALCULATIONS ON DATA OF TABLE IV

x %	(AA + Aa)	aa	AA	Aa
4 %	77.88 %	22.12 %	38.74 %	61.53 %
5 %	78.57	21.43	39.69	60.31
6 %	79.24	20.76	40.89	59.11
Observation, No. of Inds.	9,918	2,643	94	135
Percentage	78.96 %	21.04 %	41.05 %	58.95 %

It has also been noticed that the sterility concerned is associated with an abnormality represented by the behavior of chlorophyll at the ripening of seeds. While, at the ripening season, the chlorophyll in the fertile sections of the mosaic forms turns to yellow just as in ordinary fertile plants, the chlorophyll in the sterile sections still remains green. The fertile spikelets occurring in a small number on the otherwise sterile panicle appear on ripening as yellow spots scattered among green spikelets; the plants with both sterile and fertile panicles appear in the fall also as mosaic forms with green and yellow leaves. This feature of the sterile plants is in direct contrast to the behavior of the mosaic plants with the variegated and the entirely green leaves studied by De Vries and Correns.

The observations in the foregoing pages seem to parallel those made by the authors cited at the beginning of this paper. In the present investigation, however, there was observed also the transformation of allelomorphs in the opposite direction, that is, the transformation of the dominant allelomorph into the recessive allelomorph, something scarcely mentioned in the investigations referred to above. The observations in this regard were in brief as follows.

In the first place, the spontaneous occurrence of segregating families was observed again among the descendants of the families which had proved in the experiments already described to be constantly fertile. This suggests, just as did the occurrence in Family *A* and Family *B* in 1912, the probability of the AA cell changing into the Aa cell.

In the second place, a constant tendency of the dominant allelomorph to be transformed into the recessive allelomorph was observed in certain strains. In 1913, special attention was paid to such segregating families in which the excess of recessive segregates over the theoretical expectation was particularly high. Although, as already noted, the variation among the segregating families in 1913 with regard to the deviations from the recessive proportion might possibly have arisen from experimental errors associated with a certain probability of allelomorphic reversion from recessive to dominant, yet it was deemed not impossible that the very considerable excess of recessives exhibited by certain families might be caused by other reasons. This point was seemingly decided by the experiment made with Family *B*80 in 1913 (Table VI), since in this family there was noticed a constant tendency toward the allelomorphic transformation under consideration.

TABLE VI

THE SEGREGATION OF FAMILY *B*/80 AND ITS DESCENDANTS

Year	No. of Families	Parent-plants	No. of Individuals	Fertile Plants	Sterile Plants	Recessives	Deviation of Recessives	P. E.
1913....	1	Fertile	99	69	30	30.30%	+ 5.30%	2.95%
1914....	10	"	1,020	727	293	28.73	+ 3.73	0.91
1915....	5	"	435	309	126	28.89	+ 3.89	1.40
1916....	98	"	11,013	7,832	3,181	28.88	+ 3.88	0.28
Total..	114	Fertile	12,567	8,937	3,630	28.89%	+ 3.89%	0.26%
1914 (*a*).	16[1]	Sterile	199	147	52	23.62%	− 1.38%	2.04%
1914 (*b*).	13[1]	Sterile	100	5	95	95.00%	+70.00%	2.92%
1915....	59[2]	"	548	32	516	94.16	+69.16	1.25
1916....	120[2]	"	1,436	99	1,337	93.11	+68.11	0.77
Total..	192[3]	Sterile	2,084	136	1,948	93.47%	+68.47%	0.64%

[1] Derived from the family in 1913, *i. e.*, Family *B*/80.

[2] Derived from the group (*b*) in 1914.

[3] Excluding the group (*a*) in 1914.

In Table VI there is beside the *ca.* 4 per cent. excess of recessives in the families derived from fertile parents, a remarkable excess of recessives in the families descended from the sterile parents in the group (*b*) in 1914. The sterile plant of this type could not be distinguished from those which, as was shown in Table IV, gave segregating families with an excess of dominants in the intensity of the partial fertility as well as in the behavior of chlorophyll at the ripening of the seeds. Consequently, it may be presumed that although these two types of sterile plants have the same genetical constitution originally, the dominant allelomorphs resulting from the reversion of their recessive allelomorphs are of different stabilities in the dominant state; that is, in the first type of sterile plants such dominant allelomorphs are very easily re-transformed into the recessive state, while in the second type the corresponding dominant allelomorphs tend to remain in the reverted condition.

Corresponding to the excess of recessive segregates, a deficiency of dominant homozygotes among dominant segregates was also noticed. Among 153 families derived from fertile plants in the experiment above mentioned, 40 families were uniformly fertile, the remaining 113 families showing segregation. The former, therefore, is 26.14 per cent. of the total number of families, and shows 7.19 per cent deficiency from the theoretically expected percentage, 33.33 per cent., the probable error being ± 2.68 per cent.

In conclusion it may be stated that the allelomorphs concerned in this investigation are probably subject to reversible transformations, and that the probable frequency of the allelomorphic transformation may be practically constant in a certain strain, and possibly may be different in different strains. As to the conditions under which such allelomorphic transformations take place, nothing is yet certain except that these conditions are of a hereditary nature. The manner in which different intensities of allelomorphic transformations are inherited will be the subject of further investigation.

A word may be added here regarding the conception of dominance and recessiveness. Bateson's theory of "presence and absence of factors" is sometimes understood in the sense that the dominant allelomorph is regarded as due to the real presence of an hereditary material unit which is absent in the recessive allelomorph. Such a conception is not in full accordance with the idea of the reversible transformability of allelomorphs as described in this investigation. There is another possibility of the nature of allelomorphs. The dominant and the recessive allelomorphs may be supposed to represent two alternative conditions or phases of a single hereditary substance, somewhat resembling the chemical conception of polymerization. Consequently, the interchangeability between the dominant and recessive allelomorphs is not improbable theoretically.

Bussey Institution,
August 26, 1917

[Reprinted from THE AMERICAN NATURALIST, Vol. LII., January, 1918.]

MATERNAL INHERITANCE IN THE SOY BEAN

H. TERAO

THE IMPERIAL AGRICULTURAL EXPERIMENT STATION, TOKYO, JAPAN

THE soy bean, *Glycine hispida* Maxim., shows as different types two cotyledon colors, yellow and green. The beans with yellow cotyledons have two types of seed-coat colors, namely, green and yellow, while the beans with green cotyledons have always green seed-coats.[1] The inheritance of these types of cotyledons and of seed-coats has been proved by the author's experiments to be maternal. A brief notice of the experiments will be given in the following.

The green and yellow colors of cotyledons and seed-coats are obviously attributed to chlorophyll, which, on the ripening of the beans, is either changed from green into yellow or remains green. Further, according to the author's observations, the chlorophyll in the vegetative parts of the plant shows the same behavior as the chlorophyll of the cotyledons; in other words, the leaves and stems of the varieties with yellow cotyledons turn to a yellow color when they are gradually dying coincident with the ripening of the beans, while those of the varieties with green cotyledons remain green sometime after the dying of the whole plant. These facts suggest that the two types of cotyledon colors may represent two kinds of chlorophyll, one which changes into yellow under certain physiological conditions and one which is not so affected. The chlorophyll of the seed-coats, however, seems to behave somewhat differently from the chlorophyll in all

---

[1] Black and brown pigments also appear in the seed-coats of certain varieties. These pigments are entirely independent of the green and yellow colors here referred to in their inheritance, but they make the latter colors invisible or at least indistinct. By proper crosses, however, one can test whether a seed-coat covered by the black or brown pigment belongs to the green or the yellow category.

TABLE I

Soy Bean Crosses made in Studying the Inheritance of Green and Yellow Colors of Cotyledons and of Seed-coats

	Crossing No. I		Crossing No. II		Crossing No. III		Crossing No. IV		Crossing No. V		Crossing No. VI	
	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat	Cotyledons	Seed-coat
Parents												
Female...	green	green	green	green	yellow	yellow	yellow	green	yellow	yellow	yellow	green
Male.....	yellow	yellow	yellow	green	green	green	green	green	yellow	green	yellow	yellow
F$_1$-Ind......	green	green	green	green	yellow	green	yellow	green	yellow	green	yellow	green
No. Ind...	24	24	3	3	40	40	4	4	9	9	5	5
F$_2$-Ind......	green	green	green	green	yellow	green yellow	yellow	green	yellow	green yellow	yellow	green yellow
No. Ind...	3,129	1,248	322	216	11,836	825 : 288	846	436	1,815	418 : 128	169	56 : 19
						(74.1% : 25.9%)				(76.6% : 23.4%)		(74.7% : 25.3%)
F$_3$-Fam.....	green-constant		green-constant		yellow-constant		yellow-constant		yellow-constant		yellow-constant	
No. Fam..	1,248		216		1,113		436		546		74	
No. Ind...	72,501		16,498		28,231		2,341		55,354		4,635	

other parts of the plant, since, as was already noted, yellow cotyledons are accompanied by green seed-coats in certain varieties.

The crossing experiments which have been made by the author since 1910 with these different types of beans have produced the results shown in Table I, the main facts being summarized as follows.

I. The F_1 cotyledons of the crosses reciprocal to each other are of the same character as the female parents. In respect to the cotyledon colors, the F_2 and following generations show the characters of the F_1 generation exclusively, instead of a Mendelian segregation between the yellow and green colors. Hence we are probably dealing with characters which can be inherited only through the female parents.

II. The inheritance of the seed-coat colors is a more complicated phenomenon. In the cross "green cotyledons, green seed-coat" (♀) × "yellow cotyledons, yellow seed-coat" (♂), the green seed-coat is inherited through the female parent exclusively, just as in the case of the cotyledon colors; but in the reciprocal cross the green and yellow seed-coats show Mendelian segregation, the former being dominant.

The maternal inheritance observed above was not due to self-fertilization succeeding failures in artificial crossing, because several other characters showed inheritance through the male parents.

An interpretation of the inheritance phenomena under consideration is suggested as follows. In the first place, let us refer again to the two different kinds of chlorophyll assumed to be concerned in producing the green and yellow cotyledons; namely, the chlorophyll which can be changed into yellow and the chlorophyll which remains green. (These will be denoted respectively as "(Y)" and "(G)" in the later descriptions.) These characteristics of chlorophyll may be due to heritable traits of the chromatophores or of the cytoplasm, and not to hereditary elements in the nucleus. As, on the fertilization of the egg-cell, the chromatophores and the cytoplasm of the female gamete will probably remain as such without being supplemented by those from the male gamete, their characteristics would naturally be inherited only through the female parent. In the second place we may assume that a pair of Mendelian factors is concerned in the inheritance of the colors of the seed-coats. The factor "H" inhibits the chlorophyll "(Y)" in the seed-coat of the beans with yellow cotyledons from changing to yellow, producing beans with yellow cotyledons and green seed-coat; the absence of the factor "H," expressed by "h," allows the seed-coat of the bean with yellow cotyledons to remain yellow. The seed-coat of the bean with green cotyledons remains green no matter whether the factor "H" is present or absent, because the beans of this kind have the chlorophyll "(G)" which is incapable of changing the color.

The justice of the contention regarding the bean with green cotyledons, moreover, is supported by the following observations. The F_2 families of the crosses "green cotyledons, green seed-coat" (♀) × "yellow cotyledons, yellow seed-coat" (♂) were actually composed of two kinds of individuals which were distinguishable from each other by a slight difference of the intensity of green color in the seed-coats, and the numerical relation between these two kinds of individuals was approximately the Mendelian mono-hybridal segregation ratio, the darker seed-coat being dominant to the lighter one. Again, in the F_3 generation of these crosses, there were obtained three types of families, two which were uniformly of the darker and of the lighter seed-coats respectively and one which was a mixture of both. By comparing the green seed-coats of the female parents in these crosses with those of the progeny, the former was found to belong to the darker class mentioned above. These variations in the green color of the seed-coats may be regarded as being due to the influence of the Mendelian factors "H" and "h" respectively on the chlorophyll "(G)"; from which it follows that the method of inheritance in the beans with yellow cotyledons obtains also in the beans with green cotyledons.

Keeping these statements in mind the cases in Table I may be illustrated as follows:

	Crossing No. I	Crossing No. II
Parents	(G)HH (♀)×(Y)hh (♂)	(G)HH (♀)×(Y)HH (♂)
Cotyledons	green yellow	green yellow
Seed-coat	green yellow	green green
F_1	(G)Hh	(G)HH
Cotyledons	green	green
Seed-coat	green	green
F_2	(G)HH (G)Hh (G)hh 25% 50% 25%	(G)HH 100%
Cotyledons	green	green
Seed-coat	green	green

	Crossing No. III	Crossing No. IV
Parents	Y(hh) (♀)×(G)HH (♂)	Y(HH) (♀)×(G)HH (♂)
Cotyledons	yellow green	yellow green
Seed-coat	yellow green	green green
F_1	Y(Hh)	Y(HH)
Cotyledons	yellow	yellow
Seed-coat	green	green
F_2	(Y)HH (Y)Hh (Y)hh 25% 75% 25%	(Y)HH 100%
Cotyledons	yellow yellow	yellow
Seed-coat	green yellow	green

If the foregoing interpretation really represents the facts in this investigation, we may consider also crosses in which forms such as (G)Hh, (G)hh, and (Y)Hh were used as the parents, since in these crossings phenomena different from those in Table I would be expected. These expectations have been fulfilled in further experiments in which individuals from the previous experiments representing different intensities of seed-coat color were used as the parent plants. The results of these crosses, accompanied by interpretations, are shown in Table II.

TABLE II

Crosses made among the Progeny of the Hybrids Shown in Table I

		Parents		F_1		F_2	
		Female	Male	Character	No. of Individuals	Character	No. of Individuals
Crossing No. VII	Cotyledons	yellow	green	yellow	22	yellow	2,381
	Seed-coat	yellow	green	yellow	22		
	Interpret.	(Y) hh	(G) hh	(Y) hh	100%		
Crossing No. VIII	Cotyledons	yellow	green	yellow	18	yellow	1,963
	Seed-coat	green	green	green yellow	10 8		
	Interpret.	(Y) Hh	(G) hh	(Y) Hh (Y) hh	50% 50%		
Crossing No. IX	Cotyledons	yellow	green	yellow	9	yellow	1,108
	Seed-coat	green	green	green yellow	7 2		
	Interpret.	(Y) Hh	(G) Hh	(Y) HH (Y) Hh (Y) hh	25% 50% 25%		

The maternal inheritance described in this paper seems to be essentially the same phenomenon as the inheritance of the character "*albo-maculata*" which was studied by Correns[2] in *Mirabilis Jalapa* and also by Baur[3] in *Antirrhinum majus*. In each case one is dealing with chromatophore characters.

Harvard University, Bussey Institution,

---

[2] Correns, C., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. I, 1909, pp. 291–329; *Ibid.*, Bd. II, 1909, pp. 331–340.

[3] Baur, E., *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Bd. IV, 1910, pp. 81–102.

THE INHERITANCE OF DOUBLENESS IN *CHELIDONIUM MAJUS* LINN.

KARL SAX
Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from Genetics **3**: 300-307, My 1918

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

---

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

THE INHERITANCE OF DOUBLENESS IN *CHELIDONIUM MAJUS* LINN.

KARL SAX
Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS **3**: 300-307, My 1918

THE INHERITANCE OF DOUBLENESS IN *CHELIDONIUM MAJUS* LINN.

KARL SAX
Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received September 3, 1917]

The most thorough investigation of the inheritance of doubleness in flowers has been made by Miss SAUNDERS (1910, 1911, 1917). In the Petunia the double flowers set no seed and all crosses must be made with the single plant as the female parent. In the F_1 of such a cross there is either a segregation into 3 single : 1 double, or into 9 single : 7 double. All single plants selfed or crossed *inter se* produce only singles. SAUNDERS explains these results on the assumption that pollen from the single flower used carries only factors for singleness, while ovaries of the single flowers lack the factor for singleness in some cases and possibly in all. The pollen of double flowers is further assumed to be heterozygous. In the stock the inheritance of double and single flowers is explained on the assumption that two factors are involved which are linked in the pure singles, but not linked in the eversporting singles. It is also assumed that "single" factors are distributed only in the female gametes according to a system of partial linkage.

In the Welsh poppy (*Meconopsis cambrica*) SAUNDERS (1917) found that a simple 3 : 1 ratio was obtained in F_2 by crossing single and double plants. Doubleness was found to be dominant. In the hollyhock (*Althaea rosea, A. ficifolia*) the offspring of single × full double plants were intermediate in F_1 and in the F_2 produced a 1 : 2 : 1 ratio. In the carnation (*Dianthus caryophyllus*) a cross of double × single produced an F_2 ratio of 3 double : 1 single, while a cross of double × single in *Dianthus barbatus* (sweet william) gave the same F_2 ratio, but singleness was found to be dominant.

NORTON (1907) and BATCHELOR (1912) have found that doubleness in the carnation is of two types; the ordinary or standard double and the type known as "bullhead" or "buster". By crossing a full double or buster with the single the resulting F_1 is standard double. The F_1

selfed or crossed *inter se* produces an F_2 ratio of 1 single : 2 standard doubles : 1 full double or buster.

The doubling of flowers is usually due to petalody of the stamens, according to DE VRIES. This is true of the plants investigated by SAUNDERS, and has been recorded by many writers, GOEBEL (1913), MASTERS (1869), DE VRIES (1906), and others; but no statistical data have been presented to show the degree of correlation between stamen number and petal number.

The inheritance of doubleness in *Chelidonium majus* and a statistical study of the relation of petals and stamens will be considered in the present paper. A double- and a single-flowered plant growing near the BUSSEY INSTITUTION were transplanted and reciprocal crosses made. In the F_1 about sixty plants of each cross were grown and in each case produced practically an equal number of single and double plants. Seed from the F_1 singles and doubles were planted separately. Of 133 plants raised from seed of single F_1 plants, 109 were single and 24 double. Of 111 plants raised from seed of the double F_1 plants, 6 were single and 105 double. If we assume that the high number of singles resulting from F_1 singles, and the 6 singles among the doubles, were due to contamination by crossing, or possibly due to volunteers from wild plants growing near by, then it appears that singleness is dominant, and that the original cross was made with a heterozygous single. We would then expect a ratio of 1 : 1 in the F_1 irrespective of which plant is used as the female parent. In the F_2 the F_1 single segregates should give a ratio of 3 single : 1 double, while the F_1 double segregates should breed true, when selfed or crossed *inter se*. In the F_2 of this particular cross all of the doubles should be homozygous, while two-thirds of the singles should be heterozygous.

Of the 244 plants raised in the F_2 the petal number and stamen number of the flowers of 147 plants were found. An average of 20.6 flowers per plant were counted.

The average numbers of petals and stamens of the F_2 plants are shown in table 1. The mean petal number is 10.54 ± 0.31, with a standard deviation of 5.60 ± 0.22. The mean stamen number is 18.30 ± 0.26, with the standard deviation of 4.72 ± 0.19. The coefficient of correlation between stamen and petal number is — .90 ± .01. In table 2 all of the flowers of the 147 F_2 plants are plotted in respect to stamen number and petal number. The mean petal number is 10.89 ± 0.07 with a standard deviation of 5.84 ± 0.05, while the mean stamen number is

TABLE I

Average stamen and petal number of 147 F_2 plants. Chelidonium, single × double.

Stamens

Petals	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
4											1	1	4	6	6	23	10	4	1	56
5																				0
6																				0
7																				0
8											1									1
9													1							1
10									2	1	1									4
11								1		4	1									6
12						3			2		1									6
13					2	3	1	2	5	2										15
14				4	2	2	4	7	1	2										22
15						3	1	1	1											6
16				2	2	1			1											6
17	1	1	1		2			2												7
18			2		2	1	2			1										8
19					3		1													4
20		1	1				2													4
21																				0
22						1														1
	1	2	4	6	13	14	11	13	12	10	5	1	5	6	6	23	10	4	1	147

Petals
$M = 10.54 \pm 0.31$
$\sigma = 5.60 \pm 0.22$

Stamens
$M = 18.30 \pm 0.26$
$\sigma = 4.72 \pm 0.19$

$r = -.90 \pm .01$

* Not weighted for deviation in number of flowers counted.

18.14 ± 0.06 with a standard deviation of 5.15 ± 0.04. The coefficient of correlation is — .863 ± .003. The variation of the doubles is especially striking in table 3, and there is apparently a continuous gradation from single to full double.

There is no significant variation of the petal number (four) in the singles, while the mean number of stamens is 23.68 ± 0.14 with a standard deviation of 1.56 ± 0.09. Although the doubles are recessive, the variation of petal number and of stamen number is much greater than in the singles. The F_2 doubles are plotted in table 3. The mean number of petals is 14.56 ± 0.20 with a standard deviation of 2.81 ± 0.14, and the mean stamen number is 14.99 ± 0.17 with a standard deviation of 2.39 ± 0.12. The coefficient of correlation is — .58 ± .05. It is apparent that the singles, even though two-thirds of them are heterozygous, are much less variable than the recessive doubles.

The sum of the petal number and stamen number is about the same in all individuals, whether single or double. The mean sum of the petals

Table 2

Stamen number and petal number of all F_2 flowers counted. Chelidonium, single × double.

Stamens

Petals	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
3																		2	1								3
4											1		9	32	59	95	93	160	210	143	129	81	31	9	6	2	1060
5															2	2	8	6	2	2	2	3		2			29
6																1	4	1	3	1	1						11
7												1	1	1	2	1	8		2		2						18
8											1	1	3	2	7	8	4	1									27
9									2	1	2	3	6	4	6	1	6	1	1		1						34
10							1		4	6	8	6	10	7	6	2	1										51
11						1		4	4	9	19	15	16	15	4	4	2			1							94
12						2	13	18	32	38	50	40	49	26	17	14	3		1								303
13					8	3	17	11	38	26	43	34	27	15	15	7											244
14			1	2	7	2	28	11	46	35	41	20	20	8	5	3	1										230
15			1	1	9	13	23	26	29	22	31	14	16	7	1	2											195
16			4	7	11	9	24	27	27	24	25	10	5	5	5	3											186
17			4	1	11	13	13	17	16	9	23	3	3	2	2		1										118
18			7	5	9	13	22	15	21	6	7	5	8	1													119
19			7	8	16	16	23	6	15	4	4	5	1		1												106
20	3		8	9	9	9	17	8	7	6	6	7		1													90
21		1	2	3	3	8	10	8	6	4	4	1	1	1													52
22		3		2	2	3	4	3	5	2		3	1			1											29
23			1	1	2	2	2	1	3		1																13
24					1	1	1	1	1	2																	7
25						1	1	1	1																		4
26						1	2	2																			5
27									1																		1
	3	4	35	39	88	97	201	159	258	194	266	168	176	127	132	144	131	171	220	147	135	84	31	11	6	2	3092

Petals

$M = 10.89 \pm 0.07$

$\sigma = 5.84 \pm 0.05$

Stamens

$M = 18.14 \pm 0.06$

$\sigma = 5.15 \pm 0.04$

$r = -.863 \pm .003$

and stamens of the doubles is 29.49 ± 0.15 with a standard deviation of 2.24 ± 0.12, while in the singles the mean sum of petal number and stamen number is 27.68 ± 0.14 with a standard deviation of 1.56 ± 0.10. The sum of the petal number and stamen number in the doubles is significantly larger than in the singles, but with a much greater variation

TABLE 3

Average stamen number and petal number of F_2 double plants. From table 1

	Stamens													
Petals	9	10	11	12	13	14	15	16	17	18	19	20	21	
8											1			1
9													1	1
10									2	1	1			4
11								1		4	1			6
12						3			2		1			6
13					2	3	1	2	5	2				15
14				4	2	2	4	7	1	2				22
15						3	1	1	1					6
16				2	2	1			1					6
17	1	1	1		2			2						7
18			2		2	1	2							8
19					3		1							4
20		1	1				2							4
21														0
22						1								1
	1	2	4	6	13	14	11	13	12	10	4	0	1	91

Petals
$M = 14.56 \pm 0.20$
$\sigma = 2.81 \pm 0.14$

Stamens
$M = 14.99 \pm 0.17$
$\sigma = 2.39 \pm 0.12$

$r = -.58 \pm .05$

If the pedigree culture results did not show the singles to be dominant, one might expect the larger number of petals and stamens and the greater variability of the doubles to be due to heterozygosis. The behavior of the doubles may, however, be due to splitting of the stamens in some cases, in addition to petalody.

The greater variation in number of parts in the double flowers loses its significance when the doubles of the F_2 are grouped by themselves and compared with the double flowers on individual double plants of the F_2. The mean petal number of all of the F_2 double plants is 14.56 ± 0.20 with a standard deviation of 2.81 ± 0.14 and the mean stamen number is 14.99 ± 0.17 with a standard deviation of 2.39 ± 0.12 (table 3). In tables 4, 5 and 6, three F_2 double-flowered plants are plotted in respect to petal number and stamen number. In table 4 the

TABLE 4

Stamen number and petal number of flowers of a single F_2 'double' plant.

Petals \ Stamens	10	11	12	13	14	15	16	17	18	19	20	21	
9									1				1
10													0
11													0
12					1	1						1	3
13				1	1			2			1	1	6
14					1	2	1	1		1			6
15								1	1	1		1	4
16					2	2	3				1	1	9
17				1	1	2	6	1		2			13
18			1	1	1			2	3	1			9
19		1	2		1	2	2	1					9
20			3	1	1	1	4	1					11
21	1		1	1	2	2	2						9
22				1									1
	1	1	7	6	11	12	18	9	5	5	2	4	81

Petals
M = 17.23 ± 0.20
σ = 2.77 ± 0.14

Stamens
M = 15.64 ± 0.18
σ = 2.43 ± 0.13

$r = -.46 \pm .04$

TABLE 5

Stamen number and petal number of flowers of an F_2 'double' plant.

Petals \ Stamens	8	9	10	11	12	13	14	15	16	
14					1	1				2
15						5	1		1	7
16			2	5	3	1	2	1		14
17			1	3	1			1		6
18	2		3	1	6			1		12
19	2	1								3
20	2	2	3		1					8
	6	3	9	9	12	7	3	3	1	53

Petals
M = 17.15 ± 0.16
σ = 1.71 ± 0.11

Stamens
M = 11.36 ± 0.18
σ = 1.98 ± 0.13

$r = -.64 \pm .05$

mean petal number is 17.23 ± 0.20 with a standard deviation of 2.77 ± 0.14 and the mean stamen number is 15.64 ± 0.18 with a standard deviation of 2.43 ± 0.13. In table 5 the mean petal number is 17.15 ± 0.16

TABLE 6

Stamen number and petal number of flowers of an F_2 'double' plant.

Stamens

Petals	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
10									1		1				2
11							1	2		1	1			1	6
12								2		2	1	2	1		8
13							1	2	1	2	2				8
14						2	1	2	1	1	1	1			9
15							1	1		1					3
16			1	1											2
17															0
18					1										1
19	2														2
20															
	2	0	1	1	1	2	4	9	3	7	6	3	1	1	41

Petals	Stamens
$M = 13.29 \pm 0.22$	$M = 16.58 \pm 0.30$
$\sigma = 2.11 \pm 0.16$	$\sigma = 2.88 \pm 0.21$

$r = -.66 \pm .06$

with a standard deviation of 1.17 ± 0.11 and the mean stamen number is 11.36 ± 0.18 with a standard deviation of 1.98 ± 0.13. In table 6 the mean petal number is 13.29 ± 0.22 with a standard deviation of 2.11 ± 0.16 and the mean stamen number is 16.58 ± 0.30 with a standard deviation of 2.88 ± 0.21. The coefficient of correlation of all the F_2 doubles is — .58 ± .05 while the coefficients of correlation of the three F_2 double plants are — .46 ± .04, — .64 ± .05, and —. 66 ± .06, respectively. The variability of the petal number and stamen number of all of the F_2 doubles is, in general, not greater than the variability in individual F_2 double plants.

CONCLUSIONS

Doubleness appears to be a simple recessive character in *Chelidonium majus.*

There is apparently a continuous series in degree of doubling from singles to full doubles in the F_2.

There is much greater variation in the doubles, which are recessive, than in the singles, of which two-thirds are heterozygous. The F_2 doubles are however no more variable than individual double plants of the F_2.

There is a high degree of negative correlation between petal number and stamen number in the F_2, due to petalody.

LITERATURE CITED

BATCHELOR, L. D., 1912 Carnation breeding. Ann. Rept. Amer. Breeders' Ass. **7**: 199-205.

DE VRIES, H., 1906 Species and varieties; their origin by mutation. pp. xvii + 874. Chicago: Open Court Pub. Co.

GOEBEL, K., 1913 Organographie der Pflanzen. Erster Teil. pp. —.

MASTERS, M. T., 1869 Vegetable teratology. pp. xxxviii + 534. London: Ray Society.

NORTON, J. B., 1907 Heredity in carnation seedlings. Ann. Rept. Amer. Breeders' Ass. **3**: 81-82.

SAUNDERS, E. R., 1910 Studies in the inheritance of doubleness in flowers. I. Petunia. Jour. Genetics **1**: 57-69.

1911 Further experiments on the inheritance of "doubleness" and other characters in stocks. Jour. Genetics **1**: 303-379.

1917 Studies in the inheritance of doubleness in flowers. II. Meconopsis. Althaea, and Dianthus. Jour. Genetics **6**: 165-184.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, MAY 1918

TABLE OF CONTENTS

THE BEHAVIOR OF THE CHROMOSOMES IN FERTILIZATION

KARL SAX

Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS **3**: 309-327, July 1918

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

THE BEHAVIOR OF THE CHROMOSOMES IN FERTILIZATION

KARL SAX
Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received October 23, 1917]

The problems of heredity are intimately related to the two critical stages in the life cycle of the higher organisms, the reduction divisions of sporogenesis in plants and of gametogenesis in animals, and the cytological processes of fertilization. The first of these has received much attention and is generally considered to be closely correlated with the segregation of the factors which determine the characters of the next generation. The union of the gametes at the time of fertilization is equally important, although we know little of the behavior of the chromosomes at this period. Recent research has made it desirable from both a cytological and a genetical standpoint to examine critically their behavior in the higher plants.

The behavior of the chromosomes in animals at the time of fertilization is comparatively well known. In some cases the sexual nuclei unite while in the resting condition so that the male and female contribution of chromosomes can not be distinguished. It has been shown, however, that in many species the male and female chromosomes are formed before the fusion of the sexual nuclei and that they may maintain the two distinct groups during the first division of the zygote. In some species the independence of male and female chromosomes has been traced through several divisions and even to later cleavage stages. Indeed there are reasons for believing that the male and female chromosomes may maintain their independence until gametogenesis. In all cases the first division of the fertilized egg appears to be essentially similar to any other normal somatic division.

In plants there is a great deal of variation in the behavior of the sexual nuclei in fertilization. In the algae it has been shown that in some cases the first division of the zygote is a reduction division. In Spirogyra (KARSTEN 1908) it has been found that the first division of the zygospore reduces the chromosome number from twenty-eight to fourteen.

Allen (1905) has found that the first division of the oospore nucleus of Coleochaete is also a reduction division. In all cases described the gametes unite completely and male and female chromosomes are not found in separate groups.

The fungi afford an interesting variety of phenomena in connection with fertilization. As Harper (1910) points out, they have served to enlarge our conception of the sexual process elsewhere. In the rusts a fusion of two cells may occur independently of nuclear fusion as was shown by the work of Blackman (1904) and Christman (1905). The nuclei remain separate throughout the sporophytic phase until they fuse in the teleutospore just before reduction. The long period in which the nuclei exist side by side in the sporophyte without fusing and their final fusion prior to reduction is significant. There is no question but that the male and female chromosomes are independent in the sporophytic generation. No less striking are the conditions found in the Ascomycetes. Harper's (1905) work on the mildews has shown the existence of two nuclear fusions in the life cycle, one at the origin of the ascocarp where there is a fusion of differentiated gametes, and the other in the ascus. The nuclear fusion in the ascus is followed by three successive divisions which are thought to be correlated with the occurrence of the double fusion.

A most remarkable fusion which takes the place of the normal fertilization has been described in *Aspidium falcatum*, an apogamous fern, by Miss Allen (1914). In this case the sporophyte develops through a vegetative bud from the prothallus and has presumably the $1x$ number of chromosomes. Sixteen spore mother cells are present as in other ferns but these fuse in pairs to give eight cells from which a maximum of thirty-two spores may be developed. This fusion sometimes occurs while the spore mother cells are in the spireme stage so that two complete spiremes are present in the fusion nucleus. The fusion is followed immediately by the reduction division characteristic of spore formation.

The behavior of the chromosomes in fertilization has been described for many species of Gymnosperms. It was found by Blackman (1898), Ferguson (1904), and Chamberlain (1899), that in Pinus the male and female chromosomes are formed independently for the first division of the fertilized egg. The independent formation of male and female chromosomes has also been described in Tsuga (Murrill 1900), Juniperus (Norén 1907), and Abies (Hutchinson 1915). All of these accounts are in general accord with the conditions found in some other plants and in many animals.

A most unusual behavior of the chromosomes in fertilization has been described in *Abies balsamea* by HUTCHINSON (1915). The chromosomes of the male and female gametes are formed independently as is the case in most conifers. As the two groups unite the chromosomes are said to become paired side by side and to twist about one another in a manner similar to their behavior in the reduction divisions. The number of chromosome pairs is haploid. According to HUTCHINSON there is then a *transverse* segmentation of the chromosome pairs. The resulting pairs of chromosomes are diploid in number, and of about half the length of the pairs before segmentation. The chromosomes are described as then separating to form $4x$ chromosomes, half of the number passing to each pole in the first division. The description is not supported by convincing figures.

CHAMBERLAIN (1916) in *Stangeria paradoxa* finds a similar pairing of chromosomes at fertilization. Although he apparently upholds HUTCHINSON's conclusion he does not state that in this form there is a transverse segmentation of the chromosome pairs in the first division of the egg.

In the angiosperms there is no detailed account of the behavior of the chromosomes during the first division of the fertilized egg. In most cases the sexual nuclei fuse while in the resting condition. Cases have been described in Lilium (GUIGNARD 1891), Cypripedium (PACE 1907), and Fritillaria (SAX 1916), where the gamete nuclei were rarely in the spireme stage before fusion. The first division of the fertilized egg in angiosperms has been described by GUIGNARD (1891), ERNST (1902), GOLDSCHMIDT (1916), RENNER (1914) and the writer (SAX 1916), but in no case have the descriptions been complete and rarely has more than a single division figure been shown in any of the papers.

ATKINSON (1917) in a recent genetical paper on Oenothera has presented some results which he maintains can be explained only on the assumption that there is a segregation of factors in the F_1 zygote. He also states (p. 257):

> "The germ plasm is peculiarly sensitive to shock from the meeting of sperm and egg, particularly when there is a genotypic difference between the two germ plasms. This results more or less in interchange, crossing over, dominance, as well as blending, of factors in the zygote, often accompanied by selection of factors into different associations in different zygotes giving rise to more than one hybrid type in the F_1 generation of crosses."

ATKINSON's statements are largely theoretical, and, as DAVIS (1917) has indicated, have little experimental and no cytological basis, yet we must consider such possibilities in the present study.

The purpose of this study is to consider not only the behavior of the chromosomes of the gametic nuclei, but also in the "triple fusion." Although it is questionable if we may consider the triple fusion as a real fertilization, yet so far as the inheritance of endosperm characters is involved it is quite comparable to the union of the gametic nuclei. For this reason and also because of the great importance of endosperm characters in cereal breeding, we will give some attention to the chromosomes in the triple fusion in both Fritillaria and Triticum. It is also necessary to describe briefly the development of the embryo sac in Fritillaria in order to understand the chromosome number found in the first division of the endosperm nucleus.

MATERIAL AND METHODS

The material for this paper was secured from about four thousand cases of fertilization in *Fritillaria pudica* Spreng. and not less than two hundred cases of fertilization in *Triticum durum hordeiforme* Hort. var. Kubanka. Flemming's stronger solution and chrom-acetic acid were used as fixatives for the Fritillaria ovaries. At the suggestion of Dr. Osterhout about 0.5 percent of urea salts were added to the above fixatives and gave excellent results with the wheat ovaries. Besides assisting as a fixative, the urea salts reduce the surface tension of the solution and aid in the penetration of the fixative. Sections were cut from 10 μ to 20 μ thick. Modifications of Flemming's triple stain, and Heidenhain's iron alum haematoxylin were used in staining with good results.

THE CHROMOSOMES IN FRITILLARIA

A brief consideration of the chromosome number in the development of the embryo sac in Fritillaria is necessary before describing the later stages. Numerous counts of the chromosome number in the various stages of embryo sac development were made. In the heterotypic division of the megaspore mother cell twelve chromosomes pass to each pole. The second division usually appears to be normal and the four resulting nuclei each receive twelve chromosomes. These nuclei pass into the resting stage. The nuclei in the third division present considerable variation in respect to chromosome number. The two nuclei at the micropylar end of the embryo sac have the usual $1x$ number of chromosomes and when they divide twelve chromosomes pass to each pole. One of these resulting nuclei becomes the upper polar nucleus. The other three constitute the nuclei of the cells of the egg apparatus, one of which functions as the egg. One of the two nuclei nearest the chalazal end of the sac in the four-nucleate stage disintegrates. The other, which has received twelve chromosomes from the previous division, has at the time of division not twelve chromosomes, but about twenty-four, and in the division about twenty-four chromosomes pass to each pole. One of the resulting nuclei becomes the lower polar nucleus. As a result of this development of the embryo sac the egg and upper polar nuclei each contain $1x$ or twelve chromosomes while the lower polar nucleus possesses approximately $2x$ chromosomes. The lower polar nucleus and the normal antipodal nucleus are considerably larger than the other nuclei of the embryo sac, presumably because of the $2x$ number of chromosomes which they contain.

The general behavior of the sexual nuclei in Fritillaria has been described in an earlier paper (SAX 1916). The contents of the male nuclei while free in the embryo sac were found to be in an irregular dark-staining network. The male nucleus soon after coming in contact with the egg nucleus loses this netlike structure of its chromatin and passes into the usual resting condition. The union of the sexual nuclei occurs while they are in the resting condition as shown in figure 1, plate 1. The male nucleus can be recognized by its slightly smaller size. In both nuclei there are nucleoli, and the chromatin is in a reticular network. In the cases figured the nuclei are flattened at the point of contact but in some cases the egg nucleus is somewhat indented. The cytoplasm is distributed uniformly throughout the lower part of the egg cell, while the upper part is almost entirely occupied by a large vacuole. The gametic nuclei remain distinct for a comparatively long time, often until the endosperm has reached the four- or eight-nucleate stage.

The disappearance of the adjacent nuclear membranes of the sexual nuclei results in a fusion nucleus which is also in the resting stage. At first there is a trace of the outlines of the two nuclei but later the fusion nucleus shows no indication of its binucleate origin. At this stage all of the chromatin stains alike and it is impossible to distinguish the male and female chromatin as separate contributions. Such a case is shown in figure 2. The chromatin is in the resting condition and more nucleoli are present than in the nucleus of the unfertilized egg.

The fusion nucleus remains in the resting stage but a short time. The chromatin forms a fine threadlike structure and the nucleoli begin to disappear. Figure 3 shows an early spireme stage where the spireme is not completely formed. Delicate threads can be seen among the heavier chromatin threads. The spireme thread thickens until it appears as illustrated in figure 4. Here the nucleoli have not entirely disappeared and traces of the nuclear membrane may be seen. The broken appearance of the spireme is partly due to the passage of the microtome knife through the edge of the nucleus. But in many other spiremes examined it was also impossible to demonstrate the presence of a single continuous spireme.

After the formation of the spireme the nuclear membrane disappears entirely. The spireme contracts and becomes somewhat thicker just before the segmentation into chromosomes occurs. The segmentation of the spireme is shown in figure 5. The nuclear membrane has completely disappeared and the segmenting spireme has contracted. Surrounding the nuclear cavity is a dense area of cytoplasm from which delicate threads pass to the newly formed chromosomes.

A significant variation in spireme formation of the zygote has been described for Fritillaria in an earlier paper (SAX 1916, fig. 21). In this case the sexual nuclei were found in the spireme stage before fusion. This condition is very rare in the fusion of the egg and male nuclei, but is not uncommon in the nuclei of the triple fusion.

The chromosomes in the metaphase of the first division are long and often cover much of the spindle. The spindle is bipolar and the chromosomes are in a single group and not paired. The number of chromosomes at this time is twenty-four. A longitudinal section of the metaphase of the zygote is presented in figure 6. All of the chromosomes are not shown in this figure, but in this and the two following figures the proportion of chromosomes omitted, due to their presence in an adjacent section, is about the same. The cytoplasm at this time is more uniform than in the preceding stages.

As the chromosomes divide twenty-four pass to each pole. There is no evidence that the male and female chromosomes are separated in two groups. The spindle is typically bipolar. The anaphase of the first division of the zygote is shown in figures 7 and 8. In figure 7 the chromosomes are not so large as in the metaphase. In figure 8 the chromosomes are nearer the poles and they are larger than in the preceding figure. The spindle at the lower end appears to be three-parted, possibly due to the fact that it is cut somewhat obliquely. The other pole has no appearance of being divided. In neither case figured nor in many others examined is there any evidence that the chromosomes pair.

In the telophase the chromosomes form a single compact group at either pole. The fibers between the poles thicken and the cell plate is formed. A clear telophase is shown in figure 9. Although the chromatin groups are very compact the outlines of the chromosomes are still apparent.

The second division of the embryo appears to be the same as any other normal somatic division. Often one of the cells of the two-celled embryo divides before the other, but usually they divide at the same time.

The second male nucleus and the two polar nuclei usually fuse in the resting condition. Often, however, the nuclei are found in the spireme stage before they fuse and occasionally before the upper polar nucleus and male nucleus have joined the lower polar nucleus. A striking case of the latter condition is shown in figure 10. The nuclei are in early spireme stages. The difference in the size of the nuclei is evident. In this triple fusion the large lower polar nucleus contributes about $2x$ chromosomes while the upper polar nucleus and the male nucleus each contribute $1x$ chromosomes. Thus $3x$ chromosomes are contributed by the maternal parent and only $1x$ by the male parent.

The number of chromosomes in the metaphase of the first division of the "endosperm nucleus" is approximately $4x$ or forty-eight. From figure 11 it is evident that this division appears to be normal. There is no segregation of chromosomes into groups, no pairing of chromosomes, and the spindle is not multipolar.

The chromosomes of the metaphase split longitudinally and about forty-eight daughter chromosomes pass to each pole. In the anaphase shown in figure 12 it was impossible to show all of the chromosomes. Apparently an equal number of chromosomes pass to each pole and the division in every way appears to be regular.

THE CHROMOSOMES IN TRITICUM

The mature embryo sac in wheat consists of the egg cell, two synergids, two polar nuclei in the primordial endosperm, and a large number of antipodal cells. The cytoplasm of the egg cell is more or less vacuolate near the periphery, but a denser layer is found around the nucleus. The egg nucleus contains one large nucleolus and often several small ones. The chromatin is arranged in a loose irregular network. The polar nuclei come in contact with each other, but do not fuse, before fertilization. They are very large and are about equal in size. The cytoplasm of the "Endospermanlage" extends from the polar nuclei to the egg apparatus.

The male nucleus as it enters the egg cell is small, elongated and its contents are so dense that it appears almost homogeneous in structure. It takes a brilliant red stain with the safranin and is easily recognized. A male nucleus free in the cytoplasm of the egg cell is shown in figure 13. It is long and curved at the ends. The structure of the male nucleus appears almost homogeneous except for small vacuoles and darker-staining particles. There is no trace of a separate cytoplasmic sheath around the male nucleus.

The male nucleus when in contact with the egg nucleus is often more or less coiled, but has the same structure as when free in the egg cell. Such a case is presented in figure 14. Immediately around the male nucleus the cytoplasm is less dense and a few delicate threads cross this vacuolate area. This condition was also found in other preparations. The chromatin of the egg nucleus at this time is still in the resting condition.

The male nucleus apparently penetrates the egg nucleus before increasing in size. Many stages were found where the compact spireme of the male nucleus could be seen inside of the membrane of the egg nucleus. Its appearance is striking and unmistakable because of its density and darker-staining properties. In figure 15 the male nucleus is shown inside of the egg nucleus near the membrane. It has increased in size and the irregular compact spireme thread can be seen. There are several small nucleoli in the male contribution of chromatin. The chromatin of the egg nucleus is in the early spireme stage and portions of the spireme thread are often more or less parallel. In figure 16 the early spireme of the male chromatin is especially distinct. Its dark-staining closely coiled spireme is quite distinct from the loose spireme of the egg nucleus. The nuclear membrane is still apparent at this stage. In both cases figured the large nucleolus of the egg nucleus is shown quite separate from the male chromatin.

The segmentation of the two spiremes of the zygote results in $2x$ chromosomes which are unpaired. The metaphase of the first division of the fertilized egg is illustrated in figure 17. There are approximately twenty-eight chromosomes to be seen in this section. Several pieces of chromosomes, or possibly whole chromosomes, were found in an adjacent section. There is no indication that the chromosomes contributed by the male and female gametes lie in separate groups and they are not in pairs. In several chromosomes shown in this figure a longitudinal division may be seen. This longitudinal splitting of the chromosomes continues until all of the chromosomes have divided, as illustrated in figure 18. There are about twenty-one pairs shown in this figure and there are six or seven pairs in an adjacent section. These split chromosomes are comparatively long and are often curved. The daughter halves are most widely separated at the center and in some cases they appear to be slightly twisted about one another. After the completion of the longitudinal fission $2x$ daughter chromosomes pass to each pole. An anaphase of the first division is shown in figure 19. The daughter chromosomes are about as long as the mother chromosomes of the metaphase and are often curved. The spindle is clearly bipolar. The dense layer of cytoplasm so conspicuous about the egg nucleus in the earlier stages is apparent around the spindle.

The chromosomes pass to each pole in a single group. In figure 20 approximately twenty-eight chromosomes may be counted at each pole in the late anaphase. The chromosomes have shortened a little and are in compact groups. It will be noted that the dense area of cytoplasm in the egg cell is for the most part around only the upper pole, while the chromosomes of the lower pole lie in the more vacuolate cytoplasm. The chromatin of the telophase passes into the resting stage, a cell plate is laid down and the two-celled embryo is formed.

The male nucleus which unites with the polar nuclei appears to be quite similar to the one which unites with the egg nucleus. In figure 21 the triple fusion is shown. The dark-staining male nucleus is coiled at the side of one of the polar nuclei. The polar nuclei are large and of about equal size. Each contains a large nucleolus and the chromatin is in granules in an open network.

At the time of spireme formation the chromatin contributed by each of the three nuclei may be distinguished. Such a case is shown in figure 22. Here the spireme of the male nucleus is in a comparatively compact ball at the upper side of the figure. The spireme of each polar nucleus is rather open, very irregular, and quite distinct. The nucleolus and outlines of each polar nucleus may be seen, but the nuclear membranes have almost entirely disappeared.

The chromatin of the male nucleus and polar nuclei maintain their independence not only in the spireme stage, but apparently also in the early division stages. Figures 23 A and 23 B are drawn from adjacent sections of the first division of the triple fusion nucleus. This is the early metaphase when the chromosomes are on the nuclear plate. There are approximately forty chromosomes to be counted. The chromosomes appear to be in three groups, each group containing approximately an equal number of chromosomes. The spindle in figure 23 A is clearly two-parted at the upper end and more or less so at the lower end. The spindle in figure 23 B appears to be distinct from the spindles in figure 23 A. Later stages in the first division of the triple fusion nucleus were not observed, but judging from many counts of later endosperm divisions, the first division is regular and an equal number of chromosomes pass to each pole. The fact that there are about forty chromosomes in the endosperm divisions indicates that the polar nuclei each contribute 1*x* chromosomes. After the first division the endosperm nuclei divide rapidly and cell walls are not formed in the early development of the endosperm.

DISCUSSION

In many animals and in most gymnosperms the independence of the formation of the male and female chromosomes following fertilization is unquestioned. There are a few cases in the angiosperms where the independent formation in the zygote of the spiremes from the gametes has been demonstrated. In an earlier paper (SAX 1916) the writer described the gamete nuclei of Fritillaria, in rare cases, as in the spireme stage before fusion. In wheat the spireme of the male and female nuclei are formed separately even though the male nucleus is within the egg nucleus at the time of spireme formation (figures 15 and 16). In both Fritillaria and Triticum the nuclei of the triple fusion may be in the spireme stage before fusion. In Triticum the chromosomes contributed by each nucleus appear to be in more or less separate groups even in the metaphase of the first division. Although there is considerable variation in the condition of the sexual nuclei at the time of fusion, I believe that we are justified in assuming that the male and female chromosomes are formed independently in the zygote, even in cases where the nuclei fuse in the resting condition.

The behavior of the chromosomes during the first division of the egg in Fritillaria and Triticum is essentially not different from any other normal somatic division. There is no indication that the chromosomes of the male and female gametes are in separate groups, or that they pair in the first division of the zygote. In Triticum the chromosomes in the metaphase, when first split longitudinally, appear much like certain stages in Abies, which HUTCHINSON (1915) interprets as a pairing of chromosomes. But in Triticum the chromosomes of the metaphase before splitting are distinctly 2*x* in number and after splitting there are 2*x* pairs. If a pairing of male and female chromosomes occurred we would expect to find only 1*x* pairs of chromosomes.

In neither Triticum nor Fritillaria is there anything comparable to a reduction division in the fertilized egg nor are there any irregularities which might account for a zygotic segregation of factors. It is possible, as ATKINSON (1917) suggests, that there is a "shock" as the result of the meeting of genotypically different germ plasms, which may cause an irregular behavior of the first division of the zygote. The only cytological work which might support this theory is that of GOLDSCHMIDT (1916). He explains the occurrence of patrocliny in Oenothera crosses as a result of merogony. There is no good cytological evidence of any behavior which would explain a segregation of factors during the first division of the zygote. The segregation of factors in the F_1 as described by ATKINSON, might be accounted for on the assumption that in Oenothera the chromosomes of the zygote behave as described in Abies. But this assumption would lead into other problems more difficult to explain. It is much more probable, as DAVIS (1917) has suggested, that ATKINSON is dealing with genotypically impure parent species, and that his assumptions concerning the segregation of factors in the zygote are entirely unnecessary.

The behavior of the chromosomes of the zygote in Abies, as described by HUTCHINSON (1915), if verified, would be of considerable genetical significance to those who consider the chromosomes the bearers of the hereditary factors. According to HUTCHINSON the chromosomes of the male and female nuclei pair in the zygote so that there are $1x$ pairs. Each pair segments transversely, forming $2x$ pairs of chromosomes. The chromosome segments separate and $2x$ chromosomes pass to each pole. There is no longitudinal division of the chromosomes as is the case in the usual type of somatic division. If we assume that the hereditary factors are located in the chromosomes it is obvious that if homologous chromosome segments pass to opposite poles the hereditary factors will be segregated according to the usual Mendelian behavior. We would then expect a segregation of characters in F_1 individuals in crosses when the parents differ in Mendelizing characters. If we assume that not only are the hereditary factors located in the chromosomes, but also in a definite linear arrangement in the chromosomes, it is evident that the chromosomes can not divide longitudinally at one time and transversely at another time, as described in Abies, without causing chaos in the distribution of the hereditary factors. Furthermore if this process continued through several generations each chromosome would finally contain but a single factor and most of the factors would be lost. Certainly the behavior of the chromosomes in Abies, as described by Hutchinson, can not be brought into harmony with the theory of a linear arrangement of the factors in the chromosomes. To be sure the latter theory is only a working hypothesis, but the research of Morgan and his students, and other experimental work, can best be explained by it.

If in Abies there is a double "reduction," one at the time of sporogenesis, the other during the first division of the zygote, we might expect a compensating fusion at some period in the life cycle. A comparable case is found in the mildews where the double fusion is thought to be followed by a double reduction in the ascus. In view of the present study and the theoretical questions raised by Hutchinson's results, it would be well to examine more critically the behavior of the chromosomes in the first division of the zygote in Abies.

The pairing of the chromosomes in somatic cells has been described in Galtonia, Funkia, Oenothera, Thalictrum and Yucca. It appears that the pairing of the chromosomes may take place at the time of fertilization, as Hutchinson maintains is the case in Abies and as Chamberlain (1916) has described in Stangeria, or that the pairing may not occur until synapsis as is true in the rusts. There may be intermediate examples where the chromosomes pair at various times in the sporophytic life cycle. It is possible as Miss Fraser (1912) suggests, that "the clearest cases of Mendelian inheritance will perhaps be those correlated with a late association of the chromosomes in pairs." Experimental work, however, makes it appear probable that the chromosomes are quite independent, and that if there is any influence or interchange of factors between chromosomes it does not occur until synapsis. According to Harper (1910) the behavior of the chromosomes in the rusts "is certainly strongly suggestive that synapsis and its accompanying phases represent a stage of mutual influence if not of interchange of physical material between the chromosomes much more intimate than any which has preceded it in the life of the sporophyte."

In Fritillaria and in Triticum there is no evidence that the chromosomes pair in fertilization. The male and female spiremes are formed independently. At synapsis there is a pairing of male and female chromosomes. We might expect that here two spiremes are formed, one male and one female, as in fertilization, and that these spiremes or portions of these spiremes, pair side by side (parasynapsis), rather than expect that homologous chromosomes become arranged alternately end to end and then pair as in telosynapsis. In Aspidium where the spore mother cells fuse while in the spireme stage there is a reduction division immediately following. In this case there is probably a pairing of homologous chromosomes as is generally thought to occur in reduction divisions. It is more difficult to assume that here the chromosomes should follow the telosynaptic method of reduction than to assume that the spiremes conjugate side by side as in parasynapsis. In either case, however, the physical difficulties seem to be very great. If there is a somatic pairing of chromosomes in cases where the telosynaptic method of reduction occurs we might expect the male and female chromosomes to become arranged alternately end to end at or soon after fertilization.

In the development of the embryo sac in Fritillaria twenty-four chromosomes are found in the metaphase of the third division at the chalazal end of the embryo sac, and as a result of this division the lower polar nucleus receives about $2x$ or twenty-four chromosomes. A similar doubling of the chromosome number at the chalazal end of the embryo sac has been described in *Lilium martagon* by GUIGNARD (1891), MOTTIER (1897), SARGANT (1896), and STRASBURGER (1908). According to STRASBURGER this doubling is due to a premature longitudinal splitting of the chromosomes and is dependent on the food supply of the plant. In Fritillaria the lower polar nucleus which contains about $2x$ chromosomes is considerably larger than the upper polar nucleus which contains $1x$ chromosomes. Since both nuclei are surrounded by a common cytoplasm, the difference in size is probably due to the difference in chromosome number. In Triticum the polar nuclei are of equal size and so probably have the same chromosome number, presumably $1x$ each. The difference in size between the polar nuclei and the egg nucleus is apparently due to the nuclear cytoplasmic relations.

In the triple fusion in Fritillaria there are about $3x$ chromosomes contributed by the female parent and $1x$ chromosomes contributed by the male parent. If we assume that the hereditary factors are borne by the chromosomes, then the female parent contributes three sets of factors and the male parent contributes only one set. This phenomenon is of considerable importance in relation to the multiple factor hypothesis. For instance HAYES and EAST (1915) have found in a particular cross in corn that the endosperm character borne by the mother was always dominant. One of the parents used had a starchy endosperm, the other a corneous endosperm. Either way the cross was made the F_1 endosperm was always of the same kind as the endosperm of the mother parent. This type of inheritance is explained on the assumption that the two factors contributed by the mother, as a result of polar fusion, are always dominant over the single factor contributed by the male parent. The effect of multiple factors is clearly demonstrated here, and if the female parent contributes not two, but three factors, the maternal contribution should be still more potent.

It is unnecessary to consider the morphological character of the endosperm because this subject has been dealt with fully by EAST (1913). It may be added, however, that the development of the endosperm is independent of the development of the embryo. While working with Mr. E. F. GAINES at WASHINGTON STATE COLLEGE, I found about a dozen cases in wheat where the endosperm had developed normally and yet no embryo was present. One such case has been found in corn. Such a condition, although very rare, is of theoretical interest.

The significance of double fertilization has been a puzzle to many botanists. The suggestion of NEMEC (1910) seem to be the best explanation and has some experimental proof. NEMEC maintains that an endosperm whose characters are contributed by both parents is better suited to the nourishment of the embryo than an endosperm of wholly maternal origin. STINGL'S (1907) work supports this theory. He has transferred embryos of various cereals to their own and other endosperms. In most cases the embryo grew better on its own endosperm than on that of another genus. Preliminary experiments of my own in transferring hybrid corn embryos to the parent endosperms and *vice versa*, have not as yet given definite results. In view of STINGL'S results and my own work it appears that the experimental error is too large to permit small differences in adaptability of embryo and endosperm to be noted. If we assume that a hybrid endosperm is better able to nourish the hybrid embryo than an endosperm derived from the mother only, we might expect that "wider" crosses could be made among plants where the endosperm is derived from both parents.

CONCLUSIONS

A complete series of stages in the first division of the fertilized egg has been found in both *Fritillaria pudica* Spreng. and in *Triticum durum hordeiforme* Host. var. Kubanka.

In Fritillaria the male and female nuclei are of about equal size before fusion. The sexual nuclei usually unite while in the resting condition, although occasionally they are in the spireme stage at the time of fusion. The presence of a single continuous spireme in the zygote could not be demonstrated at any time. In the first division of the fertilized egg each chromosome contributed by the male and female gametes splits longitudinally and twenty-four chromosomes pass to each pole.

In Triticum the male nucleus is small and almost homogeneous in structure even when in contact with the egg nucleus. The male nucleus enters the egg nucleus and forms a separate compact spireme. At the same time the spireme of the egg nucleus is formed. In the first division approximately twenty-eight chromosomes are found in the metaphase. These chromosomes split longitudinally and the $2x$ number pass to each pole.

In both Fritillaria and Triticum the first division of the zygote appears to be essentially like any other normal somatic mitosis. The male and female chromosomes are formed independently; they are not found in separate groups, nor do they pair. There is no chromosome behavior at this time which might account for a zygotic segregation of factors.

In the triple fusion in Fritillaria the nuclei are often found in the spireme stage before fusion. The first division of the endosperm nucleus appears to be very regular. The chromosomes are not paired and there is no segregation of the chromosomes contributed by each nucleus. In this division about $4x$ or forty-eight chromosomes pass to each pole. This number is due to the fact that there is a doubling of the chromosomes at the chalazal end of the embryo sac in the third division and as a result the lower polar nucleus receives about twenty-four chromosomes. Thus in the triple fusion the female parent contributes $3x$ chromosomes and the male parent contributes only $1x$ chromosomes. This phenomenon is of interest in relation to the multiple factor hypothesis.

In Triticum the nuclei involved in the triple fusion form separate spiremes. There is evidence that the chromosomes contributed by each nucleus may remain more or less separate even in the metaphase of the first division. Each nucleus contributes $1x$ or about fourteen chromosomes.

In both Fritillaria and Triticum the chromosomes of the triple fusion are formed independently, there is no pairing of chromosomes and the first and following divisions appear to be regular.

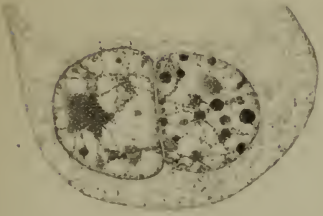
This work was done under the direction of Dr. E. M. EAST to whom I am indebted for suggestions and criticisms. I am also indebted to my wife for much assistance.

EXPLANATION OF PLATES

All drawings were made with the aid of the camera lucida. The figures were drawn from single sections with the exception of figure 22. The magnification is as follows: Figure 3, 1120 diameters; figure 21, 900 diameters; all other figures, 1200 diameters. No reduction.

PLATE I.—FRITILLARIA

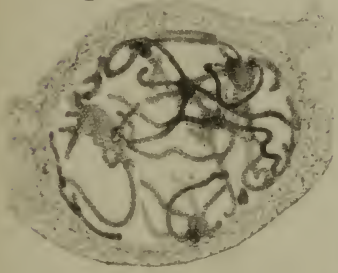
FIGURE 1.—Male nucleus and egg nucleus in contact.
FIGURE 2.—Complete fusion of male and egg nuclei.
FIGURE 3.—Early spireme of fertilized egg.
FIGURE 4.—Spireme of fertilized egg.
FIGURE 5.—Segmentation of spireme. Formation of chromosomes.
FIGURE 6.—Metaphase of the first division of the fertilized egg.
FIGURES 7, 8.—Anaphase of the first division of the fertilized egg.
FIGURE 9.—Telophase of the first division of the fertilized egg.
FIGURE 10.—Early triple fusion.
FIGURE 11.—Metaphase of the first division of the endosperm nucleus.
FIGURE 12.—Anaphase of the first division of the endosperm nucleus.



1

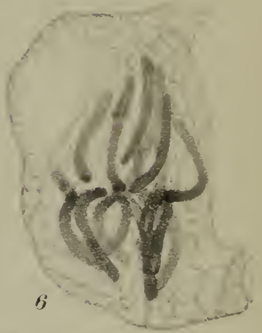
2

3



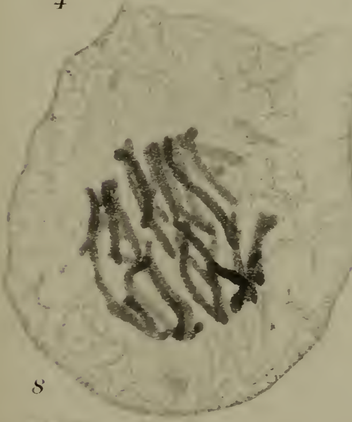
4

5

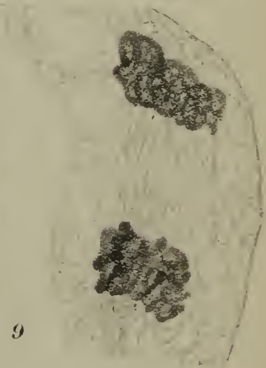


6

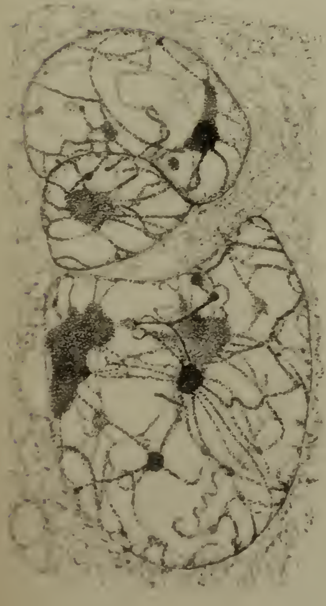
7



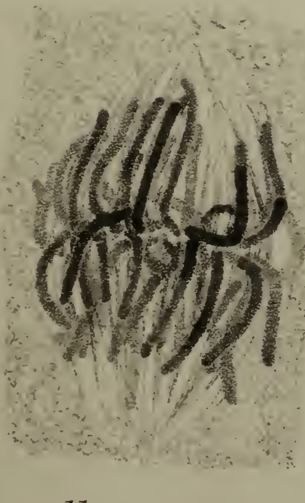
8



9



10



11

12

LITERATURE CITED

Allen, C. E., 1905 Die Keimung der Zygote bei Coleochaete. Ber. d. d. bot. Gesell. **23**: 285-292, *Taf. 13*.

Allen, R. F., 1914 Studies in spermatogenesis and apogamy in ferns. Trans. Wisconsin Acad. Sci. **17**: 1-56, *pls. 1-6*.

Atkinson, G. F., 1917 Quadruple hybrids is Oenothera. Genetics **2**: 213-260.

Blackman, V. H., 1898 On the cytological features of fertilization and related phenomena in *Pinus silvestris* L. Phil. Trans. Roy. Soc. **190**: 395-426, *pls. 12-14*.

1904 On the fertilization, alternation of generations and general cytology of the Uredineae. Ann. Bot. **18**: 323-373, *pls. 21-24*.

Chamberlain, C. J., 1899 Oogenesis in *Pinus laricio*. Bot. Gaz. **27**: 268-280, *pls. 4-6*.

1916 *Stangeria paradoxa*. Bot. Gaz. **61**: 353-372, *pls. 24-26*.

Christman, A. H., 1905 Sexual reproduction in the rusts. Bot. Gaz. **39**: 267-275, *pl. 8*.

Davis, B. M., 1917 The test of a pure species of Oenothera. Proc. Amer. Phil. Soc. **54**: 226-245.

East, E. M., 1913 Xenia and the endosperm of angiosperms. Bot. Gaz. **56**: 217-224.

Ernst, A., 1902 Chromosomenreduction, Entwicklung des Embryosacks und Befruchtung bei *Paris quadrifolia* L. und *Trillium grandiflorum* Salisb. Flora **91**: 1-46, *Taf. 1-6*.

Ferguson, M. C., 1904 Contributions to the life history of Pinus. Proc. Washington Acad. Sci. **6**: 1-202, *pls. 1-24*.

Fraser, H. I. C., 1912 The pairing of the chromosomes. New Phyt. **11**: 58-60.

Goldschmidt, R., 1916 Nochmals über die Merogonie der Oenotherabastarde. Genetics **1**: 348-353, *pl. 4*.

Guignard, L., 1891 Nouvelles études sur la fécondation. Ann. Sci. Nat. Bot. **14**: 163-296, *pls. 9-18*.

Harper, R. A., 1905 Sexual reproduction and the organization of the nucleus in certain mildews. Carnegie Inst. Washington. Publ. 37. 92 pp., *7 pls*.

1910 Nuclear phenomena of sexual reproduction in fungi. Amer. Nat. **44**: 595-603.

Hayes, H. K., and East, E. M., 1915 Further experiments on inheritance in maize. Conn. Agr. Exp. Sta. Bull. 188. pp. 1-31, *pls. 1-7*.

Hutchinson, A. H., 1915 Fertilization in *Abies balsamea*. Bot. Gaz. **60**: 457-472, *pls. 16-23*.

Karsten, G., 1908 Die Entwicklung der Zygoten von *Spirogyra jugalis* Ktzg. Flora **99**: 1-11, *Taf. 1*.

Mottier, D. M., 1897 Ueber das Verhalten der Kerne bei der Entwicklung des Embryosacs. Jahrb. f. wiss. Bot. **31**: 125-158, *Taf. 2, 3*.

Murrill, W. A., 1900 The development of the archegonium and fertilization in the hemlock spruce (*Tsuga canadensis*). Ann. Bot. **14**: 583-607, *pls. 31, 32*.

Nemec, B., 1910 Das Problem der Befruchtungsvorgänge und andere zytologische Fragen. 532 pp. *5 Taf*. Berlin: Gebrüder Borntraeger.

Norén, C. O., 1907 Zur Entwicklungsgeschichte des *Juniperus communis*. Upsala Univ. Årsskr. 64 pp., *4 pls*.

Overton, E., 1893 Über die Reduktion der Chromosomen in den Kernen der Pflanzen. Vierteljahrsschr. Naturf. Gesell. Zurich **38**: 169-186.

Pace, L., 1907 Fertilization in Cypripedium. Bot. Gaz. **44**: 353-374, *pls. 24-27*.

PLATE 2.—TRITICUM

FIGURE 13.—Male nucleus in the egg cell.

FIGURE 14.—Male nucleus in contact with the egg nucleus.

FIGURES 15, 16.—Male nucleus within the egg nucleus.

FIGURE 17.—Metaphase of the first division of the fertilized egg.

FIGURE 18.—Late metaphase of the first division of the zygote.

FIGURE 19.—Early anaphase of the first division of the zygote.

FIGURE 20.—Late anaphase of the first division of the zygote.

FIGURE 21.—Early triple fusion.

FIGURE 22.—Spireme stage in the triple fusion.

FIGURES 23A, 23B.—Adjacent sections of the early metaphase of the first division of the triple fusion nucleus.

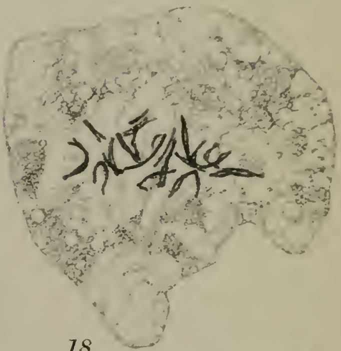
13

14

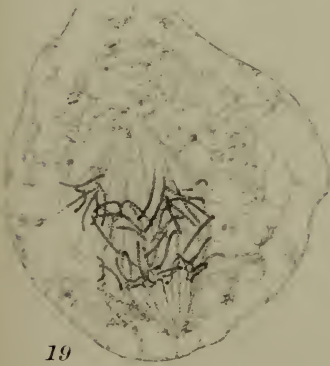
15

16

17

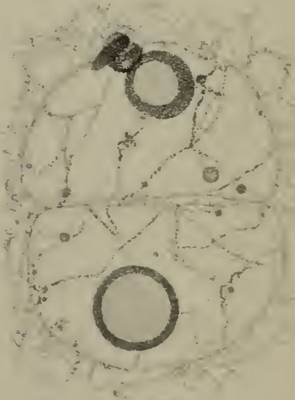


18



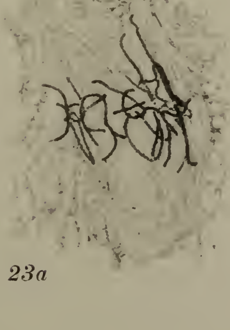
19

20

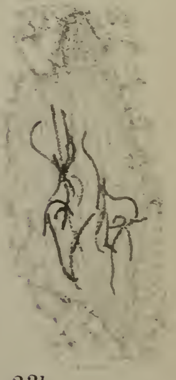


21

22



23a



23b

Renner, O., 1914 Befruchtung und Embryobildung bei *Oenothera Lamarckiana* und einigen verwandten Arten. Flora **107**: 115-150, *Taf. 12, 13.*

Sargant, E., 1896 The formation of the sexual nuclei in *Lilium martagon.* Ann. Bot. **10**: 443-477, *pls. 32, 33.*

Sax, K., 1916 Fertilization in *Fritillaria pudica.* Bull. Torrey Bot. Club **43**: 505-522, *pls. 27-29.*

Strasburger, E., 1908 Chromosomenzahlen, Plasmastrukturen, Vererbungsträger und Reducktionsteilung. Jahrb. f. wiss. Bot. **45**: 479-570, *Taf. 1-3.*

Stingl, G., 1907 Experimentelle Studie über die Ernährung von Pflanzlichen Embryonen. Flora **97**: 308-331.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JULY 1918

TABLE OF CONTENTS

STUDIES ON SELF-STERILITY I. THE BEHAVIOR OF SELF-STERILE PLANTS

E. M. EAST and J. B. PARK
Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS **2**: 505-609, November 1917

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SELF-STERILITY I. THE BEHAVIOR OF SELF-STERILE PLANTS

E. M. EAST and J. B. PARK

Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received March 19, 1917]

TABLE OF CONTENTS

INTRODUCTION

The occurrence of self-sterility

Among both hermaphroditic animals and plants forms are known in which fertilization of the eggs by sperm or by pollen of the same individual is difficult or even impossible. This condition is known as self-sterility,[1] although the term is not a happy one, since both the male and the female gametes are morphologically perfect and are functional with the complemental gametes of other individuals.

Self-sterility is probably a widespread phenomenon though its presence has been proved experimentally in comparatively few plants and in only one animal. The result, one might even say the aim, of self-sterility, however, is cross-fertilization. Regarded from this standpoint, it is to be classed with the various other specializations of animals and plants, such as morphological differences in the accessory sexual organs, dichogamy, monœcism, diœcism, etc., which tend toward the same end; and since these obvious contrivances for cross-fertilization are so numerous and so dispread, it is difficult to believe that the less easily detected self-sterility is rare, particularly as it has arisen independently in widely separated groups.

The important rôle played by cross-fertilization in the evolution of animals and plants may be attributed in some degree, therefore, to the phenomenon of self-sterility; hence, any light thrown upon its meaning is a contribution toward an explanation of the significance of cross-fertilization in general.

Among animals only *Ciona intestinalis* has been proved to be self-sterile (Castle 1896), though the condition is suspected in several other forms.

Among Angiosperms self-sterility is rather generally distributed. Knuth (1898, Vol. I, pp. 42-45) gives a list of 134 self-sterile species representing 46 families and including both monocotyledons and dicotyledons. This list is the best compilation of recorded cases and may be considered fairly complete to-day as very few additional records have

---

[1] The words self-incompatibility and self-impotence have been substituted for self-sterility by various writers. These terms seem to us to be neither more nor less objectionable than self-sterility, since neither takes into consideration the fact that the same type of infertility may exist between different individuals. The important point in the matter is that one should not confuse the phenomenon with any of those types of true sterility where there is either complete or partial incapacity for the production of gametes functional *per se*. For a discussion of the differences between self-sterility and true sterility see Kraus (1915) and Stout (1916).

appeared in subsequent publications. It is naturally somewhat inaccurate, inasmuch as several cases are recorded in which cross-pollination was merely prevented by bagging the inflorescence or by isolating the plants and self-pollination not insured. Nevertheless, at least 70 percent of the records are properly proved cases of a self-sterility that is something more than an ephemeral condition due to environmental changes or to a fleeting period of reproductive inactivity that is normal in the life history of so many plants.

There remain, then, in the neighborhood of 100 well endorsed instances of self-sterility scattered over some 35 families. These families are so different in their modes of reproduction that no general conclusion can be drawn regarding the development of self-sterility. There are legumes which are usually self-fertilized, and orchids that have developed quite wonderful floral mechanisms favoring cross-fertilization; there are showy flowers, and flowers peculiarly inconspicuous; there are flowers with perfume, and flowers without it; there are anemophilous plants, and plants that would be classed as strictly entomophilous. In certain genera, such as Passiflora, there is a general tendency toward self-sterility; in other genera, for example Verbascum and Nicotiana, closely related species behave very differently.

In other words self-sterility has arisen many times, and often in groups where there was apparently no need for it if the necessity is assumed to be that of cross-fertilization. Not only is this an irresistible argument in favor of the idea already expressed that only a small fraction of the cases of self-sterility have been discovered and that self-sterility has been a much more important factor in plant evolution than has previously been suspected, but it also indicates that certain of the mechanical devices that have received great credit for promoting cross-fertilization were inadequate for the needs of many plants.

EARLY WORK ON SELF-STERILITY

The discovery of self-sterility in plants probably should be credited to Kölreuter, the first[2] real student of hybridization, although his case is somewhat doubtful. Kölreuter (1764) found that during two years three plants of *Verbascum phœniceum* set no seed with their own apparently good pollen, although they seeded readily with pollen of *V. Blat-*

---

[2] Thos. Fairchild crossed *Dianthus caryophyllus* with *D. barbatus* in 1719, and Linneus brought his hybrid between *Tragopogon pratensis* and *T. porrifolius* into flower in 1759, but neither of them contributed to the world any important facts regarding hybridization.

taria, V. nigrum, V. phlomoides and *V. Lychnitis.* Later these plants showed sporadic fertility alternating with sterility of pollen or of eggs or of both sex-cells, so that this instance may be only one of induced true sterility due to conditions. It seems to deserve priority as an instance of self-sterility, however, for DARWIN (1872, p. 341) found *V. phœniceum* and *V. nigrum* to be self-sterile, although the related species *V. Thapsus* and *V. Lychnitis* were self-fertile.

SPRENGEL (1793), the other important hybridist of the 18th century does not mention the subject.

Several true instances of self-sterility were discovered by HERBERT (1837) in his experiments with the Amaryllidaceæ. He says:

> "Nine very fine crosses of Hippeastrum were flowering [there] at the same time; one a natural seedling from *Johnsoni* or *Regio-vittatum,* two, *Johnsoni-pulverulentum,* one *Johnsoni-vittatum,* one *psittacino-Johnsoni* crossed again by *vittato-Johnsoni,* one from *Johnsoni* by *solandriflorum,* and two from *vittato-Johnsoni* by the same. Being desirous of blending again these plants which were all cross-bred, different flowers were touched with pollen from their several neighbors and ticketed, and other flowers were touched with their own pollen. Almost every flower that was touched with pollen from another cross produced seed abundantly, and those which were touched with their own either failed entirely or formed slowly a pod of inferior size with fewer seeds, the cross impregnation decidedly taking the lead."
>
> "It is only from the superior efficacy of the pollen of another plant that we can account for the circumstances of some hybrid plants, which breed freely with plants of either parental stock and fecundate them, not producing seed readily when left to themselves; for if their pollen is able to fertilize and their ovary to be fertilized, there can be no positive sterility in the plant, though there may be a want of sufficient energy under certain, or perhaps under ordinary, circumstances."

These observations of HERBERT referred to hybrids, though he also found self-sterility in the species *Zephyranthes carinata,* and DARWIN in discussing them very properly sets them apart from the cases of self-sterility in pure species. We shall show later, however, that absolute self-sterility exists both in pure species and in hybrids, and is one and the same phenomenon. In fact HERBERT himself very nearly demonstrated this. In a letter to DARWIN (1875) written in 1839, he states that after a duplication of these experiments with like results, he was led to make similar trials on a pure species. He selected a plant of *Hippeastrum aulicum* which he had recently imported from Brazil. Three of its flowers he selfed without result; a fourth flower he crossed with pollen of a triple cross between *H. bulbulosum,*[3] *reginæ* and *vittatum* and obtained good seed.

---

[3] Probably *H. rutilum* Herb.

Later work cited by DARWIN (1875) also supports this idea. BIDWELL in New South Wales found *Amaryllis belladonna* to be partially self-sterile, though fertile to the pollen of other species. E. BERNET, of Antibes, a man having a wide experience in crossing species of Cistus, found that their hybrids when fertile (he does not mention the pure species) were completely self-impotent. His statement is that, quoting Darwin, "the flowers are always sterile when the pistil is fertilised by pollen taken from the same flower or from flowers on the same plant." "But," he says—without the italics—*"they are often fertile if pollen be employed from a distinct individual of the same hybrid nature, or from a hybrid made by a reciprocal cross."* A. RAWSON, a well known English horticulturist, found the same absolute self-sterility in various named varieties of Gladiolus that were said to have descended from Gandavensis, an old race produced by crossing *G. natalensis* by *G. oppositiflorus.* The interesting point in RAWSON's work was that none of the plants of th same variety would set seed when interpollinated. As each variety had been propagated asexually by bulbs, he was of course actually dealing with plants of the same germinal constitution, though under somewhat different environmental conditions. For this reason it is extremely improbable that these were cases of induced true sterility.

> "Altogether, Mr. RAWSON, in the year 1861 fertilised twenty-six flowers borne by four varieties with pollen taken from other varieties, and every single flower produced a fine seed capsule; whereas fifty-two flowers on the same plants, fertilised at the same time with their own pollen [which had been proved to be good by the crosses], did not yield a single seed capsule."

Returning to the phenomenon as exhibited in pure species, WM. MOWBRAY, gardener of the Earl of Mountnorris, in a letter to the Secretary of the HORTICULTURAL SOCIETY (England), dated October 29, 1830, states that he could get fruit only from *Passiflora alata* and *P. racemosa* by reciprocal fertilization.

Observations on self-sterility in this genus continued to be made later by a number of observers. The most important work was done by ROBERTSON MUNRO (1868). MUNRO found *P. alata, P. racemosa, P. cœrulea, P. Bellottii, P. kermesina, P. holosericea* and *P. fulgens* to be self-sterile, while DARWIN obtained evidence that *P. laurifolia* and *P. quadrangularis* were in the same condition. The evidence of perfect self-sterility in the first three species is incontrovertible, in the remaining species it is highly probable.

Some of the details from MUNRO's work are exceedingly interesting.

In the first place he found plants of *P. alata* to be highly fertile with their own progeny as the following quotation shows.

> "I impregnated a considerable number of these flowers with their own pollen, everyone of which proved abortive. But on impregnating eighteen flowers on the mother plant with pollen from her own self-impotent seedlings, I got eighteen fine plump ovaries full of seed."

Again, MUNRO found that self-sterile plants were sometimes cross-fertile and sometimes cross-sterile with plants of the same species and presumably of the same generation. For example, three self-sterile plants of *P. cœrulea* all produced seeds with pollen from one other plant. The same experiment on *P. alata* showed cross-sterility in two instances and cross-fertility in one instance.

A curious case of a return to self-fertility in *P. alata* through grafting was also reported by MUNRO. Mr. DONALDSON, gardener at Keith Hall, grafted a self-sterile plant upon stock of an unknown species. Though its pollen still refused to fertilize certain other plants of the same species, it was markedly self-fertile and fertile with at least one other plant. Seedlings from this plant were all self-sterile but were fertile with the mother plant.[4]

GÄRTNER (1849), who was among the most reliable of the early hybridizers, found a number of self-sterile species. *Dianthus japonicus* was sterile both with its own pollen and with the pollen of *D. barbatus*. Two plants of *Lobelia fulgens* likewise proved self-sterile. Their pollen was good on *L. cardinalis* and *L. syphilitica*, their ovules could be fertilized by the pollen of these species, but self-pollination yielded nothing. A plant of *Verbascum nigrum* was also completely self-impotent though fertile as a male with *V. Lychnitis* and *V. austriacum* and fertile as a female with *V. Thapsus*.

Similar conditions in certain exotic orchids were reported by SCOTT (abstract 1863, complete paper 1865). A duplicate of a table in his paper and a summary of his conclusions follow.

SCOTT and MUNRO (DARWIN 1875) each independently found *Oncidium sphacelatum* also to be wholly self-sterile after some three hundred attempts at self-pollination, though the species was fertile reciprocally with other Oncidiums. MUNRO in addition confirmed SCOTT's observations on *O. divaricatum* and added *O. flexuosum* to the list of self-sterile plants.

---

[4] It is likely that this phenomenon is similar to the pseudo self-fertility due to conditions, which is discussed later in this paper.

Unions between *Oncidium microchilum, O. divaricatum* var. *cupreum* and *O. ornithorhynchum.*

	Number of flowers fertilized	Total number of capsules produced	Number of good capsules	Estimated number of seeds	Estimated number of good seeds	By calculation	
						Total seeds	Good seeds
1. *O. ornith.* × *O. micro.* (No. 2)	8	3	3	20200	4242	or as 1000 to 210	
2. *O. micro.* (No. 2) × *O. ornith.*	12	0					
3. *O. ornith.* × *O. micro.* (No. 1)	8	5	4	23360	3737	or as 1000 to 160	
4. *O. micro.* (No. 1) × *O. ornith.*	12	2	0				
5. *O. divar. cup.* × *O. micro.* (No. 2)	6	3	3	22050	7938	or as 1000 to 360	
6. *O. micro.* (No. 2) × *O. divar. cup.*	18	2	0				
7. *O. divar. cup.* × *O. micro.* (No. 1)	6	4	4	26240	8922	or as 1000 to 340	
8. *O. micro.* (No. 1) × *O. divar. cup.*	6	2	2	17700	1434	or as 1000 to 420	
9. *O. micro.* (No. 1) × *O. micro.* (No. 2)	6	5	4	45800	34350	or as 1000 to 750	
10. *O. micro.* (No. 2) × *O. micro.* (No. 1)	18	0					
11. *O. micro.* (No. 1) × own pollen	24	1					
12. *O. micro.* (No. 2) × own pollen	24	0					

"By a summary comparison of these results we have the following highly interesting facts disclosed. First, we see that the male element of *O. microchilum* (No. 1) will fertilise the female element of the two distinct species *O. ornithorhynchum* and *O. divaricatum* var. *cupreum* and yet be completely impotent upon its own female element; nevertheless the susceptibility of the latter (female element) to fertilisation is shown by its fertile unions with another individual of the same species, and likewise by a fertile union with an individual of a distinct species, namely *O. divaricatum* var. *cupreum.* Secondly, the male element of *O. microchilum* (No. 2) will fertilise the female element of *O. ornithorhynchum* and *O. divaricatum* var. *cupreum,* and likewise another individual of its own species, though on its own female element it is utterly ineffective."

These observations, together with similar ones on *O. Cavendishianum* recorded by LECOQ (1862) from the experiences of RIVIÈRE were made on hot-house plants and DARWIN originally attributed their self-sterility to the peculiar conditions under which they were grown. He was forced to modify his conclusions, however, through information received from FRITZ MÜLLER. The latter self-fertilized over one hundred flowers of *Oncidium flexuosum* at Desterro, Brazil, where it is native, without obtaining a single seed, but he did discover the important fact[5] that each plant *was fertile with the pollen from any other plant.*

SCOTT and MÜLLER each independently made the further discovery that the tissue of the style of the self-sterile plants was penetrated freely by the pollen tubes after selfing, though fertilization did not subsequently occur.

As DARWIN noted:

> "Another observation made by FRITZ MÜLLER is highly remarkable, namely that with various orchids the plant's own pollen not only fails to impregnate the flower, but acts on the stigma, and is acted on, in an injurious or poisonous manner."

We have not been able to find any confirmation of these results, and it seems entirely probable that the apparently poisonous action of the pollen after an "illegitimate" pollination, might have been due to the action of bacteria or fungi, since the work was done under tropical conditions. But the facts are so exceptional that we give DARWIN'S (1875, vol. 2, p. 112) account.

> "FRITZ MÜLLER observed the poisonous action of the plant's own pollen in the above mentioned *Oncidium flexuosum, O. unicorne, pubes* (?), and in two unnamed species. Also in two species of Rodriguezia, in two of Notylia, in one of Burlingtonia, and of a fourth genus in the same group. In all these cases, except the last, it was proved that the flowers were, as might have been expected, fertile with the pollen from a distinct plant of the same species. Numerous flowers of one species of Notylia were fertilised with pollen from the same raceme; in two day's time they all withered, the germens began to shrink, the pollen masses became dark brown, and not one pollen grain emitted a tube. So that in this orchid the injurious action of the plant's own pollen is more rapid than with *Oncidium flexuosum* Eight other flowers on the same raceme were fertilised with pollen from a distinct plant of the same species; two of these were dissected and their stigmas were found to be penetrated with numberless pollen tubes; and the germens of the other six flowers became well developed. On a subsequent occasion many other flowers were fertilised with their own pollen, and all fell off dead in a few days; whilst some flowers on the same raceme which had been left simply unfertilised adhered and long remained fresh. We

---

[5] It is probable that cross-sterility existed, but was not discovered.

have seen that in cross unions between extremely distinct orchids the pollen long remains undecayed; but Notylia behaved in this respect differently; for when its pollen was placed on the stigma of *Oncidium flexuosum,* both the stigma and pollen quickly became dark brown, in the same manner as if the plant's own pollen had been applied."

Müller suggests an explanation of this phenomenon which must be pleasing to the minds of strict Natural Selectionists. He believes it to be an advantage to the species to have its pollen positively deleterious rather than simply neutral, because the flowers would then soon drop off, and the energies of plants no longer be directed toward nourishing a part which would not finally function.

Another quotation from Darwin (*ibid.*, p. 113) is interesting both for the facts contained and for the deductions of Müller.

"The same naturalist found in Brazil three plants of a Bignonia growing near together. He fertilised twenty-nine flowerets on one of them with their own pollen, and they did not set a single capsule. Thirty flowers were then fertilised with pollen from a distinct plant, one of the three, and they yielded only two capsules. Lastly, five flowers were fertilised with pollen from a fourth plant growing at a distance, and all five produced capsules. Fritz Müller thinks that the three plants which grew near one another were probably seedlings from the same parent and that from being so closely related, they acted very feebly on one another. This view is extremely probable for he has since shown in a remarkable paper (Müller 1873) that in some Brazilian species of Abutilon, which are self-sterile, and between which he has raised some complex hybrids, that these, if near relatives were much less fertile *inter se,* than when not closely related."

This work of Müller (1873) consisted in noting the fertility of various matings of 8 species of Abutilon that he denotes by the letters A, C, E, F, M, P, S and V, the individual plants being distinguished by subscripts. Thus the plants $EF.F_1$ and $EF.F_2$ are similar combinations formed by crossing species E with species F and crossing the first generation hybrids thus formed with F_1 and F_2. The principal results were as follows:

Number of flowers	Mother plant	Source of pollen	Number of fruits	Average No. of seeds
9	$F.EF_1$	Others of same stock		
20	$F.EF_1$	$F.EF_2$ $EF.F_1$ and $EF.F_2$	3	1.3
10	F.EF	FE and FE_2	10	4.5
11	F.EF	EF_2 and EF_3	10	4.6
10	F.EF	F.	9	4.6
6	F.EF	$F.CF_1$ and $F.CF_2$	6	4.5
1	F.EF	FS_1	1	4.7

He says that the results following the intercrossing of sister plants were not due to bad pollen, as on other plants it was completely potent; the pollen of $F.EF_2$ producing fruit full of seeds on FS_1, that of EF.F on FE_2, that of $EF.F_2$ on F, and that of $F.EF_1$ on F, $F.CF_2$, FS_1 and FS_2. In explaining the phenomenon he follows DARWIN in supposing inbreeding to be the cause.

Most of these observations and investigations were known to DARWIN who not only published historical accounts in the "Origin of species" and "Variation of plants and animals under domestication," but between 1860 and 1880 carried out numerous experiments on the subject which were reported in a series of papers in the JOURNAL OF THE LINNEAN SOCIETY and other places and were brought together in the three classics, "On the various contrivances by which British and foreign orchids are fertilised by insects" (1862), "The effects of cross- and self-fertilisation in the vegetable kingdom" (1876), and the "Different forms of flowers on plants of the same species" (1877).

DARWIN'S investigations on fertilization in the orchids are only remotely related to the subject in hand, but his experiments on heterostyled dimorphic forms are, we believe, concerned with an analogous phenomenon. The "illegitimate" unions according to DARWIN include certain matings other than self-pollination, but the greatly decreased fertility after self-pollination in practically all of these species as well as the absolute self-sterility of so many forms indicate that the condition is one like ordinary self-sterility though complicated by a linkage with style length and with pollen size. The work of BATESON and GREGORY (1905) on the inheritance of heterostylism in Primula has done something toward clearing up these relationships, but much remains for the future. As these investigations of DARWIN are readily available and cannot, at present, add materially to our discussion of self-sterility on account of moot points, they will not be described further; but we shall abstract from the experiments on those plants usually considered to be genuinely self-sterile.

DARWIN (1876) investigated rather thoroughly the conditions in five self-sterile species, *Eschscholtzia californica, Abutilon Darwinii, Senecio cruentus, Reseda odorata* and *R. lutea.*

A plant of *Eschscholtzia californica* had been accidentally found to be self-sterile by FRITZ MÜLLER (1868, 1869) while working in southern Brazil. This induced him to investigate its behavior through six generations, during which time he found all of the plants to be completely self-sterile though fertile between themselves. As DARWIN had found

English plants comparatively self-fertile and as HILDEBRAND had discovered no complete self-sterility in plants grown in Germany, he obtained from MÜLLER seed of the Brazilian plants known to be self-sterile and from them raised seedlings. These while not wholly self-fertile, tended toward fertility, which fact DARWIN attributed to the lower English temperature. A second generation of seedlings proved to be still more self-fertile. Conversely, seed of English stock sent to Brazil proved to be more self-fertile than the native race, though one plant thus exposed to the climate of Brazil for two seasons, was wholly self-sterile.

These results were paralleled by the behavior of *Abutilon Darwinii* which is self-sterile in its native Brazil, but became moderately self-fertile *late in the first flowering season* in DARWIN's greenhouse.[6]

DARWIN made no extensive experiments on self-sterility with Brazilian plants in collaboration, so to speak, with FRITZ MÜLLER; but this was not for the lack of material, for in a letter to FOCKE (1893), MÜLLER says the number of self-sterile species of plants in Brazil is very large, and that different species of the same genus often behave differently in regard to self-pollination. He observes that self-sterility is often associated with unusual vegetative vigor and that species of Oxalis having trimorphic flowers which are all self-sterile make unusually vigorous growths. This condition observed by MÜLLER is doubtless merely another example of the hybrid vigor or heterosis so common among both plants and animals, and shows the reason, of course, why self-sterility has been maintained by natural selection.

DARWIN's experiments on *Senecio cruentus* are noteworthy only because the varieties used were descendants of garden hybrids.

Two plants of a purple-flowered and one plant of a red-flowered variety were found to be self-sterile and cross-fertile.

The experiments with *Reseda odorata* were more detailed. Those of 1868 are shown in tabular form, the letters representing individuals and the subscripts pollinations. As may be seen, the seven plants used were absolutely self-sterile. The number of pollinations made allow us no doubts about the matter, F and G being selfed many times as well as the others, though in these two cases no figures were reported. Sixteen cross-matings, on the other hand, were all fertile.

In the spring of 1869, four other plants were raised from fresh seed and isolated under nets. Three of these proved to be wholly self-fertile, while the fourth was not completely self-sterile.

---

[6] Cf. our results on flowers late in the season.

DARWIN's experiments on *Reseda odorata* in 1868.

	Male parents						
Female parents	A	B	C	D	E	F	G
A	S_{16}	F	F				
B	F	S_{18}	F	F			
C	F	F	S_{19}	F	F		
D	F	F	F	S_{15}	F		
E	F		F	F	S_{8}		
F						S	
G							S

Much surprised at these divergent results DARWIN raised six more plants in 1870. Of these, two were almost self-sterile and four were completely self-fertile. The former produced altogether five seeds, which were grown the following year. These plants made a luxuriant growth, but were almost completely self-sterile like their parents [an indication of pseudo-fertility]. The progeny of the self-fertile plants was not followed.

These varying results were attributed by DARWIN to a difference in inherited sexual constitution. He says in his general conclusions (1876, p. 346):

"Finally, the most interesting point in regard to self-sterile plants is the evidence which they afford of the advantage, or rather of the necessity, of some degree or kind of differentiation in the sexual elements, in order that they should unite and give birth to a new being. It was ascertained that the five plants of *Reseda odorata* which were selected by chance, could be perfectly fertilised by pollen taken from any one of them, but not by their own pollen; and a few additional trials were made with some other individuals, which I have not thought worth recording. So again, HILDEBRAND and FRITZ MÜLLER frequently speak of self-sterile plants being fertile with the pollen of any other individual; and if there had been any exceptions to the rule, these could hardly have escaped their observation and my own. We may therefore confidently assert that a self-sterile plant can be fertilised by the pollen of any one out of a thousand or ten thousand individuals of the same species, but not by its own. Now it is obviously impossible that the sexual organs and elements of every individual can have been specialised with respect to every other individual. But there is no difficulty in believing that the sexual elements of each differ slightly in the same diversified manner as do their external characters; and it has often been remarked that no two individuals are absolutely alike. Therefore we can hardly avoid the conclusion, that differences of an analogous and indefinite nature in the reproductive system are sufficient to excite the mutual action of the sexual elements and that unless there be such differentiation fertility fails."

These inductions are cleverly drawn and clearly expressed, but they are not all justified by the data in DARWIN's possession. The matings between self-sterile plants made by HILDEBRAND, MÜLLER and DARWIN were neither individually nor collectively sufficient to establish the point that "a self-sterile plant can be fertilized by the pollen of any one out of a thousand or ten thousand individuals of the same species," and it is upon this supposition that the generalization is based. Further, MUNRO, whose work was known to DARWIN, had found cross-sterility in Passiflora.

As it is not proposed to make this review a check list of species which are, as a whole or in part, self-sterile, but rather to set forth the known facts concerning the behavior of self-sterile plants and to outline the various theories that have been suggested to interpret the phenomenon, we shall pass DARWIN's conclusions without further comment. His work properly stands as the outpost of advance in the subject until the rediscovery of Mendel's Law in 1900. The method of analysis of pedigree cultures foreshadowed by VILMORIN but really initiated by MENDEL has made a methodological revolution. It seems fitting, however, to close this part of our paper with the work of a botanist who, though making no outstanding contributions to the subject, was a contemporary of and an aid to DARWIN, and who from the chronological standpoint links the work of DARWIN to that of the present day.

HILDEBRAND worked and wrote indefatigably upon questions of fecundation in plants from 1863 until 1908. His first paper (1863), on dimorphism in *Primula sinensis* appeared almost simultaneously with that of DARWIN, and since that time in the neighborhood of seventy contributions on similar subjects have appeared under his name.

HILDEBRAND (1866) published some rather extensive experiments with *Corydalis cava* in which he showed that the plants were absolutely self-sterile although both pollen and ovules were functional. But his investigations were noteworthy with respect to the large number of species in which he established a high probability of self-sterility, rather than for any fundamental researches on the genetic problem concerned. We will mention only one other paper, therefore, merely to show the large numbers of self-sterile plants that are sometimes (possibly often) to be found in a single family when said family is even partially investigated.

In 1896 he published on the Cruciferæ and found *Hesperis tristis, Lobularia maritima* (=*Alyssum maritimum* Lam.), *Cardamine pratensis, Rapistrum rugosum, Iberis pinnata* and *Sobolewskia clavata* fully self-sterile, *Aethionema grandiflorum* and *Hugueninia tanacetifolia* (=*Nasturtium tanacetifolium* Hook.) nearly self-sterile, and only *Draba verna* and *Brassica rapa* fully self-fertile.

RECENT WORK ON SELF-STERILITY

The work of the last decade on self-sterility has been less concerned with the discovery of new cases than with an interpretation of the phenomenon in keeping with modern biological thought. Several noteworthy investigations on both plants and animals have appeared.

JOST (1907) repeated HILDEBRAND'S experiments on *Corydalis cava,* and unlike the latter, observed a small percentage of self-fertility. In his experiments 93 selfed plants yielded 6 capsules, whereas 42 crossed plants produced 30 capsules. Self-sterility was also noted in *Secale cereale* (a variety *montanum*) and *Lilium bulbiferum.* The immediate cause of the different behavior of these plants after self-pollination and after cross-pollination was found to be the difference in rate of pollen-tube growth. In Secale, pollen tubes were found to have penetrated the micropyle in about eight hours after cross-pollination, although after self-pollination the tubes had merely reached the base of the pistil after twenty-four hours. Pollen tubes also appeared to grow somewhat faster than after self-pollination when crosses (?) were made between flowers on the same plant, but in view of the fact that asexually propagated plants from a single seed appear to behave very similarly this observation may not be correct. In this connection it should be mentioned that FOCKE (1890 and 1893) found that *Lilium bulbiferum* plants of the same clonal variety were completely cross-sterile, although sister seedlings were cross-fertile. Similar observations on asexually propagated pome fruits have been made by WAITE (1895) and LEWIS and VINCENT (1909), but in these cases "fruitfulness" rather than "fertility" was noted.

To explain his results JOST had recourse to the old concept of "Individualstoffe." He believes that individuals not only of the same species but of the same family differ qualitatively in their chemical composition, that the gametes of any plant possess the "Individualstoff" of that plant, and that pollen tubes grow well only in tissues having a different "Individualstoff."

In 1912 a very important paper by CORRENS appeared in which a Mendelian interpretation of results was proposed. His experimental work began with a hybrid between *Petunia nyctaginiflora* and *Petunia violacea* that had been produced in 1901, and of which 11 individuals had passed through the winter. Six of these plants were found to be self-fertile, three completely self-sterile and two nearly self-sterile. Among the self-sterile plants certain combinations proved easy to make, while others were impossible. It was sometimes impossible even to cross the self-sterile with the self-fertile plants [probably pseudo-fertile]. For several reasons, however, CORRENS found Petunia unsatisfactory and the work was dropped until 1910; it was then recommenced with *Cardamine pratensis,* a Crucifer that had been shown to be wholly self-sterile by HILDEBRAND (1896).

Concerning the "cause" of self-sterility, borrowing the term from the author, he gives the following facts: The pollen grains germinated on the stigma of the self-pollinated flowers, but produced only short tubes that did not penetrate the tissues of the stigmas, while after cross-pollination the pollen tubes were found in the upper part of the ovaries after only 48 hours.

The pedigree culture investigations began with two plants, B having very light lilac flowers, and G having flowers of a more intense lilac. These plants were crossed reciprocally, the combination B♀ × G♂ being designated No. 1 and the other No. 2. From each of these matings, 30 plants were raised, and formed the basis of the remaining experiments. They were numbered 1a, 1b, 1c, - - - - 2a, 2b, 2c, etc.

These plants were first tested for their fertility when used as females by crossing each individual with the pollen of two unrelated plants from Lake Zürich and Schwabia respectively. These pollinations were successful without an exception, proving that pollen from a single plant could fertilize each of the 60 F_1 sibs.

From 3 to 15 pollinations were then made upon every F_1 plant with the pollen of each parent B and G. About half of these pollinations were uniformly fruitful or uniformly unfruitful as the case might be, but the other half showed variations in behavior that made classification of the results difficult. For example out of ten pollinations of plant 1o with the pollen of B, 6 were successful and 4 unsuccessful. This plant was classed as fertile with B. Again, plant 1k pollinated 7 times with the pollen of G yielded 3 good capsules, 2 poor capsules and 2 failures Correns classes this plant as sterile with G with a question mark. These results seem at first sight to indicate a definitely graduated fertility in Cardamine. This is not impossible; but, arguing from our own experience (*Nicotiana alata*), it appears to be more probable that the plant is in a rather unstable condition physiologically and can be influenced easily by external conditions.

Correns did endeavor to test the question of the influence of age of plant on fertility by (1) making 17 duplicate pollinations the next year with pollen from a plant raised from a cutting of B, and by (2) making 18 reciprocal pollinations from the F_1 plants upon B and G. The pollinations with pollen from the cutting of B made in 1912 checked with those made in 1911 with pollen from the original plant B in a remarkable manner. Of the reciprocals, 7 were successful both ways, 5 failed both ways, 4 were rather indefinite but similar, while only one showed a conflicting result (2 failures one way and 3 successes the other).

In spite of these facts, however, it is apparent from Correns's account that the plants were at all times kept in as fine condition as possible so that the behavior under a poor environment or during different phases of the flowering period was really not determined. What these experiments did do was to prove beyond a reasonable doubt the physiological similarity of cuttings with respect to cross-fertility and cross-sterility, and to indicate that reciprocal crosses always behave in the same manner. Unfortunately for the latter thesis, however, there are a few conflicting results in his table 8, though this he does not mention. Of the 53 reciprocals recorded there, 31 give the same results, 17 give different results, while 5 are questionable.

Correns concluded that the behavior of the F_1 individuals with the pollen of the parents was such as to indicate equal-sized classes of definitely fertile or definitely infertile plants, the behavior of the reciprocals being the same. His classification gave the following groups:—fertile with B, 32; sterile with B, 28; fertile with G, 30; and sterile with G, 30.

He further concluded that the action of an F_1 individual toward one parent was wholly independent of its action toward the other, and that the population could be divided into 4 classes with reference to the behavior of the individuals toward both parents, as follows:

Fertile with both B and G, type bg,	16 plants
Fertile with B, sterile with G, type bG,	16 plants
Fertile with G, sterile with B, type Bg,	14 plants
Sterile with both B and G, type BG,	14 plants

An explanation of these facts was sought by assuming that each parent B and G carried at least one transmissible factor, *B* and *G* respectively, which actively inhibited pollen-tube growth, besides at least one inactive factor, *b* and *g* respectively. The formulae for these plants would then be *Bb* and *Gg,* and when they are crossed four equal-sized classes of zygotes will be formed *BG, Bg, bG* and *bg,* because *B* and *b,* and *G* and *g* segregate at reduction. These four F_1 classes should behave when back-crossed with each parent in the manner shown above.

There seems to be no reason in his hypothesis why plants of the type *bg* should not be self-fertile though this is not the case. In fact all of the 60 F_1 plants are assumed to be self-sterile although two cases showing some self-fertility (probably pseudo-fertility) are shown in table 8c. But this discrepancy is probably due to an imperfect description of the hypothesis by the author, as the relation between self-fertile and self-sterile plants is evidently meant to be left out of consideration.

The intra-class and inter-class pollinations between the F_1 plants of which he made about 700 (tables 8a-8d), hardly come up to expectations, but there is a regularity that cannot be overlooked.

Compton (1913 a) confirmed Darwin's report that both self-fertile and self-sterile plants occur in the mignonette, *Reseda odorata.* From experiments on crossing these two races he obtained the following facts:

(1) Self-sterile plants when bred *inter se* threw self-sterile offspring only. This was thought to indicate that self-sterility is a Mendelian recessive. (2) Certain self-fertile plants, when self-fertilized gave self-fertile offspring only. When crossed with self-sterile plants the same result was obtained. These plants Compton regarded as homozygous dominants. (3) Other self-fertile plants, when self-fertilized, gave approximately 3 self-fertile to 1 self-sterile offspring. The same plants crossed with self-sterile individuals produced about one-half self-fertile and one-half self-sterile progeny. These he regarded as heterozygous. All of these facts are satisfactorily interpreted by the hypothesis that self-fertility is a simple dominant to self-sterility.

In a later paper Compton (1912) suggests, as Jost had previously done, the presence in the pistil of diffusible substances which stimulate or retard pollen-tube growth after cross- or self-pollination respectively.

The growth of pollen tubes in the style and the growth of fungus hyphae in a host appealed to Compton as analogous, and he suggests that self-sterility may be due to agents similar to those which govern immunity or susceptibility in animal or plant.

These results confirm a Mendelian hypothesis already suggested by Baur (1911) without reporting detailed results. He crossed the self-sterile *Antirrhinum molle* with the self-fertile *A. majus* and obtained only self-fertile offspring. The F_2 generation consisted of both self-fertile and self-sterile plants, the former being in the majority. Baur gave these hybrids to Lotsy (1913) who raised a large F_2 generation with similar results although he was inclined to believe that the plants showed variable degrees of self-fertility and self-sterility. Neither Compton, Baur nor Lotsy touched the question of the behavior of self-sterile plants among themselves.

Since self-sterility was discovered in the Ascidian *Ciona intestinalis* by Castle (1896), its reproductive behavior has been studied by Morgan (1905, 1910), Morgan and Adkins (Morgan 1913), and Fuchs (1914a). Morgan and Adkins showed that these animals vary in degree of self-sterility. Perfectly self-sterile individuals were the exception, but self-fertility never equaled cross-fertility. Individuals also varied in the ease with which their eggs might be fertilized by the sperm of other individuals. The following matings were made with the results noted in percentage of eggs fertilized:

♂ ♀	A	B	C	D	E
A	0	87	92	84	96
B	38	0	35	98	97
C	93	96	0	97	96
D	91	98	77	0	89
E	96	92	60	74	0

FUCHS (1914 a), however, has criticized MORGAN'S work, maintaining that 100 percent of segmenting eggs can be obtained in every cross with normal ova if sufficiently concentrated sperm suspension be used. He showed, among other things; that (1) an increased concentration of sperm suspension caused an increase in the number of eggs self-fertilized, (2) a greater concentration of sperm was usually necessary to bring about any self-fertilization than would cross-fertilize 100 percent of foreign eggs, and (3) contact with suspension of own sperm decreased the ease of later cross-fertilization.

The work of FUCHS suggests a physico-chemical basis for self-sterility, since contact of eggs with their own sperm appears to cause changes in the egg membranes which inhibit entrance of own sperm and to some extent of foreign sperm, yet his criticism of MORGAN'S statements is not to the point for by the submission of the eggs to different sperm concentrations he has increased the number of variants under investigation.

MORGAN (1913, p. 217) explained his facts by means of this hypothesis:

> "This failure to self-fertilize, which is the main problem, would seem to be due to the similarity in the hereditary factors carried by the eggs and sperm; but in the sperm, at least, reduction division has taken place prior to fertilization, and therefore unless each animal was homozygous (which from the nature of the case cannot be assumed possible) the failure to fertilize cannot be due to homozygosity. But both sperm and eggs have developed under the influence of the total or duplex number of hereditary factors; hence they are alike, i.e., their protoplasmic substance has been under the same influences. In this sense, the case is like that of stock that has long been inbred, and has come to have nearly the same hereditary complex. If this similarity decreases the chances of combination between sperm and eggs, we can interpret the results."

This interpretation of self-sterility endeavors to give a modern rendering of DARWIN'S idea that the condition is analogous to the decreased fertility often resulting from other modes of inbreeding. From his other numerous observations on cross- and self-fertilization, DARWIN felt instinctively that such an analogy should exist, even though self-sterile plants were continually cross-pollinated and must of necessity have a mixed ancestry. MORGAN'S contribution was to show in a general way how such a similarity might come about. His suggestion is unquestionably stimulating and we have been glad to acknowledge our indebtedness to it (EAST 1915).

One should not ascribe more breadth to the hypothesis than the author really intended, however; for certain coördinate problems that may or may not have the same underlying cause, were not included in its scope. For example, it assumes nothing regarding the origin of self-sterility or the difference between self-sterility and self-fertility. At first sight one feels that there is a great weakness in its failure to account for self-fertility, since the eggs and sperms of self-fertile races also develop under the influence of the total or duplex number of hereditary factors, and it is difficult to see why this should decrease the attraction between eggs and sperm in some cases and not in others. But the *difference* between self-fertile and self-sterile organisms is not of necessity the same problem as the *behavior* of self-sterile organisms.[7] This distinction is manifest if one refers to COMPTON'S work. In his material the difference between self-fertility and self-sterility is that of a single Mendelian factor,— self-sterility being recessive. But COMPTON does not attempt to account for the behavior of his self-sterile plants.

DARWIN, on the other hand, made no serious attempt to interpret the behavior of self-sterile plants, or to describe the fundamental difference between self-fertile and self-sterile races. He was concerned chiefly with the origin of self-sterility. The basic reason for the evolution of self-sterility, he thought, lay in a *necessity* for cross-fertilization. In this we believe he was unwise. The benefits of cross-fertilization, no one doubts. With the vigor of heterozygosis as the immediate advantage for natural selection to grasp, with the immense ultimate advantage of multiplicity of forms brought about by Mendelian recombination, one can see reason in all the host of devices for producing cross-fertilization in animals and plants,—including even bisexuality itself. But this does not mean that cross-fertilization is an inevitable need, as DARWIN believed was so clearly demonstrated by his observations on the deleterious effects of inbreeding. It is rather merely an asset in the struggle for existence, as recent experiments have shown.[8] Consequently emphasis should be placed on the assured benefits of cross-breeding and not on the doubtful evils of inbreeding. One can understand therefore why self-sterility might be desirable, and why it should be retained by natural selection after coming into existence, but the cause of its origin must still be denoted by that useful word *chance,* the veil of ignorance.

In view of these facts—and all of the important facts regarding self-sterility have been cited—the fundamental questions involved are almost as obscure now as they were when DARWIN left them. But the work of

---

[7] STOUT (1916) continually confuses these two problems.

[8] See EAST and HAYES (1912) and the papers there cited.

MORGAN, CORRENS and COMPTON encourages the hope that their solution, if one may use that term for scientific description, will be accomplished. An interpretation in harmony with modern biological conceptions which will in its turn be helpful, ought at least to be possible when all of the facts are at hand.

Since the historical part of this paper was written, STOUT (1916) has published a bulky memoir on self-sterility in *Cichorium intybus*. A large portion of this paper is devoted to destructive criticsm. DARWIN and his contemporaries, BAUR, COMPTON, CORRENS, EAST, JOST, LOTSY, MORGAN and SHULL are "placed upon the carpet" and dealt with severely. One wonders whether all of these writers can be wholly wrong in the views that have been assailed, and if not, just wherein the differences of opinion lie. We cannot help but feel that they are due largely to his misconceptions of the views of the various writers concerned.

As examples of what is meant by this statement, let us mention two of the points on which STOUT lays great stress. He feels strongly that self-sterility is a markedly variable character, and that this has not been recognized by previous writers. But since the existence of variability in the somatic expression of self-sterility has been admitted unanimously by the writers with whom we are acquainted, the true point at issue is not this, but rather the question whether any considerable part of the variation in this character is the result of genetic differences. This question has been investigated in Nicotiana, and there the variation seems to be almost wholly due to environmental changes, as is shown later in this paper. Considered with this point in mind, a reasonable and constructive interpretation of our own and many other self-sterility data can be given. Where before there was chaos a certain order appears. STOUT'S failure to recognize these truths is probably the reason why he has been unable to make any constructive analysis of his own numerous data for the fact that some of his families arising from selfed seed behaved exactly as the families arising from crossed seed shows that he is often (at least) dealing with a pseudo self-fertility (see p. 531).

Now this argument of STOUT'S, we gather, is meant to be only a particular instance advanced in favor of his general view that characters are (always?) too variable genetically to be represented properly by fixed Mendelian factors. The justice or injustice of such a contention cannot be discussed here, but we should like to point out that in assuming—as is so often done—that geneticists commonly believe in an elemental stability of characters, the attitude of the great majority of such workers is misconstrued. If we have interpreted Mendelian investigators' views correctly, they believe that characters are variable, but in different degrees in different species; and that there is adequate evidence to show that most characters in most species are so constant throughout the number of successive generations ordinarily available for experimental purposes when viewed under the conditions most likely to eliminate variables other than heredity, that the *abstract* idea of fixed germinal factors can be used properly and helpfully in genetic analysis.

As a second case where we believe STOUT has not represented fairly the views of the writers criticized, the section of his paper entitled "Relation of vegetative vigor and fertility to inbreeding and cross-breeding" may be cited. STOUT criticizes in particular the views of DARWIN, SHULL, and EAST and HAYES on this subject. He rests his case on a paper by BURCK (1908) in which the writer holds, that (quoting STOUT):

> "(1) plants that are regularly self-fertilized show no benefits from crossing, (2) that nowhere in wild species is there evidence of an injurious effect from self-fertilization, and that there is abundant evidence of continued vigor and high fertility resulting from long-continued self-fertilization, and (3) that the advantage derived from crossing within or between garden varieties appears when there is doubtful purity; and is due to the fact that both vigor and fertility have already been decreased by hybridization, and that when crosses do give increased vigor and fertility the cross has restored in increased measure the original nuclear organization of the parent species."

The logic of the third statement is too delightful for comment, being worthy indeed of Mother Eddy. Vigor is decreased by hybridization. Vigor is increased by hybridization. It is increased by restoring "nuclear organization." Not only is nuclear organization restored, but it is restored in *"increased measure."*

The second statement has never been denied by modern writers, to our knowledge. It was emphasized by EAST and HAYES (1912), who pointed out why the advantage of cross-fertilization in plants should be stressed rather than the disadvantage of self-fertilization. This advantage, if one may recall it, lies in the fact that n inherited variations can produce but n forms under self-fertilization, and may produce 2^n forms under cross-fertilization by Mendelian recombination.

The first statement is simply not in accord with the facts. We are astonished that one who has the acquaintance with the literature that

STOUT has shown, should quote it with approval. Every hybridist of experience from KÖLREUTER (1760) to the present day has cited so many data diametrically opposed to it that the matter is no more worthy of discussion than is a denial that the earth is round.

Of course as to the interpretation of the facts one may hold a difference of opinion. The hypothesis of heterosis advanced independently by SHULL and EAST has, we think, served a useful purpose. The last word has not been said, however, and data accumulated by H. K. HAYES and D. F. JONES in their continuation of the experiments reported by EAST and HAYES (1912) have led the senior author to modify his views on several of the points there discussed, though not on the main conclusions. But in the meantime it is disconcerting to have our published statements misunderstood and misinterpreted. For example STOUT says (p. 419) "EAST and HAYES believe that heterozygosity gives an increase of both vigor and fertility in proportion to the number of heterozygous factors in the organism." There are two errors in this statement. Neither SHULL nor EAST has maintained that crossing increases fertility. The number of flowers and fruit is often increased, but no data have appeared which indicate a decreased percentage of nonfunctional gametes. Second, EAST and HAYES used the words "roughly proportional to the number of heterozygous factors." Leaving out the word "roughly" and taking the statement from its context, conveys a very wrong impression for it was *not* assumed that *every* germinal factor affected vigor and it was expressly stated that one could *not* assume equal effects for different factors. Again STOUT achieves a remarkable misinterpretation of the results reported in table 5 of this same paper. Here 42 inter-specific crosses are reported, of which 14 show decreased vigor (this figure should be 13 instead of 14 owing to a typographical error in reporting the first cross, *N. alata* × *Forgetiana,* which was 125 percent of the parental average in height, instead of 25 percent). STOUT leads his readers to infer that this table is the sole basis of the conclusions regarding heterozygosis, and that the conclusions are incorrect because, as he states: "There was increased vigor in only 17 cases, but there is no apparent reason why, if it is simply heterozygosity that increases vigor, more of the combinations should not show increased vigor."

Now what are the facts. The statements on the previous page (p. 27) of the paper make it clear that many varietal crosses were made (over 100 in Nicotiana alone to that date), *which showed vigor equal to, or greater than the parental average.* While not expressly stated, it may be inferred that none was found with decreased vigor. If it had been otherwise it would have been stated. Multiplication of such data was thought unnecessary in view of the exceedingly numerous results of Kölreuter, Knight, Gärtner, Naudin, Focke, Darwin and others, on the increased vigor of such hybrids. This table then, *as is shown on pages 29 and 30,* was submitted for the particular purpose of trying to establish a wholly different thesis, viz., that as germ plasms become more and more unlike, there comes a time when hybrids show (1) an inability to form germ cells (sterility), and (2) difficulty in somatic cell division. Our typographical error was unfortunate, but in view of the text given the statement made by Stout is an inexcusable perversion of our work.

We have mentioned but two out of a goodly number of misconstructions of work with which we have been concerned. We have done this because we believe that they are paralleled in the author's criticism of most of the writers mentioned above, and because we realize that if we undertook to point out these misunderstandings in the case of other writers, the answer would be that it was merely a difference of opinion.

On the other hand, Stout has given us a classification of types of sterility, and has reported a really immense amount of data. We hope that he will give a more constructive analysis of them later.

THE MATERIAL USED AND THE GENERAL PLAN OF THE PRESENT INVESTIGATIONS

The investigations described in this paper may be said to have been begun in 1910, when, in connection with some genetic studies on size in the genus Nicotiana, the two species *Nicotiana Forgetiana* (Hort.) Sand. and *Nicotiana alata* Lk. and Otto var. *grandiflora*[9] Comes were found to be self-sterile. These two species have been made the basis of our experiments, though later some work was done upon *Nicotiana angustifolia* R. and *P.* var. *crispa*[9] Cav., *N. commutata* Fisch. & Meyer, and *N. glutinosa* L., in which self-sterility had been discovered.

The characters of these species and of *Nicotiana Langsdorffii* L., a self-fertile species used, are described in Comes (1899), Setchell (1912), and East (1913, 1916).

From the technical standpoint the material has been ideal. Any combination of the three species *N. Forgetiana, N. alata,* and *N. Langsdorffii* can be made, the F_1 hybrids being completely fertile (in proper cross-fertile combinations). *N. glutinosa* and *N. angustifolia,* however, can

---

[9] Hereafter *N. alata grandiflora* will be known as *N. alata* and *N. angustifolia crispa* as *N. angustifolia.*

neither be crossed together nor with the other species. The plants of each race grow rapidly and vigorously, and are not easily affected adversely by sudden changes in environmental conditions. They are not subject to serious parasites. Cuttings root well, and with care old roots will live through a second and occasionally even a third season. Emasculation and pollination are easy to perform, and seed production in fertile crosses is high.

N. Forgetiana, *N. alata* and *N. angustifolia* belong to the subgenus Petunioides, a fact worthy of note because nearly all of the species of this section have both showy flowers and abundant nectar which attract insects and thus promote cross-pollination. Even *N. glutinosa* has rather conspicuous blossoms, though belonging to the subgenus Rustica in which most of the species have small and unattractive flowers that are self-pollinated naturally. In other words all four of these species probably had evolved structural modifications which aided cross-fertilization long before the development of their self-sterility. We are dealing, therefore, with plants desirable both from the viewpoint of the experimentalist and of the student of evolution, a most unusual combination.

The general problem presented by this material obviously was to discover the facts regarding self-sterility, and to determine whether these facts might be fitted by a simple mathematical or chemico-mathematical description. It has been attacked along three distinct lines: (1) pedigree cultures; (2) histological studies of pollen tubes in crossed and in selfed pistils, and in inter-specific and inter-generic crosses; and (3) physiological studies of pollen tubes cultivated on artificial media.

Work along this general plan has been carried on at the Bussey Institution of HARVARD UNIVERSITY continuously since 1910, though it has not been our sole interest. It was our good fortune to have the very efficient aid of Dr. O. E. WHITE, then a graduate student and assistant at HARVARD UNIVERSITY, during the winter of 1911-12. The junior author's connection with the work began in February 1914, and has continued until the present time. In addition, Miss GRACE SHEERIN and Miss BERTHA KAPLAN have assisted in the pollination work for limited periods of time.

It being impracticable to present and to examine these various data within the limits of a single article, we propose to take up only a portion of the pedigree culture work in this paper, leaving the remaining questions to be treated later. The pedigree culture investigations have thus far involved four studies: (a) the effect of environment on self-sterility;

(b) the relations existing between self-sterile plants in intra-specific and inter-specific crosses; (c) the relations between self-sterile and self-fertile plants; (d) selective fertilization. The first two studies will be discussed here.

The usual precautions used by plant geneticists have been carefully observed, including castration of all flowers on self-sterile plants used as pistillate parents. This safeguard would not be worthy of especial mention except for the fact that it is wholly disregarded in STOUT's recent paper (1916). We shall show in a later paper that effective pollen mixed with "own" pollen causes scarcely any acceleration of "own" pollen tubes in Nicotiana. But we cannot find that STOUT determined this for chicory, and to take for granted that there is no such effect seems to us a laxity in a scientific work.

Every important fact described has been confirmed independently by each of us, and certain of the data that have been remarkably orderly (for example, table 11) have been collected by several persons in such a manner that personal equations were largely eliminated.

It may be noted here that a preliminary report of some of the work which we now report in detail was published in 1915 (see EAST 1915). With more data in hand more definite ideas on the subject have been possible, hence several differences will be noted between the statements made then and now. It is scarcely necessary, however, to point out every difference in the interpretations, as we shall endeavor to give in full our reasons for the present conclusions.

THE EFFECT OF THE ENVIRONMENT ON SELF-STERILITY

In beginning the description of our experiments with a section on the effect of environmental changes on self-sterility a chronological inversion is made which needs explanation, particularly as carefully planned experiments designed to show the effect of individual environmental factors when all others are controlled have not been carried out. Work on the relation between self-sterile plants was started with the idea, that even though DARWIN were correct in supposing that self-sterility is seriously affected by changes in the environment, conditions might be kept so constant that no difficulties would be encountered. Indeed, this is probably the case, since no particular difficulties were experienced during several years in spite of *certain* environmental factors being constantly varied. There came a time, however, when troubles arose which were puzzling for a considerable period. Our inquiries regarding the effect of the environment on self-sterility have finally removed the stumbling-block and have made a clear and reasonable analysis of the pedigree culture work possible.

In brief these conclusions are as follows:

1. Self-sterility is a condition determined by the inheritance received, but can develop to its full perfection only under a favorable environment. This is not a strange conclusion, for perhaps particular environmental combinations are necessary for the full development of all positive somatic characters. But certain characters are much more seriously affected than others by the environmental variations likely to be met under ordinary conditions. For example, BAUR (1911) showed that *Primula sinensis rubra* produces red flowers when grown at a temperature of 20° C. and white flowers at a temperature of 30° C.; EAST and HAYES (1911) found that the red pericarp characteristic of a certain maize variety developed in sunlight but not in shade; Miss HOGE (MORGAN et al., 1915) discovered that in a Drosophila mutant with supernumerary legs the character was only called out when the animals were kept at 10° C. Self-sterility is such a character. It develops fully only under conditions which promote a normal healthy vegetative growth, and during the active part of a flowering period.

2. At the end of a flowering period and under conditions adverse to vegetative growth, self-sterility declines until a few seeds may sometimes be obtained after self-pollination. Occasionally even a full capsule is produced. The immediate cause of this partial return to a pseudo-fertility is the acceleration of pollen-tube growth that obtains under these conditions. Since we have reason to believe that the difference between a fertile and a sterile combination in these plants is the ability of the pollen grain through something inherent in its constitution to call forth in the tissue of the style in the former and not in the latter case a secretion which accelerates pollen-tube growth, it follows that in weakened style tissue some change has occurred that renders this secretion more easily produced.

3. Self-sterility can be restored in weakened plants by allowing them to go through a period of rest and then, by proper treatment, bringing them into flower anew as vigorous plants. Truly self-fertile plants cannot be forced into self-sterility by any treatment. This last conclusion is of course largely a conclusion by analogy and is not subject to rigorous proof.

4. Self-sterile races differ in their norms for self-sterility. Thus in

N. Forgetiana and in *N. angustifolia* the character is much more stable than in *N. alata* and *N. glutinosa*. In many ways this behavior indicates the existence of multiple allelomorphs for self-sterility.

The basis for these conclusions is the whole of our experience with self-sterile plants, which, it is scarcely necessary to say, cannot be cited statistically in this place. But the following facts will show, we hope, that they are well founded.

Cross No. 1 between *N. Forgetiana* and *N. alata* was made in 1909 using *N. Forgetiana* as the female. At that time both of the parents were thought to be self-fertile because a carefully bagged inflorescence of each species had yielded seed; but when the plants of the F_1 generation turned out to be self-sterile, the status of the parents was investigated more carefully. Over two hundred plants of *N. Forgetiana* have been tested under various conditions. Plants growing out of doors both on good soil and on poor soil have been tested throughout the growing season. Greenhouse-grown plants have been tested not only throughout a normal flowering period (about 3 months), but have been forced through an abnormally long flowering period during the test. Plants well nourished have been compared with plants poorly nourished, and plants well watered with plants under conditions of drouth. Both old roots and cuttings brought into a second flowering period in fine condition have been compared with much pruned old roots and cuttings in poor condition.

Only 3 cases of seed production have been observed. 2 plants at the end of their flowering period under conditions adverse to vegetative growth produced 1 and 2 capsules respectively having about 50 seed each (the normal is *ca.* 300) out of 14 tests. The third plant was not tested until near the end of its flowering period. At that time it was noted that it seemed to be self-fertile. Under test it did indeed produce several fine seed capsules after self-pollination and would undoubtedly be called a self-fertile plant were there not the following reasons for considering it an unstable self-sterile (see description of *N. alata*).

1. The plant when first tested was in a late flowering stage, yet produced capsules only in about half the tests.

2. After pruning and resting for a time the plant was brought into vigorous flower a second time. The tests during the first two weeks of this period (about 20 flowers) were all negative. The plant seemed to be perfectly self-sterile. Gradually, however, self-fertility returned as the flowering period waned.

3. Twenty-four plants grown from selfed seed of this individual, tested during the height of their flowering period, all proved self-sterile.

We are therefore forced to concede the probability that an error of manipulation or of record was made in 1909, although we may have happened upon a plant like the one just described since the original selfing was done at the end of the flowering season. Be that as it may, the conclusion is inevitable that *N. Forgetiana* (and *N. angustifolia* has yielded similar results) is a self-sterile species of remarkable stability, which only occasionally (1 in 300?) produces a plant that shows some self-fertility under adverse conditions.

Table 1

Progeny of pseudo self-fertile N. alata plant used in cross No. 2. Grand-progeny of original pseudo self-fertile plant. Subscripts show number of pollinations made.

Ped. No. ♀	No. selfings sterile	No. selfings giving capsules			Plants with which cross-fertile ♂	Plants with which cross-sterile ♂
		1-10 seeds	10-50 seeds	250-300 seeds		
53	6		1		57	54_2
54	5					53_2, 57_2, 58_2
56				3		53, 57, 58, 59
57	3					58
58	1				53, 59	314
59	2					314, 53_4 54, 56_3, 57_3
61	3					
62	4	4		2		58, 79
64	3	1				58
65	6					79
66	12	1				58, 62, 71, 79
67	3					
68	4					
70	5	1	1			
71	3		1	1		314, 58
72	3					
73	4					
74	1					
75	8					
76	2	1		2		66
77	2					
78	9					66
79	3	1				58, 66

1 pollination 53 × 54 and 2 pollinations 59 × 53 produced 1-10 seeds each.
314 = *N. Forgetiana.*

N. alata, on the other hand, has proved to be more unstable[10] in its self-sterility; or better, it has proved to have a norm more nearly inter-

---

[10] *N. glutinosa* appears to behave like *N. alata,* but has not been tested very thoroughly.

mediate between the extremes complete self-sterility and perfect self-fertility. But fundamentally it is a self-sterile species like *N. Forgetiana.*

Numerous *N. alata* plants have been tested for self-sterility under the same conditions as described above for *N. Forgetiana.* The results have been similar in that the plants were practically always completely self-sterile during the early part of a vigorous flowering season. But under adverse conditions during the latter part of the flowering period, rather a high percentage of the plants produced capsules with from 1 to 50 seeds each. Only 2 plants have been found, however, that appeared to be almost completely fertile from the middle of the flowering period onward under normal conditions. Of these plants more is to be said.

Assuming that no mistake was made in 1909 and that selfed seed was actually obtained from a field-grown plant of *N. alata,* we have records of its progeny for three generations.

Twenty-five seedlings from this seed were grown in 1914. These plants were tested for self-sterility as field-grown plants, though not as thoroughly as might be desired. 2 plants showed some self-fertility,—no tests having been made until the latter part of August. From 1 of them selfed seed was obtained and a second generation grown. 23 of these plants were tested in the greenhouse with the results shown in table 1.

Fourteen of these plants produced no seed when selfed; 9 showed some degree of self-fertility. This fertility apparently occurred only

TABLE 2

Progeny of pseudo self-fertile N. alata plant No. 56. Great-grand-progeny of original pseudo self-fertile plant.

Ped. No.	No. selfings sterile	No. selfings giving capsules		
		1-10 seeds	10-50 seeds	250-300 seeds
80	9	2	2	
81	1			
83	7			
84	3			
85	10	2	1	1
86	1			
87	5			
89	7			
90	8			
91	8		1	
92	1	1		
93	8		2	
94	4			
95	3			

when the flowering season was waning and the plants were under adverse conditions, as was stated before; but it cannot be proved that this was always the case, for one cannot draw a definite line between vigorous and weakened plants. 3 plants, excluding No. 56, produced some full capsules, but in these cases the remaining self-pollinations and sterile cross-pollinations show that the plants were not truly self-fertile. Plant No. 56, however, showed no direct indications of self-sterility in connection with the 3 self-pollinations tried. More pollinations should have been made on this plant at the beginning of a second flowering period. Unfortunately, it was discarded. The evidence of self-sterility, therefore, is wholly circumstantial. It is, that though having functional ovules No. 56 was sterile to the pollen of plants 53, 57, 58 and 59, and though having functional pollen it was sterile crossed on plant 59.

A small population was grown from the selfed seed of this plant. It is shown in table 2.

Although 5 of the plants produced some seed, if one considers the date of manipulation and the state of the plants, the evidence is all in favor of the idea that this was an effect of external conditions. There is no reason whatever for believing that any of the plants were truly self-fertile.

All told then, we have three generations of *N. alata* plants, each generation being grown from selfed seed produced from plants apparently weakened at the time of seed production, without the occurrence of a single plant which behaved in every way like a truly self-fertile individual. It seems to us, therefore, that this selfed seed might be thought of as having been produced artificially.

If this be the correct view of the matter, it is clear that there is no reason why fusion between gametes produced by a self-sterile plant cannot occur provided the male generative nucleus enters the embryo sac. Such unions may take place without affecting the self-sterility of the progeny. Even by the selection of apparently self-fertile plants for three generations no tendency toward the formation of a self-fertile race is indicated. Just how broadly one may generalize from these data is still problematical, but the two following conclusions are certainly more than guesses.

(1) Unless a male gamete complementary to every female gamete is formed, there is no selective fertilization, for *full* capsules have been found on plants that in the early part of the season and in crosses showed they were really self-sterile. Other evidence militating against selective

TABLE 3

Progeny of N. alata No. 58 × N. alata No. 56.

Ped. No.	No. selfings sterile	No. selfings giving capsules		
		1-10 seeds	10-50 seeds	250-300 seeds
96	5	1	3	
97	5	1		
98	11	1		
99	4			
101	4			
102	4			
103	8			
105	8		2	
106	7			
107	3			
108	4			
109	1	3	2	
110	3			
111		3		
113	1			
116	4			
117	6			
118	7			
119	3			
120	5	1		
121	2			
122	7			
123	5	1		
124	5			
126	1			
127	8			
128	4			
133	1	3		
135	3			
136	3	2		
137	3			
139	9	3	1	
140	4			
141	2			
144	4			
146	6			

fertilization which will be presented in a later paper has also been obtained by a different method of attack.

(2) It follows therefore that self-sterility behaves as a sporophytic character and is not the result of incompatibility between gametes.

One other bit of evidence regarding *N. alata* should be presented here. It is the behavior of the progeny of a cross between the self-sterile plant No. 58 and the apparently self-fertile plant No. 56. These data are reported in table 3.

Here again we find a considerable percentage of plants, a third to be exact, giving a few capsules having from 1 to 50 seeds each. Here again it was the plants near the end of their flowering season, the plants that had been cut back strongly, the plants that were producing flowers on one or two weakened branches, that gave the seeds. To be sure, as in other families, one or two plants apparently vigorous behaved in the same way near the end of the flowering season. But the correlation between *weakened failing* branches at the end of their flowering period and *tendency toward self-fertility* was very high even when judged only by external appearances.

The remaining data on this subject cannot be discussed in this place without repetition, since they include nearly all our pedigree culture work. And at any rate they are important only as corroborative evidence, for in our regular experiments extremely weak and old flowering branches were seldom used. For this reason we rarely had to contend with any approach toward self-fertility in self-sterile plants. But the phenomenon when met lent support to our hypothesis. Furthermore, *cross-sterile combinations behaved in the same way.*

These conclusions have been a great aid to us in analyzing our pedigree culture facts. Without them the data from two or three of our populations, where pollinations were carried on up to the end of the flowering season, would have been somewhat chaotic. They reveal, for example, that *N. alata* is just as much of a self-sterile species as *N. Forgetiana* though the expression of the character is affected more easily by external conditions. They show clearly why selection for three years accomplished nothing. The selected extreme was a non-inherited fluctuation. It is clear also why crosses between these apparently self-fertile plants and plants unquestionably self-sterile, yielded no truly self-fertile offspring in either the F_1 or F_2 generations. The plants were really self-sterile; they were pseudo-fertile, and will be so called.

In this connection it may be recalled that DARWIN (1876) found that self-sterile plants of *Abutilon Darwinii* became partly self-fertile *at the end of their flowering season.*

Keeping these things in mind, one is able to classify the pedigree culture results with great accuracy, though there are five possibilities of error.

1. There may be error of record. This we believe to be slight, owing to our various methods of checking results.

2. A true sterility either partial or complete may exist. This usually can be discovered by a microscopical examination of the pollen, and may be tested by reciprocal crosses. The reciprocal cross test has never

brought to light a case of ovule sterility and pollen fertility, but the converse is sometimes true.

3. Combinations made but once and failing must be reported as sterile; but this is an error about 4 times per hundred, since this is the ratio of failure found in combinations known to be fertile, by reason of an imperfect technique or other unknown causes. We cannot correct accurately for this error, but it must be considered when discussing exceptions to a general scheme which other data fit.

4. Combinations may fail once and succeed once in two trials, or in very rare cases fail twice and succeed twice in four trials. Experience has shown that if the capsules are normal in size and full of seed, the combination is fertile. Fertile combinations *always* give full capsules. There is no partial fertility in fertile combinations except as *true* sterility exists in some degree (see error 2). Conversely, it is possible of course to meet with a pseudo self-fertile plant like *N. alata* plant No. 56, which under adverse conditions might give full capsules of normal size after a "sterile" combination had been made. But under the environmental conditions that usually obtained during our work, this would be extremely rare,—to the best of our knowledge and belief not over 1 per 200 plants.

5. Combinations may give capsules with from 1 to 50 seeds as well as failures. These are sterile combinations. They probably occurred in only three families, because only in these families were the plants utilized during the *whole of their flowering period.* Unfortunately it must be admitted that a few errors of record may have been made with these cases. A small number of apparently successful matings were not recorded until the capsules had opened. Since the capsules were of normal size and each had contained a number of seeds, these combinations were recorded fertile, but the matter is not certain.

It is not believed that these errors are serious even when taken together but some allowance must be made for them in considering the few exceptions noted in the analyses we have made of the tables that follow.

INTER-SPECIFIC PEDIGREE CULTURE EXPERIMENTS

All of the crosses reported in this paper are between species or varieties believed to be self-sterile for the reasons set forth in the foregoing section. But because certain plants were used which under the peculiar conditions at the time of the test for self-sterility yielded some selfed seed, these plants are distinguished by the term "pseudo self-fertile." Their behavior in these crosses is further evidence that the term is justified.

Cross No. 1. N. Forgetiana × *N. alata* (*self-sterile* × *self-sterile*)

The cross to be described first is that mentioned previously in connection with the discovery of self-sterility in the genus Nicotiana. It was made in 1909, using *N. Forgetiana* as the female and *N. alata* as the male.

The F_1 generation

The F_1 population consisted of vigorous plants twenty-five[11] percent *taller* than the average of the two parents and was extremely uniform in size and in color of flowers, though the latter were not so dark a red as those of the male parent. A few individuals tested for fertility in 1910 and others from the same original cross again tested in 1912, all proved to be self-sterile. The actual tests made, some 20 plants altogether, were too few to claim self-sterility for every individual, but careful observation of about 50 other plants in the field indicated this to be the case. These observations were made by estimating the number of capsules which developed naturally on each plant, it having been determined that on self-fertile plants of an allied species, *N. Langsdorffii*, from 10 to 20 times as many capsules develop as on self-sterile plants of *N. alata*, though the ratio of flowers formed on the two species is only about 3 to 1.

No extended experiments were carried out to test the fertility of these plants in intercrosses. 6 intercrosses between sister plants were made and each was successful, but whether some cross-sterility existed or not is unknown. The pollen, however, was good in every plant examined (about 30).

The F_2 generation

From these 6 intercrosses between pairs of F_1 plants almost a thousand individuals were grown. They showed a most remarkable variation in all their characters, the range including the modal values of both grandparents. The frequency distributions for length and for breadth of corolla have been discussed in another paper (EAST 1913), and it will suffice to note here that while the coefficient of variation for length of corolla in the F_1 generation was $8.28 \pm .38$ percent, in the F_2 generation it was $22.57 \pm .39$ percent.

---

[11] By a typographical error the height of this cross is made 25 percent instead of 125 percent in table V, EAST and HAYES 1912.

There was also a great range in color of corolla, which even with the considerable number of subsequent generations grown, has not been analyzed to our complete satisfaction. 4 Mendelian factors appear to describe the breeding results best, giving the 7 forms, red, magenta, light red, light magenta, light red on exterior of corolla only, light magenta on exterior of corolla only, and white. Red is epistatic to magenta, and the darker colors are epistatic to the lighter ones.

These details are given in order to emphasize the fact that here we have two races sufficiently distinct from each other to be designated as separate species, which cross easily and give a fertile F_1 generation and a wide range of forms in the F_2 generation. The fertility of the F_1

TABLE 4

Result of matings on 20 plants of the F_2 generation of cross No. 1
N. Forgetiana × N. alata.

Plants used as males

Plants used as females	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	S		F					F			F	F								
2		S									F	F	F							F
3	F		S			F		F			F	F			F		F			
4				S				F			F	F								
5	F				S		F	F	F	F	F	F	F	F	F	F	F	F	F	F
6				F		S		F			F		F	F			F			
7			F				S				F				F		F			
8	F		F	F		F	F	S		F	F	F	F	F	F	F	F			
9				F				F	S			F		F						
10					F			F		S	F	F	S	F	F	F	F			
11					?	F		F		F	S	S	F	F			F			
12			F		F					F	S	S	F	F	F	F	F	F	F	F
13								F			F	F	S		F		F			
14			F		?			F	F			F		S			F			
15					F			F			F	F			S					
16					F					F	F	F		F		S		F	F	
17					F					F	F	F	F		F		S			
18					F		F	F			F	F						S	F	
19			F		F			F						F			F	F	S	
20					?			F					F							S

generation indicates absence of any selective elimination of gametes or zygotes in its daughters, and the variation exhibited by these daughters shows conclusively that the original parents really did differ by a considerable number of hereditary factors. These matters are important in connection with the inbreeding experiment that followed.

About 40 plants from the F_2 generation were crossed and selfed on a rather large scale. One of these experiments in which 20 plants coming from 2 intercrosses between F_1 plants were used, is shown in table 4. The vertical columns give the number of the plants when used as males; the horizontal rows are the same plants when used as females. The result of each mating made is denoted by the letters F for fertile and S for sterile.

It was planned to make all possible combinations of these plants; but this proved to be impracticable, and only 154[12] were accomplished. The pollinations on the plants of this generation as well as those on the succeeding generations included in this experiment were made under various conditions of sunshine, temperature, moisture, food supply and age, but these variables appeared to have no influence on fertility. The results always checked. A small number of matings were made in the open field in August and September, 1911. The remainder were performed in the greenhouse. A part of these were made upon some of the old plants that had been transplanted during the late fall, and the others upon cuttings from the plants in the field which were again ready for operation in April, 1912. *But in all the work on the 20 plants tabled it should be noted that pollinations were made during the height of the flowering period when the plants were in good condition. Nevertheless, there may have been errors. If such did occur, cross-fertility would have been favored; since at the time the work was done upon the F_2, F_3, and F_4 generations of this cross, pseudo self-fertility was not suspected.*

The plants were each selfed from 2 to 10 times, an average of 4 times per plant, without a single seed being obtained.

Of intercrosses, 132 were made. 3 of these are indicated by question marks on the table. This is because plant 5 had defective pollen, it being the only one of the twenty in which the pollen did not show from 90 to 100 percent of morphologically perfect grains. None of the crosses where this plant was used as the male gave capsules over half-filled with

---

[12] A few of the figures given here differ from those given in the preliminary report on this work (EAST 1915). This is due to rechecking the results and to the addition of a few more data. There have been no essential changes and the present figures are believed to be correct.

seeds, but since 7 matings had from 30 to 100 seeds per capsule, and since the reciprocal matings were all successful we have classed them as fertile. The matings questioned, 11 × 5, 14 × 5, and 20 × 5, ought also to be classed as fertile, since the reciprocals were fertile, but as they yielded only 2 to 10 seeds per capsule, they have been omitted from these next calculations.

Of the remaining 129 intercrosses, 126 were successful; 4 of them produced capsules having less than 50 percent of the ovules fertilized (2 pollinations each being made), the remainder produced full capsules. There were few failures among these intercrosses, though from 2 to 12 repetitions of the matings were made in almost every case. It seemed as though an intercross possible at one time could be made at any other time at the first attempt. In other words, there seemed to be no variability in ease of cross-fertilization. The failures in the fertile intercrosses were less than 4 percent, and these were complete failures which may be attributed to the technique used.

Twenty-eight intercrosses between these plants and other plants of the F_2 generation were also made with 28 successes. In addition, 92 other combinations were made between plants not shown in the table. They are not reported in detail because only a few matings per plant were made; but the gross results were 89 successes and 3 failures.

Altogether among these matings there were 54 pairs of reciprocals each of which gave the same result.

The failures in the intercrosses remain to be considered. The table shows 3 cases; of which 10 × 13 was tried 2 times; 11 × 12, 12 times; and 12 × 11, 6 times. The last pair are reciprocals, but we shall treat reciprocals separately for the present. Of the other 3 cases, 2 of them were tried 3 times, but the third was made only once, which of course does not settle the matter. Thus there were 4 definite cases, 1 probable case, and 1 questionable case of cross-sterility, a matter of 2.4 percent (6 out of 249).

The F_3 generation

Out of the many fruitful combinations of F_2 plants, 29 F_3 families were grown,—50 to 150 individuals of each being transplanted from the greenhouse to the field with due care that random samples were obtained. Field examinations as described above, indicated a total absence of self-fertile plants, and from 3 to 6 attempts to self individuals of each family resulted in failures.

The progeny of 2 red-flowered plants of the F_2 generation furnished

TABLE 5

Result of matings on 12 plants of the F_3 generation of cross No. 1, N. Forgetiana × N. alata.

Plants used as females	Plants used as males 1	2	3	4	5	6	7	8	9	10	11	12
1	S		F	F	F		F		F		F	
2		S		F	F		F		F	F	F	F
3	F		S		F		F			F	F	
4	F	F		S		S		F	F	F		
5			F		S			F	F		F	F
6	F		F	S	F	S		F	F	S		F
7	F	F	F		F	F	S	F	F		F	S
8		F	F	F		F		S		F	F	F
9	F		F		F	F			S		F	F
10			F	F	S	S	F	F		S	F	
11	F		F	F			F	F		F	S	F
12							F			F		S

the material for the continuation of our intercrossing experiment. Most of the work was done on 12 plants as set forth in table 5. Fruitless self-pollinations averaging over 3 per plant proved they were self-sterile. 102 cross-pollinations were made: 75 are shown in the table; 27 were made in a less systematic manner with 11 other plants of the same family. These resulted in 95 successes and 7 failures. Again the "possible" combinations were almost always successful. The unsuccessful matings were 4 × 6, 6 × 4, 6 × 10, 10 × 6, 7 × 12, and 10 × 5. Combination 6 × 4 was made twice and combination 7 × 12 once, the remainder were made three or more times. The first 4 matings consist of 2 pairs of reciprocals. The reciprocal of 7 × 12 was also made, but proved to be fertile. This is evidence that with further trials 7 × 12 would also have been successful, for we have *invariably* found reciprorocals to behave alike when a number of pollinations sufficient to determine definitely the status of the cross has been made. In fact 26 reciprocals gave the same result in this population. The remaining combination showing cross-sterility was between plants 21 and 27. Eliminating combination 7 × 12, therefore, 6 percent gross of cross-sterility is shown in the F_3 generation.

TABLE 6

Result of matings on 10 plants of the F_4 generation of cross No. 1, N. Forgetiana × N. alata.

Plants used as females	Plants used as males 1	2	3	4	5	6	7	8	9	10
1	S		F	F	F		F		F	F
2	F	S	F	F		F	F	S	F	
3			S		F				F	F
4	F			S	F	F	F		F	
5		S			S	F		S	F	F
6	F		F			S	F			F
7	F	F		F	F	F	S			F
8	F		F		S		F	S		F
9	F	F	F		F		F		S	
10	F		F		F	F	F		F	S

TABLE 7

Result of matings on 20 plants of the F_5 generation on cross No. 1, N. Forgetiana × N. alata.

Plants used as females	Plants used as males 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	S		F	S	F			F	F	F	F	F	F	F	F	F	F			
2	F	S	F	S	S				F		F	F	F	F	F	S	S	F	F	S
3			S	F	F			F	F	S	S									
4																				
5													F							
6	F					S	F	F	F	F	F	F	F							F
7	F	F	S	S	F		S	F	S	S	S									
8					F			S	F	F										
9		F			S				S	F	F	F	F	F						
10			S		S					S										
11											S									
12			F		F		F	S	F	F	F	S	F							
13			S										S							
14			F		F	S	F	F	F	F	F	F	F	S						
15			F		F	S	F	F	F	F	F	F	F	S	S	F				
16			F		F	F	F	F	S	F	F	F	F	F	F	S	F	F	F	S
17			F		F	F	F	S		F	S	S	F	F	F	F	S			
18		F	S		F	F	S	F	F	S	S	F	S	F	F		F	S	F	
19			F		S	F	F	F		F	F	F	F	F	F		F		S	S

The F_4 generation

Only 2 of the F_3 combinations were grown during the next season and the pressure of investigations along other lines was such that but little work was done upon them. Field examination and tests on 21 plants, however, showed us no self-fertility. 10 of the progeny of 2 red-flowered F_3 plants, had 52 matings made upon them, 15 being reciprocals giving duplicate results. In addition 6 random matings with other plants of the family were tried with 1 failure. There were 48 successful and 4 unsuccessful matings on the 10 plants shown in table 6. The fertile matings yielded good capsules as usual with 3 exceptions, there being but 7 complete failures out of over 200 pollinations. Of the unsuccessful combinations, pollinations were made as follows: 2 × 8, 4 trials; 5 × 2, 6 trials; 5 × 8, 4 trials; 8 × 5, 5 trials; and 8 × 12, (not shown in the table) 4 trials. Each of these cases is fairly certain, therefore, and gives us a gross cross-sterility ratio of nearly 9 percent.

The F_5 generation

Only 1 F_5 family was studied, but as it was planned to discontinue this particular experiment, considerable attention was given to it. As was also true of the F_3 and F_4 generations, the work was carried on under field conditions. Similarly again, it was produced by mating two red-flowered sibs.

A random sample of 20 plants was marked for work, and 439 pollinations made (table 7). Of these pollinations 92 were wholly unsuccessful attempts to secure selfed seed made on 17 plants, an average of 5.5 pollinations per plant. Thus there is no question about the self-sterility of each plant tested. Plants 4, 5 and 20 were not tested. Plant 4 had such bad pollen that results with it are valueless, and plants 5 and 20 were somewhat sickly. Plant 9 also had such poor pollen that the seed capsules were not full, but a classification of the matings where it was used could be made without any serious chance of error. 274 pollinations were made on the 119 intercrosses that proved fertile. Only 12 of these attempts failed, and 5 of them were on crosses between No. 9 and No. 3. Thus only 4 attempts per hundred failed in the intercrosses that were classed as fertile from records of other pollinations, showing conclusively, we think, that inbreeding had produced no quantitative diminution in fertility among "possible" combinations, the percentage of failures in fertile crosses in the F_2 generation being about the same.

The remaining 73 pollinations were unsuccessful attempts to obtain seed in 33 intercrosses. The details are shown in table 8.

TABLE 8

Record of unsuccessful cross-pollinations made on the F_5 generation of cross No. 1, Nicotiona Forgetiana × N. alata.

Mating	Pollinations	Mating	Pollinations	Mating	Pollinations
1 × 4	1	7 × 9	1	16 × 20	3
2 × 4	1	7 × 10	1	17 × 8	2
2 × 5	1	7 × 11	1	17 × 11	2
2 × 16	2	9 × 5	3	17 × 12	3
2 × 17	2	10 × 5	1	18 × 3	3
2 × 20	3	12 × 8	3	18 × 7	3
3 × 10	2	13 × 3	2	18 × 10	3
10 × 3	2	14 × 6	3	18 × 11	3
3 × 11	2	15 × 6	3	18 × 13	2
7 × 3	3	15 × 14	2	19 × 5	2
7 × 4	3	16 × 9	1	19 × 20	4

It will be seen that only 1 reciprocal cross was made on these plants and this was by accident. A large number of reciprocals had been made on other crosses always with the same results when tried a sufficient number of times to make classification conclusive. It was decided therefore, to make as many distinct matings as possible in order to make a thorough test of the mating proclivities of the plants under observation. The result is that the percentage of cross-sterility found in the F_5 generation is not strictly comparable with the percentages found for the earlier generations where matings were made at random and each mating counted. To be sure a few reciprocal matings[13] were made in F_5, but the percentage is very much less than in the preceding generations. The gross cross-sterility found in F_5 was 21.7 percent, if the 8 crosses where only 1 pollination was made be counted. By the theory of error 1 of these cases might be excluded, while for certain other reasons (see table 9) error is suspected in another case, but since this correction would reduce the cross-sterility percentage by only 1.2, the figures 21.7 will be allowed to stand.

Eight other intercrosses between other plants of this same population were also made. We have not thought it necesssary to include them in the table because the attempts at crossing were so sporadic, but the percentage of cross-sterility would scarcely be changed, for 7 out of 8 intercrosses were fertile.

A number of other facts appear in the data shown in tables 7 and 8, which are not apparent without careful study. In accordance with their behavior in intercrosses, the plants may be grouped into 5 classes in

---

[13] Seven reciprocals were made altogether in this family with like results.

which there is intra-class sterility and inter-class fertility, with very few exceptions. This grouping is shown in table 9. The two columns at

Table 9

Plants of F_3 generation of cross No. 1, N. Forgetiana × N. alata, grouped in accordance with their behavior in intercrosses.

Group	Ped. No.	Number cases fertile within group					Number cases sterile within group				
		A	B	C	D	E	A	B	C	D	E
A	3	0	5	2	3	1	5	0	0	0	0
	7	0	4	3	3	1	4	1?	0	0	0
	10	0	3	3	3	1	3	1?	0	0	0
	11	0	4	3	1	1	3	1	0	0	0
	13	0	5	3	2	1	2	0	0	0	0
	18	0	5	3	3	–	5	0	0	0	–
B	2	5	2	2	1	1	0	3	0	1	0
	5	4	1	2	3	1	1?	3	0	0	0
	9	5	1	3	2	1	1?	2	0	0	0
	16	6	2	3	3	1	0	3	0	0	0
	19	6	2	3	3	–	0	2	0	0	–
	20	–	0	1	–	–	–	3	0	–	–
C	6	5	4	0	3	1	0	0	2	0	0
	14	6	5	0	3	1	0	0	2	0	0
	15	6	5	0	3	1	0	0	2	0	0
D	8	4	4	3	0	1	0	0	0	2	0
	12	6	5	3	0	1	0	0	0	2	0
	17	4	3	3	0	1	1	1	0	2	0
E	1	5	4	3	3	0	0	0	0	0	0

the left show the division into groups, and the pedigree numbers of the plants within each group. The next 5 columns show the number of individual cases of cross-fertility within each group. For example, plant No. 3 was fertile with 5 plants of group B, with 2 plants of group C, with 3 plants of group D, and with the single plant comprising group E. The last 5 columns show the number of individual cases of cross-sterility within each group. The exceptional cases where there is inter-class sterility or intra-class fertility are printed in bold-face type. By utilizing the mating record of a plant either when used as a male or female in making the classification, all of the plants could be grouped excepting number 4 which had very bad pollen. It is excluded on this account.

The number of exceptions appear at first sight to be rather large but it must be remembered that one exceptional mating makes two irregularities appear in the table. If 7 is sterile with 9, 9 is sterile with 7, for example, and both exceptions are noted.

Number 2 and number 17 are anomalous plants; the remainder behave very regularly. 2 is sterile with 17 where one would expect to find fertility: this is also true of the mating 17 × 11. Both of these matings were made twice, which establishes the sterility rather definitely. In addition 2 is fertile with both 9 (thrice) and 19 (twice) of the same group, though it properly belongs in group B from its sterility with 5, 16 and 20, and its fertility with at least 1 plant of each of the other groups. The mating between 2 and 9 was fertile only 3 times in 6 trials, however, and may indicate a *pseudo-fertility due to external conditions.* The cross was made reciprocally; 2×9 was fertile in both trials, but 9×2 was fertile but once out of 4 trials.

Eliminating plants 2 and 17 from consideration, there are left only 4 unconformable matings. There are 2 cases of inter-class sterility, 9 with 7 and 10 with 5. Each of these matings was made but once, however, and their sterility is questionable because 4 times per 100 one obtains no seed in matings that otherwise prove fertile. The exceptional fertile matings, 5 with 16 (thrice) and 16 with 19 (twice), on the other hand, appear to be definitely established.

If one admits the possible fertility of combinations 9 × 7 and 10 × 5, then, 16 plants allow themselves to be grouped into five classes A, B, C, D, and E, with no anomalous behavior whatever. Each is cross-sterile with every plant of its own class and cross-fertile with every plant of every other class with which it is tested. True, 3 anomalies remain, plants 2, 16 and 17. Number 17 of class D shows a perfectly regular behavior except with plant 11 of class A and plant 2 of class B. Plants 2 and 16 show their irregularities only within their own class except in the cross between 2 and 17, which leads us to suspect pseudo-fertility.

The conclusion seems just, therefore, that this grouping is real and significant, since the great majority of these plants (in this sample of the population, 84 percent) shows an absolutely regular behavior and the small minority of exceptional plants presents but a few irregularities.

If one admits the justice of this classification there comes the question of the number and composition of such groups in the F_5 generation of this cross. 19 plants form a very small sample of such a population. What is the composition of the whole population? The first thing to be noted is the varied size of the groups. The number of individuals in each class is 6, 6, 3, 3, and 1, respectively. Even with a due allowance for the smallness of the sample, it is clear that there is little probability of the plants being distributed in equal-sized classes. It is hardly more probable that the distribution will fit a Mendelian $(3/4 + 1/4)^n$ expansion. It is reminiscent, however, of a normal binomial expansion $(1/2 + 1/2)^n$. The resemblance is possibly illusory, but 0, 3, 6, 6, 3, 1 is too much like 1, 5, 10, 10, 5, 1 to escape notice, particularly as on the theory of random sampling it is possible for the whole population to contain from 1 to 3 more classes. Be that as it may, we can certainly conclude that the F_5 generation of this particular cross contains *no more* than from 6 to 8 groups—the chances are practically negligible that there might be 10—which are intra-class sterile and inter-class fertile, and within which the distribution of individuals bears some similarity to that of a normal frequency distribution.

Let us now consider whether a possible meaning can be attached to the results obtained in this experiment.

Argument on cross No. 1

We early assumed a working hypothesis in part similar to and in part different from that of MORGAN, viz.; first, self-sterility is heritable; second, as regards that part of the constitution of pollen grains which affects the behavior of self-sterile plants all pollen grains produced by each plant are alike, i.e., with reference to self-sterility pollen grains behave as if they were sporophytic; third, under normal conditions the pollen tubes produced by pollen from any self-sterile plant will not grow in styles of that plant with a rapidity sufficient to reach the ovules during the "life" of the flower, on account of this "likeness" of constitution; fourth, pollen tubes will grow with a rapidity sufficient to allow fertilization to occur if the constitutions of the two proposed parental plants *differ* from each other in any of these essential factors, by reason of a stimulus possibly analogous to that which makes growth more vigorous in first generation hybrids.

The first assumption has been demonstrated more or less clearly by all who have worked upon self-sterile plants. It is proved for self-sterile Nicotiana species both by the experiments reported here, and by those to be published later on the relation between self-fertile and self-sterile plants.

The second assumption is proved circumstantially by the fact that reciprocal matings always duplicate each other. Direct experiments showing that selective fertilization does not occur have also been made, and will be the subject matter of another paper.

If there be any justification for the third and fourth assumptions, a cross between two self-sterile species differing by a large number of hereditary factors (expecting some of the differences to be effective) should show a high degree of cross-fertility in the F_1 and F_2 generations, followed by an increasing percentage of cross-sterility in later generations produced by the closest possible inbreeding. The reason for such a belief is, of course, the well-known fact that inbreeding increases homozygosis. Such being the case, plants ought to appear with "like" constitution as far as the factors affecting cross-fertility are concerned, and these should be cross-sterile to each other. If the factors affecting cross-fertility are relatively few in number, a small number of intra-sterile, inter-fertile groups should be found after a comparatively limited amount of inbreeding. This, broadly speaking, we believe to be a plausible interpretation of the facts found. A detailed interpretation is given later.

In general, the F_2 generation of such a cross—between species—might be expected to show an approach to the maximum limit of cross-fertility, since the F_2 generation usually shows greater variability than succeeding generations. But in the case of self-sterility where the self-sterile plants must be supposed to differ in constitution among themselves, this is probably not strictly true. If one could test a large series of F_2 populations from various original and F_1 matings, he ought to find a variable degree of cross-fertility, with the maximum reached only in certain cases.

In this instance, no claim can be made that we are dealing with the maximum. We can only report the results for this case, pointing out that in crosses No. 2 and No. 3, the cross-fertility is much lower.

One of the best systems of inbreeding in the case of self-sterile plants is to mate sister plants in successive generations, for such crossing, after an original mating *Aa* × *Aa,* by Mendelian recombination ultimately gives a population in which *AA* and *aa* each approach ½ and *Aa* approaches 0. Expectation of homozygosis in successive matings is $\frac{1}{2}$, $\frac{5}{8}$, $\frac{11}{16}$, $\frac{24}{32}$ - - - - 1 (JENNINGS 1916). This system seemed to suit our purpose better than any scheme of mating parent with offspring, because of the difficulty of keeping plants alive for several years.

It is regretted that so little is known about the cross-fertility of the F_1 generation, but this bit of ignorance does not affect our test seriously. This really begins with the inter-cross of two self-sterile F_1 plants, which were similar in appearance, but were producing numerous different types of gametes, as is proved by the extremely variable F_2 generation.

The cross-sterility[14] of the F_2 generation was 2.4 percent, if the sixth case of sterility where only one pollination was made, be included. The result on the 20 plants tested rather thoroughly was 3 cases of cross-sterility out of 131 matings. The result on the other twenty-odd plants tested less thoroughly was 3 cases of cross-sterility out of 120 matings. And this percentage of cross-sterility may have been too low, as was mentioned before, because of our failing to suspect pseudo cross-sterility at this time. But taking this low estimate of cross-sterility at its face value, it is clear that no hypothesis of Individualstoffe (Cf. JOST 1905) is necessary to account for the results. The presence of even 6 cases of cross-sterility in 251 matings eliminates this requirement definitely.

The number of classes which would be necessary to give such an amount of cross-sterility, on the assumption of inter-class fertility and intra-class sterility, depends upon what is presupposed as to the frequencies within the classes.

As we shall have a number of such estimations to make, let us consider the matter here. It is always dangerous to calculate *a posteriori* probabilities. But because this danger is realized, and the probabilities calculated must be used with caution, it seems best to use as simple an approximation as possible. Therefore, we have assumed that if S and F represent the total number of sterile and of fertile matings found, the probable error of the determination $\frac{S}{S+F}$ is $\pm \frac{.6745}{S+F}\sqrt{\frac{(S)\,(F)}{S+F}}$. In obtaining this figure, self × self is added to the cross-sterility of course, S representing the total of sterile combinations. The fraction $\frac{S}{S+F}$ then gives us a measure of the probable number of classes for

---

[14] In our preliminary paper (EAST 1915) judgment was withheld as to the validity of the apparent cases of cross-sterility in the F_2 generation of this cross. The recovery of a misplaced data card with records of duplicate cross-pollinations made on the combinations that had shown apparent cross-sterility, by Dr. WHITE, gives us the grounds for our present conclusions.

$\frac{S}{S+F} = \frac{\Sigma(C_a^2 + C_b^2 + \ldots\ldots\ldots C_r^2)}{\Sigma(C_a + C_b + \ldots\ldots\ldots C_r)^2}$, where r is the number of classes, and C_a, C_b, etc., are the number of individuals within each class.

If the classes are of equal size, the ratio of sterility to total number of combinations is $\frac{1}{n}$ where n is the number of classes; for if there are x individuals in each class the sterility is $\frac{nx^2}{n^2 x^2} = \frac{1}{n}$. If on the other hand, the distribution of individuals within the classes is that of the coefficients of the point binomial, these coefficients must be substituted.

With these two assumptions as to distribution, the following percentages of sterility to total number of matings is found:

Number of classes	Equal size	Point binomial	Number of classes	Equal size	Point binomial
4	25.0	31.3	15	6.6	15.0
5	20.0	27.3	16	6.2	14.5
6	16.7	24.6	17	5.9	14.0
7	14.3	22.6	18	5.6	13.6
8	12.5	20.9	19	5.3	13.2
9	11.1	19.6	20	5.0	12.8
10	10.0	18.5	21	4.8	12.5
11	9.0	17.6	22	4.5	12.2
12	8.3	16.8	23	4.3	11.9
13	7.7	16.1	24	4.2	11.7
14	7.1	15.5	40	2.5	9.0

Should one wish to make the calculation from cross-sterility only on account of the self-sterility determinations being selected values the formula becomes

$$\frac{S_c}{S_c + F} = \frac{\Sigma(C_a^2 + C_b^2 + \ldots\ldots\ldots C_r^2) - \Sigma(C_a + C_b + \ldots\ldots\ldots C_r)}{\Sigma(C_a + C_b + \ldots\ldots\ldots C_r)^2 - \Sigma(C_a + C_b + \ldots\ldots\ldots C_r)}$$

but this correction is unnecessary under most circumstances.

Taking now the gross returns on the F_2 generation at their face value, 2.4 percent cross-sterility, or 15.8 percent total sterility on the 40 plants used, the number of classes of approximately equal size necessary to account for the results is between 8 and 14. But the groups which were afterward found in the F_5 generation, were not of equal size. Their frequencies resembled rather those of a point binomial. Assuming such a distribution within the classes of F_2, the number of classes would lie between 12 and 25.

These class number determinations have been made roughly on purpose. There are three reasons for doing this.

In the first place, there is reason to believe that the proper percentage of cross-sterility was not obtained. Our calculations were made by including with the matings listed in table 4, 28 matings of plants shown in table 4 with other plants, and 92 matings made rather unsystematically between about 20 plants not shown in that table. Data as to the age, condition, flowering period, etc., of these plants were not recorded. Furthermore, fertility and sterility were usually recorded merely as *F* and *S* without data as regards the percentage of seeds in the capsules. For our present purpose, therefore, they have *not* the value of the data recorded in table 4.

Probably the correct way to treat the data of table 4 would be as follows. Consider every mating as if it were made reciprocally whether actually accomplished or not. For example, 5 × 1 is fertile; then assume 1 × 5 to have been fertile even though that mating was not attempted, since reciprocals always have given the same results. If this be done the records show 184 cases of cross-fertility, 4 cases of cross-sterility and 20 cases of self-sterility. Another question then arises. These plants supposedly were *all* in good condition and in general were mated only at the height of the flowering season. But we did not at that time suspect pseudo cross-fertility, and made no particular attempt to clear up doubtful cases, as was done later on crosses No. 2 and 3. Now crosses 3 × 17, 5 × 15, 6 × 8 and 19 × 14, although made twice each, showed less than 50 percent of the ovules fertilized. The reciprocal of 6 × 8 was clearly fertile, so this mating remains in the "fertile" column. But there is good reason from analogous results in the other families for considering the other 3 matings as sterile. The mating 5 × 15 may be questionable, but as 5 had such bad pollen we cannot be certain of the placing of mating 15 × 5, as was stated earlier. If then we remove these matings from the fertiles to the steriles, which seems the logical thing to do, there are 178 cases of cross-fertility, 10 cases of cross-sterility and 20 cases of self-sterility. The total percentage of sterility is 14.4 (30:208), with very little selective advantage to sterility on account of self-fertilizations.

With these facts in view, we believe it reasonable to assume that between 8 and 14 approximately equal-sized intra-sterile classes or between 12 and 25 intra-sterile classes with the individuals distributed according to the point binomial coefficients, are represented in the F_2 generation,—these being taken as distributional extremes.

The second reason for approximating the number of classes is because the number of individuals investigated is comparatively small, and the probability that they are not a fair sample of the population correspondingly large.

The third reason is that the probable upper limit of the number of classes is all that is essential to our purpose. *The point is, that should the answer lie between 27 and 81 classes, the difference could be accounted for by 1 additional Mendelian factor pair.* The number of actual classes in the F_2 generation of a Mendelian population is 3^n where n represents the number of allelomorphic pairs; and 3^3 is 27, while 3^4 is 81.

Thus it is clear that with the assumptions made previously regarding the cause of self-sterility, our probable maximum cross-fertility can be interpreted by 3 (possibly 4) effective allelomorphic pairs.

For the same reasons for which it was thought best to *correct* the gross percentage of cross-sterility found in the F_2 generation, the later generations of this cross ought to be revised.

Considering then only the matings of the F_3 generation shown in table 5, if one counts reciprocals fertile or sterile as the case may be with the mating made, there are 98 fertile combinations and 6 sterile combinations. But mating 1 × 5, made twice, yielded capsules only 30 and 35 percent full, respectively; and mating 9 × 3, made thrice, yielded capsules only from 20 to 30 percent full. If, as seems probable, these are really sterile matings, the ratio of cross-sterility to the total number of cross-combinations becomes 10 to 104 or 10 percent, and the ratio of total sterility to total number of combinations becomes 22 to 116 or 19.1 percent.

Similarly correcting the results listed in table 6 for the F_4 generation, we find 16.2 percent of cross-sterility in the cross-combinations and 26.2 percent of total sterility in all combinations, with indications that plants 2, 5 and 8 belong in one class, plants 6 and 7 in a second class, and plants 9 and 10 in a third class. This result is obtained thus: there are listed 68 fertile and 6 sterile combinations, but matings 10 × 9 (made twice), 6 × 7 and 7 × 6 are now classed as sterile because they uniformly gave capsules less than 40 percent full.

The cross-sterility of the F_5 generation has already been analyzed sufficiently carefully in explaining table 9. Measured as above it is 22.2 percent.

Unquestionably the samples of the populations from which these results were obtained were so small and the number of matings so few, *that the probable errors are large; but rough as the determinations may be, we think that no one can question the general conclusion that in these three generations from repeated sib matings cross-sterility has increased immensely.*

The cross-fertility of F_2 in this cross, as compared with the cross-fertility in those to be described next, is high. It may not be the maximum cross-fertility possible in a population from one original mating, but it is the highest found in 16 families that we have studied rather thoroughly. High as it is, nevertheless, the probable maximum number of inter-fertile, intra-sterile classes which it contains is *less than 25,* and this number may be interpreted by the permutations of 3 Mendelian allelomorphic pairs. Further the probable number of these classes in the F_5 generation can hardly be more than 8, a figure which may be interpreted by only 2 effective allelomorphic pairs. We were decidedly in error, therefore, when in 1915 we said (EAST 1915): "This is a straight mathematical problem and it is hardly necessary to say that it is insoluble by a strict Mendelian notation such as CORRENS sought to give." In justice it should be said, however, that at that time, the existence of cross-sterility in the F_2 generation was uncertain through a supposed lack of confirmatory data which was really in our possession and had been overlooked.

Cross 2. N. alata × N. Forgetiana (pseudo self-fertile × self-sterile) and cross 3. N. Forgetiana × N. alata (self-sterile × pseudo self-fertile)

The two crosses to be described next are reciprocals made with the same two individuals. It was our intention to repeat the cross just described together with its reciprocal, and to make a more thorough study of the first hybrid generation. At the same time we intended to study the relation between self-sterility and self-fertility by crossing *N. Forgetiana* with a fertile plant of *N. alata,* since *N. alata* was then supposed to be a mixed population consisting of self-sterile and self-fertile plants. Both of these crosses were made. In crosses No. 2 and No. 3 the "self-fertile" daughter of the original supposedly self-fertile plant described on page 534 was used as the *N. alata* parent. Soon after work was started on these plants, our evidence was so conclusive that *N. alata* was always self-sterile and that this particular individual showed only pseudo-fertility caused by external conditions, that we decided to use *N. Langsdorffii* as the self-fertile strain in a series of crosses and to continue this work as a repetition of cross No. 1.

TABLE 10

Result of matings on F_1 plants 0 to 39 of cross No. 2, N. alata × N. Forgetiana and on plants 40 to 52 of cross No. 3, N. Forgetiana × N. alata. Number of pollinations shown by subscripts.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
0	44, 46_3	22_2, 34, 38_3, 49
1	2, 3, 4, 6, 41	8_2
2	4, 18, 41, 44, 52	9, 22, 23_2
3	2, 9, 14, 23, 29	4_4, 6_2, 18_3, 41_3, 46
4	2_2, 9, 10, 44_2	18
5	2, 3, 6, 9, 10_2, 18_2, 46	8_2, 44_2
6	5, 10_2, 43, 44	3_2, 4_3, 18_2, 40_2
7	2, 13, 22, 44	18_3, 46
8	6, 9, 10, 39, 40, 46_3	5_3, 44_4
9	3, 18, 44, 52_2	2_4, 10, 23_2, 37, 48
10	4, 6, 18, 40, 44	2_2, 23, 24_2, 27_3, 34_3, 48_2
11	2, 8, 12, 15, 34, 44, 46	
12	9, 16, 22, 43	6_3, 18_3, 46_3, 52
13	3, 8, 18_2, 44, 46	2, 9_2, 15_3, 21_2, 34_7
14	18_2, 20, 43	10, 34_1
15	1, 3, 16_2, 17, 18, 20	9_5, 13_2, 14, 23_7, 44
16	13, 14, 18, 25, 43_3, 46	17_2, 29_3
17	14, 18, 19, 20, 22, 30	16, 26_5, 44_3
18	2_2, 9_2, 21_2, 23, 28, 34, 36, 44	3, 46_3
19	17, 22, 28, 34, 44	18_2
20	2, 8_2, 9, 16, 18, 20_2, 21, 22_2, 26, 36, 40, 44	43_2
21	4, 12, 16, 18, 46	2, 9_4, 22_2, 25, 27_2, 37
22	12, 42, 44	14, 23_4, 24, 36, 48_3
23	41	9_2, 10_3, 37, 48_2
24	3_2, 6, 20, 26, 28, 44	10_2, 22_2, 23, 30, 37
25	8, 33, 44_2, 46_3	2_2, 9, 23_3, 27
26	9, 18, 22, 23_2, 25, 40, 48	28, 29_3, 44_3
27	3_3, 18, 32, 44, 46	2, 9_2, 30_3, 34_3, 48
28	2_2, 3, 23_2, 27, 39, 46_2	8, 26_2, 29_3, 44_3
29	2, 14_3, 18_2, 22, 23, 24, 25, 30, 34, 37, 41, 46	5_2, 26, 28, 31_4, 44_3
30	8_3, 29, 33, 44_2, 45, 46	9, 21_4, 22_3, 27
31	22, 32, 52	8_2, 29, 36, 44
32	9, 21, 23, 29, 30, 34, 43, 44	18, 33, 46_2
33	8, 16, 23, 31, 46	18_5, 32_2
34	28, 41, 44, 46	10_2, 23_2, 24, 37_2
35	3, 9, 18, 21, 27, 30, 34, 37, 42	8_3
36	8_2, 33, 44_2, 46	10_3, 23
37	39, 42_2, 43, 44, 46_2	9_2, 10_3, 22, 23_4, 34_3, 38
38	28, 35, 39, 42, 43, 46_2	34_3, 37_3, 47
39	9, 44	18, 40_2, 42_3
40	22, 43, 44, 47, 49	6, 33_5, 46_2
41	10, 37, 44, 48	33_2, 10, 46_4
42	20, 44	39_3, 41, 45_2
43	5, 27, 33, 38, 39, 40_2, 42, 44, 46, 51	
44	10, 14, 23, 34, 45	
45	18, 44, 48	46_2, 52
46	10, 22, 37, 44, 51	52_4
47	20, 42, 44, 45, 46, 51, 52	38_2
48	40, 41, 43, 46	10, 23_2, 24_2, 27_2, 34
49	42, 44, 45	0, 9, 27, 34_3, 47
50	18, 39, 51, 52	9, 27_5, 37_2
51	9, 18, 23, 39, 45, 46, 50	8, 29
52	10, 23, 29, 37, 51	3_2, 4_2, 6, 18_2, 41_2, 45_3, 46_2

It is reasonable to consider these crosses in a sense to be repetitions of cross No. 1, but one must not assume that they are duplicates of cross No. 1. Both *N. alata* and *N. Forgetiana* must consist of plants which differ among themselves in the factors that affect self-sterility, hence only by following through a number of F_1 generations where these species are involved could one expect to find results duplicating those of cross No. 1. The data are none the less interesting, however, because the crosses are only similar and not identical.

The F_1 generation

All of the individuals resulting from this cross were grown in a greenhouse as potted plants. The F_1 generation came into blossom during the latter part of the winter. Conditions were extraordinarily favorable for growth and the pollinations were all made while the plants were vigorous, hence scarcely any trouble arose over classification of the results.

Our study was made on a population of 53 plants. Pedigree numbers from 0 to 39 inclusive represent cross No. 2, *N. alata* × *N. Forgetiana;* pedigree numbers 40 to 52 inclusive represent cross No. 3, *N. Forgetiana* × *N. alata.*

Each plant was selfed one or more times, and all proved absolutely self-sterile. Further *each plant* was *back-crossed* with pollen from a single plant of each of the parent species *with complete success in every instance.* The plants used in this work were not the individuals that entered into the cross under discussion, however, for unfortunately these were not available.

The numerous cross-pollinations made are shown in table 10. There were 103 reciprocal matings. Of these 100 gave duplicate results, 39 pairs being fertile and 61 pairs sterile. The three which did not check are:

2 × 3,	sterile,	1 pollination	classed as fertile
3 × 2,	fertile,	1 pollination	
6 × 52,	fertile,	1 pollination	classed as sterile
52 × 6,	sterile,	1 pollination	
37 × 21,	fertile,	1 pollination	classed as sterile.
21 × 37,	sterile,	1 pollination	

Since but one pollination was made in each of these cases we have made our decision as to fertility or sterility by a consideration of the circumstantial evidence. The behavior of these plants in other crosses shows conclusively that 3 should be fertile with 2, 6 sterile with 52, and 21 sterile with 37. They have been classed accordingly. That this grouping is correct is further shown by the fact that the mating 3 × 2 (classed as fertile) was made at the height of the flowering season, while the matings 6 × 52 and 37 × 21 (classed as sterile) were respectively the last and next to the last matings made on those plants.

In spite of the fact that plants 0-39 are from cross No. 2, *N. alata* × *N. Forgetiana,* and plants 40-52 are from cross No. 3, *N. Forgetiana* × *N. alata,* they behave as one family in inter-crosses. The entire population can be grouped into 6 classes in which there is inter-class fertility and intra-class sterility (table 11). The following explanation may be necessary to make it clear just how table 11 was obtained from table 10. Table 10 shows all of the matings; but in the form given it is not easy to see at a glance every combination in which a particular plant was used, both as male and as female. It was necessary, therefore, to make a new table in which the pedigree numbers in the column at the left were tabled as males, and the pedigree numbers in the columns headed "Fertile matings" and "Sterile matings" were tabled as females. Thus plant 2 used as a female was fertile with pollen from plants 4, 18, 41, 44, and 52, and sterile with plants 9, 22 and 23; but pollen from plant 2 was fertile on plants 1, 3, 4, 5, 7, 11, 18, 20, 28 and 29, and sterile on plants 9, 10, 13, 21, 25 and 27. It is clear, therefore, that instead of the 8 matings on plant 2 that table 10 appears to show, there are really 21, the 3 reciprocals of course being counted but once.

These tables were combined for analysis. In the interest of economy only one is shown, however, since the second can easily be made from the first.

The four exceptions in this huge set of matings are in reality negligible though they are emphasized in the table by bold-faced type. Matings 15 × 44 and 31 × 36 were sterile, though they do not belong to the same class. Plant 15 was sterile to 4 plants of class A and fertile to 2 plants of class B, 3 plants of class C, and to the isolated individuals forming classes D and F. It is unquestionably a member of class A. Plant 44 was sterile to 7 individuals in class C and fertile to 17 plants of class A, 12 plants of class B and to the singletons forming classes D, E and F. This evidence places it unmistakably as a member of class C. Plant 31 is also a member of class C as evidenced by 3 sterile matings within that class and by fertile matings with 1 plant of class A and 3 plants of class B. Plant 36 is like plant 15 thrown into class A by its sterility with 3 others of that class, and by its fertility with 3 individuals

TABLE II

Plants of F_1 generation of reciprocal cross between N. Forgetiana and N. alata, grouped in accordance with their behavior in inter-crosses. Plants 0-39 are products of cross No. 2; plants 40-52 are products of reciprocal cross No. 3.

Group	Ped. No.	Number cases fertile within group						Number cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	0	0	1	1	—	—	—	4	0	0	—	—	—
	2	0	6	5	1	—	1	8	0	0	0	—	0
	9	0	7	6	1	—	—	13	0	0	0	—	—
	10	0	7	3	—	—	—	10	0	0	—	—	—
	13	0	4	3	—	—	—	5	0	0	—	—	—
	14	0	2	4	1	1	—	4	0	0	0	0	—
	15	0	2	3	1	—	1	4	0	1	0	—	0
	21	0	5	2	1	—	—	8	0	0	0	—	—
	22	0	6	5	1	—	—	9	0	0	0	—	—
	23	0	6	5	—	—	—	11	0	0	—	—	—
	24	0	2	4	1	—	—	7	0	0	0	—	—
	25	0	2	5	—	—	—	5	0	0	—	—	—
	27	0	4	3	—	1	—	10	0	0	—	0	—
	30	0	4	5	—	—	—	5	0	0	—	—	—
	34	0	5	4	—	—	1	11	0	0	—	—	0
	36	0	3	2	1	—	—	3	0	1	0	—	—
	37	0	5	3	—	1	—	9	0	0	—	0	—
	38	0	3	2	—	1	—	4	0	0	—	0	—
	47	0	5	2	1	—	—	2	0	0	0	—	—
	48	0	4	1	—	1	—	7	0	0	—	0	—
	49	0	3	1	—	—	—	5	0	0	—	—	—
	50	0	3	1	—	—	—	3	0	0	—	—	—
B	3	8	0	5	—	—	—	0	6	0	—	—	—
	4	4	0	2	—	—	—	0	4	0	—	—	—
	6	2	0	4	—	1	—	0	6	0	—	0	—
	7	3	0	1	—	—	—	0	2	0	—	—	—
	12	3	0	1	—	1	1	0	4	0	—	0	0
	18	12	1	9	1	—	—	0	11	0	0	—	—
	19	2	0	3	—	—	—	0	1	0	—	—	—
	32	6	0	3	—	1	—	0	3	0	—	0	—
	33	4	1	3	0	1	—	0	4	0	—	0	—
	39	4	0	4	—	1	—	0	3	0	—	0	—
	40	5	0	3	1	1	—	0	5	0	0	0	—
	41	6	0	3	—	—	—	0	6	0	—	—	—
	42	5	0	2	1	1	—	0	3	0	0	0	—
	45	4	1	2	—	—	—	0	3	0	—	—	—
	46	14	1	7	—	1	1	0	9	0	—	0	0
	52	7	0	3	—	—	—	0	8	0	—	—	—
C	1	2	4	0	—	—	—	0	0	1	—	—	—
	5	3	4	0	—	1	—	0	0	3	—	0	—
	8	6	5	0	1	—	1	0	0	7	0	—	0
	16	5	4	0	1	1	—	0	0	2	0	0	—
	17	4	2	0	1	—	—	0	0	3	0	—	—
	26	6	2	0	1	—	—	0	0	4	0	—	—
	28	6	5	0	—	—	—	0	0	4	—	—	—
	29	9	6	0	—	—	—	0	0	7	—	—	—
	31	1	3	0	—	—	—	1	0	3	—	—	—
	35	7	3	0	—	—	—	0	0	1	—	—	—
	44	17	12	0	1	1	1	1	0	7	0	0	0
	51	4	5	0	—	1	—	0	0	2	—	0	—
D	20	9	3	5	—	1	—	0	0	0	—	0	—
E	43	5	8	4	1	—	—	0	0	0	0	—	—
F	11	3	2	2	—	—	—	0	0	0	—	—	—

of class B, with 2 of class C, and with the lone plant of class D. In view of this evidence and the fact that in these two matings but one pollination was made in each case, they are much more likely to be errors of record or of technique than true exceptions to our classification.

The other two exceptions, matings 45 × 18 and 33 × 46, were fertile where from the evidence of numerous other matings they should have been sterile. Here again but one pollination was made in each case; and, coincidence though it may be, *each pollination was the last mating made on that particular plant.* What is more probable than that this is a pseudo fertility appearing during the wane of the flowering season of the two mother plants, No. 45 and No. 33?

Six groups appear in table 11, but there is proof of the existence of only five. Groups A, B, C, D and E are definitely established. Plant 11, on the other hand, is an isolated individual rather than a class. It does not belong to groups A, B, or C; but unfortunately it was not crossed either with class D (plant 20) or with class E (plant 43), hence one cannot say that it does not fall into one or the other of these two classes.

In the three large groups the distribution of individuals is 22, 16 and 12. About all that can be said about the type of this distribution is that the classes appear not to be of equal size. On the other hand, it is interesting to note that the plants of both cross No. 2 and cross No. 3 fell into the three groups as if they were samples of the same population. There were 40 plants of cross No. 1, and 12 plants of the reciprocal cross No. 2. In the classes A, B and C the proportions were 18, 10, 10 and 4, 6, 2, respectively. This similar behavior of the progeny of reciprocals seems to us strong corroboratory evidence in favor of the conclusion that reciprocal crosses always behave in like manner as regards self-sterility.

It is interesting here to check our *a posteriori* probabilities with the facts. There were 278 fertile matings made in this family, of which 39 were reciprocals, making 478 (278 × 2—78) fertile combinations altogether. There were 167 sterile matings, of which 61 were reciprocals, making a total of 212 (167 × 2—122) cross-sterile combinations. If to the cross-sterile combinations, the 53 self-sterile combinations be added, there is a total of 265 sterile combinations out of 743,—a percentage of 35.6 ± 1.2. Assuming a point binomial distribution of individuals we should expect 4 intra-sterile classes for this percentage of sterility; but since we must discount the selection of self-combinations a little, perhaps 5 classes may be taken as the probable expectancy.

It was planned to continue the study of this family—considering it as a single cross—on populations obtained by back-crossing a representative of each of the large classes A, B, and C with both parents, and by intercrossing the same three individuals among themselves. This rather Herculean task has not been finished. The progeny of a part of these matings was investigated as thoroughly as time permitted in 1915-16, but much remains to be done. These families came from the following combinations:

Family D, *N. alata* plant 53 × plant 44 of class C
Family E, *N. alata* plant 58 × plant 44 of class C
Family F, plant 34 of class A × *N. Forgetiana*
Family G, plant 44 of class C × *N. Forgetiana*
Family H, plant 44 of class C × plant 10 of class A
Family I, plant 44 of class C × plant 34 of class A
Family J, plant 52 of class B × plant 23 of class A
Family K, plant 52 of class B × plant 44 of class C

In families D and E we have two *N. alata* plants 53 and 58 crossed with the same plant of cross 3 (table 11), No. 44 a member of class C. Families F and G were produced by crossing individuals of classes A (34) and C (44) with the same plant of the other parent species *N. Forgetiana.* The four remaining families are true F_2 generations formed by mating two F_1 plants. There is a duplicate test of plant 44 (class C) with two plants of class A, 10 and 34. Then there is a test of plant 52 (class B) with plant 23 of class A and plant 44 of class C. Thus plant 44 of class C enters into two back-crosses with *N. alata,* one back-cross with *N. Forgetiana,* and matings with two individuals belonging to class A and one individual belonging to class B.

Family D,—*N. alata* plant 53 × plant 44 of class C, cross No. 3

The first of the eight F_2 populations of crosses No. 2 and No. 3 was produced by back-crossing. Plant 53 of *N. alata* (table 1), a plant apparently[15] fertile with sister plants 57 and 58, and sterile with sister plants 54, 56 and 59, was crossed with the pollen of plant 44 of class C, cross 3. In a manner of speaking, it may be called $P_1 \times F_1$, if it be remembered that plant 53 is not the same plant of *N. alata* used in making cross No. 3.

Table 12 shows the self-pollinations made on 39 plants. They behaved in much the same manner as the *N. alata* plants recorded in tables 1-3. One-third of them produced some seed, though from 1 to 10 failures

---

[15] See page 533.

TABLE 12

Family D.—Record of self-pollinations on progeny of N. alata plant 53 × plant 44 of F_1 *of cross No. 3*

Ped. No.	No. selfings sterile	No. of selfings giving capsules with		
		1-10 seeds	10-50 seeds	250-300 seeds
151	11			
152	15			
153	6			
154	10			
155	14			
156	10	1		
157	1			
158	4			
159	2			
160	2			1
161	1			
162	8			
163	3			
164	7			
165	3	2		6
166	10	2		
167	7			
168	1			
169	1			
170	9			
171	5		2	
172	1			
173	2			
174	10			
175	1			1
176	3			
177	10	2		
178	11		5	
179	5			
180	4			
181	5			
182	8		1	
183	5		1	
184	3			
185	1	4		
186	6		1	
187	8	4		
188	16			
189	9			

were also recorded for the same plants. The remaining plants produced no capsules. There was an extremely high correlation between this partial fertility which we have regarded as false, and the close of the reproductive period. Yet one cannot say that every plant can be made to produce seeds at this phase of the life cycle, even under adverse conditions. This may be the case, but we have been unable to demonstrate it. 4 plants in this family, however, gave a very nice demonstration of the fact that complete self-sterility returns with the return of a new flowering season. A number of these plants were selfed at various times during two flowering periods, and plants 156, 166, 177 and 178, though giving a

TABLE 13

Family D.—Record of cross-pollinations on progeny of N. alata plant 53 × plant 44 of F_1 of cross No. 3 outside of family D.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
152		204 Family E
153		204 Family E
167	201 Family E	
171	201 Family E	
174	58 *N. alata*	

TABLE 14

Family D.—Record of cross-pollinations on progeny of N. alata plant 53 × plant 44 of F_1 of cross No. 3.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
151	159	
152	160	185
153		152
154	151	153
155		154
157	154	
159		
160		174
161		162
162		163_2, 168
163	185	
168	173	
170	168	
172	175	
173	159_2	
174		
175		185
177	168, 182_2	183
179	177	
180	177	
181		183
182	160, 183	185
183		177
184	185	188
185	160, 174	
186	185	160?
187		185
188	185	

few poor capsules at the end of the first flowering season, showed complete self-sterility from the beginning to the height of the second flowering period. Then, in two cases, the slight degree of fertility shown at the end of the first flowering season returned. 3 plants produced full capsules. No. 160 and No. 175 yielded 1 each, both according to the late

TABLE 15

Family D.—Progeny of N. alata plant 53 × plant 44 of F_1 of cross No. 3 grouped in accordance with their behavior in inter-crosses.

Group	No. Ped.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	Ind.	A	B	C	D	E	Ind.
A	152	0	1	—	—	—	—	2	0	—	—	—	—
	153	0	—	—	—	—	—	2	—	—	—	—	—
	154	0	—	—	—	—	2	2	—	—	—	—	0
	155	0	—	—	—	—	—	1	—	—	—	—	—
	175	0	—	—	—	—	1	1	—	—	—	—	0
	182	0	1	—	2	—	—	1	0	—	0	—	—
	185	0	3	1	—	2	—	4	0	0	—	0	—
	187	0	—	—	—	—	—	1	—	—	—	—	—
B	160	3	0	—	—	—	—	0	2	—	—	—	—
	174	1	0	—	—	—	—	0	1	—	—	—	—
	186	1	0	—	—	—	—	0	1	—	—	—	—
C	161	—	—	0	—	—	—	—	—	1	—	—	—
	162	—	—	0	—	—	—	—	—	3	—	—	—
	163	1	—	0	—	—	—	0	—	1	—	—	—
	168	—	—	0	1	—	2	—	—	1	0	—	—
D	177	1	—	1	0	—	2	0	—	0	1	—	0
	181	—	—	—	0	—	—	—	—	—	1	—	—
	183	1	—	—	0	—	—	0	—	—	2	—	—
E	184	1	—	—	—	0	—	0	—	—	—	1	—
	188	1	—	—	—	0	—	0	—	—	—	1	—

TABLE 16

Family E.—Record of cross-pollinations on progeny of N. alata plant 58 × plant 44 of F_1 of cross No. 3.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
191		197
192		191
193		44_3, 58_3
194		58_2
195		193, 204
197		199
199		195
200		204
202		197
204		152 Family D
205		204

season expectation. No. 165, on the other hand, was somewhat of an exception to the usual rule, in that it produced 6 full capsules out of 11 pollinations. There were 2 failures and 2 small capsules with from 1-10 seeds each from pollinations made during the height of the flowering season. Toward the end of the flowering period the plant was tested again and yielded 6 good capsules out of 7 flowers selfed.

Five plants of family D were crossed with individuals outside of that group, as is shown in table 13. 2 plants, 167 and 171, were fertile with the pollen of plant 201 of family E, while 2 other plants, 152 and 153, were sterile to the pollen of plant 204 of family E. Plant 174 was fertile with *N. alata* plant 58.

Only 36 cross-matings were made between plants of this family (table 14). Of these, 16 were failures. In spite of this small number of intercrosses, 20 out of 28 plants can be shown to belong to not over 5 classes wherein the plants are intra-class sterile and inter-class fertile (table 15). The other 8 plants show only 1 or 2 cases of cross-fertility and no cross-sterility, and may or may not belong to separate groups. Their fertility with the other classes is shown in the column marked "Indeterminate."

There are no exceptions in table 15. Each plant in every group is wholly intra-class sterile and inter-class fertile as far as it was tested. But these five groups are not necessarily independent. A is not B, C, D, E, 151, 157, or 172; B is not A; C is not A, D, 170 or 173; and D is not A, C, 179 or 180. Therefore B may be C, etc., and the existence of only three groups is demonstrated.

An estimation of the number of classes by formula is hardly desirable on account of the small number of combinations made per plant, though the total number of combinations is larger than appears at first sight because only 1 reciprocal (sterile) was made. There are really 70 combinations of which 30 are sterile, a cross-sterility percentage of 42.8.

Family E.—*N. alata* plant 58 × plant 44 of class C of cross No. 3

Family E resulted from a cross between *N. alata* plant 58 and plant 44 of class C, cross No. 3. The interesting thing about the family is its lack of fertility not only when selfed but also in crosses. 10 plants were mated together in such a manner that the chain of evidence was not broken, as can be seen by studying table 16, with no evidence whatever of any fertility between them. *They all belong to one class showing perfect intra-class sterility.* In addition, if one may assume that all of the individuals would have behaved as plants 193 and 194, the group was sterile to the 2 parents. Plant 204 was also sterile reciprocally with plant

152 of family D, and as a male with plant 153 of family D. The only sign of cross-fertility shown was when pollen from plant 201 (which also belonged to family E) was used on plants 167 and 171 of family D, yet in appearance the pollen of these plants was perfectly good.

It is unfortunate that the behavior of more plants of this family was not investigated, but a good many plants needed attention at the same time during the period these were in flower, and the importance of establishing definitely whether the entire family belonged to one class was overlooked until too late. It is clear, however, that if other classes existed, they must have contained relatively fewer individuals than the one found.

Judged by its parents family E appears to be a duplicate of family D. *N. alata* plant 58 was apparently fertile to its sister plants 53 and 59, and sterile to its sister plants 54, 56, 57, 62, 64, 66, 71 and 79; plant 53, the female parent of family D, was apparently fertile to plants 57 and 58,

TABLE 17

Family F.—Record of self-pollinations on progeny of plant 34 of F_1 of cross No. 2 × plant AA of N. Forgetiana.

Ped. No.	No. selfings sterile	No. of selfings giving capsules with		
		1-10 seeds	10-50 seeds	250-300 seeds
207	9			
211	8			
212	4			
214	11			
215	1			
216	22			
217	12			
218	8			
219	5			
225	11	1		
227	3			
228	12			
229	1			
230	10			
231	10			
232	9			
233	1			
234	1			
235	5			
236	6	1		
237	6			
239	9			
240	11			
241	1			
242	12		1	
243	18			
244	1			

and sterile to plants 54, 56 and 59 of the same family. But considering the behavior of *N. alata* plants 53-79 of table 1 as a whole there is good reason to believe that they all belong to 1 intra-sterile class and that the fertility of matings 53 × 57, 58 × 53 and 58 × 59 is pseudo-fertility. For this reason one might expect family D and family E to behave similarly; but unless one assumes the existence of other classes of low frequency in family E, their behavior was different.

Family F.—Plant 34 of class A × plant AA of *N. Forgetiana*

Family F resulted from crossing plant 34 of class A, cross No. 2, with a plant of *N. Forgetiana;* but, as in families D and E, it was not a true back-cross, since the plant of *N. Forgetiana* used was not the individual that participated in the original mating.

Selfings were made on 27 hothouse-grown plants with the results shown in table 17. It will be noticed that only 3 individuals produced any seeds at all. No. 225 yielded 1 capsule containing 8 seeds in 12 tests; No. 236 produced 1 capsule containing 7 seeds in 7 trials; and No. 241 finally produced a single capsule having about 30 seeds after 12 pollinations. This is a considerably smaller seed production than was recorded for family D, and we believe it to be due to the fact that family F came into blossom somewhat later than family D, thus making it practicable to conclude the pollinations during the height of the flowering season.

A few pollinations were made between plants of this family and plants of family G, the results of which are set forth in table 18. They will be discussed when describing that family.

We were able to make 151 cross-matings on this family, with the results shown in table 19. Some of these matings, unlike the self-pollinations were made rather late in the flowering season. These made trouble in some cases, and had to be repeated several times before a proper decision as to fertility or sterility could be made. In all there were 17 matings that gave seeds in some tests and none in other trials. If the capsules were full and the majority of pollinations succeeded, the mating was called fertile; if the capsules were small and poorly filled, and the majority of the pollinations failed completely, the mating was called sterile.

These 17 matings, we believe, are listed correctly, but there are a few matings made but once during the latter part of the season which may be recorded erroneously.

In addition, plant No. 225 had poor pollen and decision as to the

TABLE 18

Family F.—Record of cross-pollinations on progeny of plant 34 of F_1 *of cross No. 2 × plant AA of N. Forgetiana outside of family F.*

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
216	278 fam. G.	247 fam. G.
219		250 fam. G.
239		247 fam. G.
241	250 fam. G.	
243		247 fam. G.
244	247 fam. G.	

TABLE 19

Family F.—Record of cross-pollinations on progeny of plant 34 of F_1 *of cross No. 2 × plant AA of N. Forgetiana.*

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
207	211, 216, 225	
209	212, 216, 231	
211	209_3, 214, 216	212_2, 215
212	214_2, 216_4, 231	
214	209, 211, 216_2, 217, 219, 228	
215	214, 217_2, 219, 222	
216	212, 217_3, 219_2, 223	239
217	216_2, 218, 219_2	212
218	217, 219	
219	214_2, 215, 216, 217_4, 218_2, 227	228
221	227	
222	217_2, 218, 219_2	
223	216, 225_3, 227, 228, 230, 236	
224	217, 219, 223, 225_2	
225	216, 217_2,, 219, 221, 223, 228, 230_2, 234_2, 235	
226	227_2, 228, 230, 234_3	223
227	219_2, 224, 225_3	
228	222, 223_2, 225_2, 227, 230	219
229	209, 214, 216, 219, 231_4	
230	223, 225_2, 227, 234, 236	
231	212, 214, 219, 229_5	
232	236, 239_2, 243	219, 234
233	223, 234, 239	
234	225, 226, 230_3, 239_3	219, 228, 232_2
235	236_2, 239	232
236	232, 234_2, 239_2, 243	233
237		235_2
238	239, 243_2 244_2	
239	219, 232, 235, 236, 240	243_2
240	234, 236, 239, 243	
241	234_2, 236, 244_3	239, 243_3
242		239, 243_2
243	234, 244_2	239_4, 241, 242
244	236, 238_2, 239_2, 241_2, 243_2	
245	238_2, 241_2, 243, 244	

character of three matings (with 219, 227 and 230) was made on the basis of the successes obtained when No. 225 was used as female.

There were 23 unsuccessful and 128 successful cross-matings in this family. Of these combinations, 55 were reciprocals fertile in both matings and 10 were reciprocals sterile both ways.

Eighteen of the plants can be grouped into 6 inter-class fertile, intra-class sterile groups of 2 or more plants each (table 20), but these groups are not necessarily independent. A is not B, C, D or F; B is not A, C, D, E or F; C is not A or B; B is not A, B or F; E is not B or F; and F is not A, B, D or E. Therefore, C may be D, E or F; D may be C or E; E may be C or D; and F may be C. But since 2 of these alternatives are mutually exclusive, it is definitely established that at least 4 of these groups are independent of each other.

This matter is shown more clearly in table 21, where the 17 other plants which exhibited no cross-sterility are also listed. From this table by the process of elimination cited above it can be shown that 5 separate inter-class fertile, intra-class sterile groups must exist. Since there are 16 plants unplaced because they have had only a few cross-matings made upon them, however, it may be well to compare the number of classes proved with the number to be expected from the percentage of sterility

TABLE 20

Family F.—Progeny of plant 34 of F_1 of cross No. 2 × plant AA of N. Forgetiana grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	219	0	2	1	—	—	—	3	0	0	—	—	—
	228	0	—	—	2	—	—	2	—	—	0	—	—
	232	0	2	—	—	0	1	2	0	—	—	1	0
	234	0	3	—	1	—	2	3	0	—	0	—	0
B	216	1	0	2	1	—	—	0	1	0	0	—	—
	239	3	0	—	—	1	2	0	4	—	—	0	0
	241	1	0	—	—	—	1	0	2	—	—	—	0
	242	—	0	—	—	—	—	—	2	—	—	—	—
	243	2	0	—	—	—	1	0	3	—	—	—	0
C	211	—	1	0	—	—	—	—	0	2	—	—	—
	212	—	1	0	—	—	—	—	0	1	—	—	—
	215	1	1	0	—	—	—	0	0	1	—	—	—
D	223	1	1	—	0	—	2	0	0	—	1	—	0
	226	2	—	—	0	—	—	0	—	—	1	—	—
E	235	0	1	—	—	0	1	1	0	—	—	1	0
	237	—	—	—	—	0	—	—	—	—	—	1	—
F	233	1	1	—	1	—	0	0	0	—	0	—	1
	236	2	3	—	1	1	0	0	0	—	0	0	1

TABLE 21

Family F.—Progeny of plant 34 of F_1 of cross No. 2 × plant AA of N. Forgetiana grouped to show inter-class fertility.

	A	B	C	D	E	F	207	209	214	217	218	221	222	224	225	227	229	230	231	238	240	244	245
A		7	1	3		3			2	1	1		2	1	3	2	1	2	1		1		
B	7		2	1	1	4	1	1	1	1					1		1			2	2	3	2
C	1	3					1	2	3	1			1						1				
D	3	1				2								1	1	2		2					
E		1				1									1								
F	3	4		2	1													1			1	1	
207		1	1												1								
209		1	2						1								1		1				
214	2	1	3					1		1							1		1				
217	1	1	1						1		1		1	1	1								
218	1									1			1										
221															1	1							
222	2		1							1	1												
224	1			1						1					1	1							
225	3	1		1	1		1			1		1		1		1		1					
227	2			2								1		1	1			1					
229	1	1						1	1										1				
230	2			2		1									1	1							
231	1		1					1	1								1						
238		2																				1	1
240	1	2				1																	
244		3				1														1			1
245		2																		1		1	

found, on the theory of a distribution of individuals corresponding to the frequencies of the coefficients of the binomial expansion. In family F there are 128 fertile matings, of which 55 are reciprocals, a total of 146 (128×2—110) fertile combinations. Likewise there are 23 sterile matings, of which 10 are reciprocals, a total of 26 (23 × 2—20) sterile combinations. This amounts to a cross-sterility of 15.1 percent. Adding the 35 self-combinations to the steriles, gives 61 cases of sterility out of 207 combinations,—a percentage of 29.4. We should expect only about 5 intra-sterile classes in this population, therefore, unless a very broad allowance is made for *selection* of matings that were sterile.

TABLE 22

Family G.—Record of cross-pollinations on progeny of plant 44 of F_1 of cross No. 3 × plant AA of N. Forgetiana outside of family G.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
247	44 ♀ parent, F_1 plant	
249	44 ♀ parent, 351_3, fam. H, 467_2, fam. I	
258	34_2 F_1 plant	
278	219 fam. F, 374 fam. H, 467 fam. I	
281	405_2 fam. I	
293	44 ♀ parent, F_1 plant	
308	34_2 F_1 plant	

Family G.—Plant 44 of class C, cross No. 3 × plant AA of *N. Forgetiana*

Family G was produced by mating plant 44 of class C, cross No. 3, with the same plant of *N. Forgetiana* used in producing family F. In all, 53 hothouse-grown plants had some work done upon them, although in a few cases only one mating was made. These plants were studied during a complete flowering season, but nearly all of the work was completed before the period of decline in reproductive vigor so that only a few cases of pseudo-fertility were found. 31 of the plants were selfed from 1 to 19 times with the production of a few seeds in one attempt at selfing only (308). In 12 other matings there was some conflict in the results. These were classified, as before, by recording as fertile those that gave full capsules in two or more trials even though one trial failed, or by recording as sterile those in which a majority of the trials failed even though a portion of the pollinations did produce a few seeds (less than 15 percent of normal).

Table 22 records the crosses made when plants outside of family G

TABLE 23

Family G.—Record of cross-pollinations on progeny of plant 44 of F_1 of cross No. 3 × plant AA of N. Forgetiana.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
247	248_7, 250_4, 253_4, 256, 263, 276	
248	247	
249	247_2, 250_2, 256	
250	247_3, 249	253
251	270	
252	247_2, 249, 256, 257	250, 255
253	247_3, 256, 262	255
255	249, 262	252
256	253	
257	255, 256_2	
258	247, 257, 269	270_2
259	258_3, 262	
260	251_2, 255, 262	
262	266, 271	
263	250, 253	258_2
265	263, 266, 269, 276_2, 278	
266	263, 265, 270_2, 281	
267	251	
268	284	289
269	270, 281	
270		260
271	274	
272	255, 256, 270, 281	
273	275, 276, 281	
274	269, 275_2	270_2
275	258, 270_2, 274, 278	
276	270, 275, 281	
278	269, 274, 285, 289	281_2, 284_2
279	289	281
281	276_3, 284	275, 278
283	270	276
284	281, 285, 289	
285	289, 293, 306, 309	304_3
286	278, 284	289
288		289
289	265, 269, 284, 293_2	286, 306
290	258, 278, 289	
291		284
293	274, 285_2, 289, 290	284
295	310	
297	289	
298	284_2	
303	285_2, 304, 306_2	
304	293, 306_2, 309, 310	307
305	312	311
306	284, 293, 304_3, 309, 310	289
307	310	304
308	312	
309	304_4, 310_3, 311	308
310	304, 308, 309_2, 311, 312	
311	308_4, 309_2, 310_2	
312	309, 310_2	311_3

were used as pollen parents. The 11 matings tried were all successful. 3 back-crosses were made with plant 44, 2 with plant 34 of F_1, 2 with plants of family H and 3 with plants of family I. It should be noted, however, that of 7 crosses of plants of family F with pollen from individuals of family G, 4 were failures. On the other hand, G family pollen was fertile on 3 plants of family H (table 27) and on 1 plant of family I (table 30).

Table 23 shows the cross-matings made within family G. There were 126 successful matings,—19 being pairs of reciprocals,—making 214 successful combinations. 29 matings were sterile, including 5 pairs of reciprocals,—48 combinations in all. 314 combinations have been made, therefore, 100 being sterile (52 selfs + 48 crosses) and 214 fertile. The probable sterility is thus 31.2 percent ± 1.8 percent.

Table 24 shows 27 plants of this family grouped in accordance with

TABLE 24

Family G.—Progeny of plant 44 of cross No. 3 × plant AA of N. Forgetiana grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group						No. cases sterile within group					
		A	B	C	D	E	F	A	B	C	D	E	F
A	250	0	1	—	—	—	—	2	0	—	—	—	—
	252	0	—	—	—	—	—	2	—	—	—	—	—
	253	0	1	—	—	—	—	2	0	—	—	—	—
	255	0	1	—	—	—	—	2	0	—	—	—	—
B	258	—	0	1	—	—	—	—	2	0	—	—	—
	260	1	0	—	—	—	—	0	1	—	—	—	—
	263	2	0	—	—	—	—	0	1	—	—	—	—
	270	—	0	1	—	—	—	—	3	0	—	—	—
	274	—	0	3	—	—	—	—	1	0	—	—	—
C	275	—	3	1	—	—	—	—	0	1	—	—	—
	278	—	1	1	2	1	—	—	0	2	0	0	—
	279	—	—	0	1	—	—	—	—	1	0	—	—
	281	—	—	1	—	—	—	—	—	3	—	—	—
	284	—	—	1	4	—	—	—	—	3	0	—	—
	291	—	—	0	—	—	—	—	—	1	—	—	—
	293	—	1	0	2	2	—	—	0	1	0	0	—
D	268	—	—	1	0	—	—	—	—	0	1	—	—
	286	—	—	2	0	—	—	—	—	0	1	—	—
	288	—	—	—	0	—	—	—	—	—	1	—	—
	289	—	—	4	0	1	—	—	—	0	4	0	—
	306	—	—	2	0	2	—	—	—	0	1	0	—
E	285	—	—	3	2	0	—	—	—	0	0	1	—
	304	—	—	1	1	0	—	—	—	0	0	2	—
	307	—	—	—	—	0	—	—	—	—	—	1	—
F	305	—	—	—	—	—	1	—	—	—	—	—	1
	311	—	—	—	—	—	0	—	—	—	—	—	2
	312	—	—	—	—	—	1	—	—	—	—	—	1

TABLE 25

Family G.—Progeny of plant 44 of cross No. 3 × plant AA of N. Forgetiana grouped to show inter-class fertility.

	A	B	C	D	E	F	247	248	249	251	256	257	259	262	265	266	267	269	271	272	273	276	283	290	295	297	298	303	308	309	310
A		3					3		3		2	2		2						1											
B	3		5				2			2		1	1	1	1	2		3	1	1		1	1	1							
C		4		9	3										1	1		2		1	2	2		2			1				
D			9		3										1			1						1		1		1		1	1
E			4	3																								2		2	2
F																													2	2	2
247	3	2						1	1		1											1									
248							1																								
249	3						1				1																				
251		2															1														
256	2						1		1			1								1											
259		1									1																				
257	2	1												1																	
262	2	1											1			1			1												
265		1	1	1												1		1				1									
266		2	1											1	1																
267										1																					
269		3	2	1											1																
271		1												1																	
272	1	1	1								1																				
273			2																			1									
276		1	2				1								1						1										
283		1																													
290		1	2	1																											
295																															1
297				1																											
298			1																												
303				1	2																										
308						1																									1
309				1	2	2																									1
310				1	2	2																			1				1	1	

their behavior in inter-crosses. There are 6 classes as tabled with a frequency of 3, 5, 7, 5, 4, 3. There are 3 exceptions among the fertile matings, 275 × 278, 281 × 284 and 305 × 312. Only one pollination each was made on the first and third of these combinations, but the second was made reciprocally—*the last of the flowering season*—one pollination each way. *There were no sterile exceptions.*

Though 6 intra-sterile groups are tabled, there is definite proof of the existence of only 3 classes. This is easily seen by referring to the table. Classes C, D and E must be different, but the other 3 groups might have proved to fall in with them had the proper crosses been made. Nor can the existence of more than 4 intra-class sterile groups be proved even by the complete table of inter-class fertility shown as table 25. By our probability formula also the presumption is that there are but 4 or 5 classes, whether the distribution of individuals be according to the coefficients of the binomial expansion or into classes of equal size.

Family H.—Plant 44 of class C, cross No. 3 × plant 10 of class A, cross No. 2.

Family H was one of the 30 true F_2 populations possible from combinations of the 6 different F_1 classes. It was produced by crossing plant 44 of class C, cross No. 3 with pollen from plant 10 of class A, cross No. 2. 70 plants were grown in the greenhouse. Self-pollinations were made on 33 of these individuals with the results listed in table 26. In view of previous results it seemed hardly necessary to self every member of the population. If this had been done a truly self-fertile plant might have been discovered, of course, but it is exceedingly improbable. Of those selfed, 5 did produce some seed,—the amounts being shown in the table. These capsules were all produced at the very end of the flowering season, except 1 with 8 seeds in it on plant 316. There is a chance that these seeds were produced by foreign pollen, though it is hardly necessary to "explain" such a rare exception to the general rule.

This family was studied through a long flowering season. Many matings were made, and the work completed before we were certain of the effects of environment on self-sterility. For this reason some of the matings made toward the end of the season were not tested as thoroughly as should have been done. Further, no records of the number of seeds were taken in the case of several capsules that were not full. Thus it is altogether likely that several matings marked fertile were in reality sterile. The maximum number of such errors, we should judge from a careful examination of our records ought not to be over 10.

It is also probable that the usual experimental error of 4 failures per hundred in actually fertile matings obtains in cases where a mating was made but once and proved sterile. There were 63 such matings in the intra-family crosses, thereby making 3 such errors probable. The remaining combinations were judged by several matings and by reciprocal crosses, and are likely to be correct.

It is clear that the errors mentioned above are largely compensatory when figuring the percentages of fertility or sterility in the matings made, but they will stand revealed when endeavoring to group the individuals in intra-sterile classes.

The record of back-crosses and crosses made with plants outside of

TABLE 26

Family H.—Record of self-pollinations on progeny of plant 44 (F_2, cross No. 3, class C) × plant 10 (F_2, cross No. 2, class A).

Ped. No.	No. selfings sterile	No. of selfings giving capsules with			
		1-10 seeds	10-50 seeds	50-150 seeds	250-300 seeds
314	1				
315	4		2	2	
316	9	1	3		
317	4				
318	3				
321	1				
324	1				
330	1				
331	2				
332	6				
333	1				
334	1				
335	3				2
336	1				
340	1				
342	3				
347	1				
350	3		1		
351	1				
353	1				
354	10				
358	9		1		
362	4				
363	7				
368	4				
370	1				
371	3				
373	4				
374	2				
378	1				
381	2				
382	2				
385	1				

TABLE 27

Family H.—Record of cross-pollinations on progeny of plant 44 (F_1, cross No. 2, class C) × plant 10 (F_1, cross No. 2, class A) outside family H.

Ped. No. ♀	Fertile with parents ♂	Sterile with parents ♂	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
314	44, 10_2			
315	44_2			
317	44_2	10_4	311 fam. G	34_3 F_1
318		10		
319		10_2	311 fam. G	
320	10_2			
321		10_4	311 fam. G	
322		10_3		
324		10		
327	44_3	10_2		
328	44_2			
329	44_3			
330		10_4		
331	44_4	10		
334		10		
335	44_2, 10	10		
337		10	477 fam. J, 524 fam K	
339				18 F_1
340		10		
342	44_2, 10 poor	10_3		467 fam. I
349		10		
350	44	10_2		
351		10		
354	44_2	10_4	467 fam. I	34_4 F_1, 401 fam. I
362	10, 8 seeds	10_3		34_2 F_1
363	44	10_4		
365	44			
366		44		
367	10	10		
368	10_3		467 fam. I	
371	44		467 fam. I	
373	44_4, 10			
374	44_3			401 fam. I, 467_2 fam. I
378	44			
379	44_4	10_2		
381	44, 10		405 fam. I, 415 fam. I	
382	44_2, 10_2			
384	44			
385	44_2	10		

family H, are shown in table 27, but they can be discussed best after dealing with the intra-family matings.

Excluding selfings, 312 intra-family matings were made on 56 plants. If we take all of these plants to be self-sterile,—a reasonable assumption even though a few of them were not selfed—448 combinations out of a possible 3136 were attempted. The figure 448 is the sum 153 × 2 = 306 fertile matings, minus 100, the number of fertile reciprocals, plus 159 × 2 = 318 sterile matings, minus 132, the number of

TABLE 28

Family H.—Record of cross-pollinations on progeny of plant 44 (F_1, cross No. 2, class C) × plant 10 (F_1, cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
315		316, 317, 318_2
316	320, 324	317_2, 318, 321, 331
317	320	315_2, 318, 321, 327_2, 328_3
318	320_2, 328	315_3, 316, 317_5, 321_2, 324
319	347	315, 316, 317_5, 354_2, 381
320	317, 318, 321, 322, 324_2, 328_2, 354_2, 381	342, 351
321	320_2, 335_2, 381	315_2, 316_2, 322_2, 328_2
322	320_2, 325, 381_2	321, 324, 328, 329
324	320_3, 325, 342, 367_2, 379_2	322, 327, 328, 331, 354_2
325	317, 322_2, 324, 329	
327	351	330, 336_3, 337_2, 340_2, 345
328	335, 337	317, 324, 327, 329, 342
329	325, 347	324_3, 327, 328
330	335	327, 334, 374
331	335_3	316_3, 327, 328_2, 329, 330, 336
333	336_2	
334	335	331_2, 337, 374
335	321, 324, 327, 328, 329, 331	320, 336, 381_2
336	328, 351_2	327_2, 331, 337_2, 342, 345
337	339	327, 336, 340_3
338	327, 337, 341, 342	
339	318, 327, 336, 337_2, 340, 342_2	338
340		327, 337_2, 342_3, 345, 346
341	327_2, 331, 337_2, 340_4, 342_4	
342	347_2, 351, 373_2, 381	336, 340, 345, 354_2, 371, 374
345		327, 337_2, 342
347	337_3, 340, 342, 349_2, 354	
348	342, 347	351
349	351_2	342_2
350	381_2	334, 337, 340, 349, 354_2, 359, 363
351	349_2, 350, 353, 354_2, 362	320, 368, 381_2
352	327, 342, 349_3	348
353	351_2	354_2, 362_3
354	351_2, 371	317_6, 337, 350, 363_2, 374_3
355	342_2, 351, 354_2, 381	
358		354_4, 362
359	347, 351, 355_2, 366_2	342, 354_2, 362, 371_2
360		362, 363_3
362	368, 381_2	340, 354, 358, 363, 365
363	351, 366, 368_2	350_2, 354, 365
365	355, 368	354, 359, 362, 363, 374
366	351, 354_2, 360, 363, 365, 368_2	
367	354_2, 370_3, 371	378
368	354, 363, 371, 374	320_2, 367, 381_6
370	367_2, 368_3, 373, 378	371, 372, 374
371	366, 368, 381_2	365_2, 374_7
372	367_3, 368, 381	371_2, 374
373	354_2, 367, 370_2, 374_3, 385, 371_4	320_2, 368, 381
374	373, 378, 381	371_6
378	373, 381_7, 383	379_2
379	374_4, 381_2, 383	354_2, 373_3
381	317_3, 340, 341, 342_2, 354_4, 374_2, 378	351, 367, 368_2, 373
382	354_2, 374, 379	367, 368, 373_2, 381
383	378_4, 384	367
384	381	378_2
385	381_2	378

TABLE 29

Family H_1—Progeny of plant 44 (F_1, cross No. 2, class C) × plant 10 (F_1, cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group					No. cases sterile within group				
		A	B	C	D	Ind.	A	B	C	D	Ind.
A	315	0	—	—	—	—	5	—	—	—	—
	316	**1**	1	—	—	—	6	0	—	—	—
	317	0	2	—	—	1	8	0	—	—	0
	318	**1**	1	—	1	—	5	0	—	0	—
	319	0	0	—	—	1	4	**1**	—	—	0
	321	0	3	—	—	—	6	0	—	—	—
	322	0	2	—	—	1	4	0	—	—	0
	324	**2**	3	1	—	1	7	0	0	—	0
	327	0	3	—	2	1	10	0	—	0	0
	328	**3**	2	—	—	—	8	0	—	—	—
	329	0	1	—	—	2	5	0	—	—	0
	330	0	1	—	—	—	4	0	—	—	—
	331	0	1	—	—	1	8	0	—	—	0
	334	0	1	—	—	—	5	0	—	—	—
	336	**1**	1	—	1	1	5	**1**	—	0	0
	337	**1**	—	—	2	2	7	—	—	0	0
	340	0	1	—	1	2	7	0	—	0	0
	342	**1**	6	—	2	3	9	**1**	—	0	0
	345	0	—	—	—	—	5	—	—	—	—
	346	0	—	—	—	—	1	—	—	—	—
	349	0	2	—	—	1	2	0	—	—	0
	350	0	2	—	—	—	7	0	—	—	—
	353	0	1	—	—	—	2	0	—	—	—
	354	**1**	7	0	—	3	13	0	**1**	—	0
	358	0	—	—	—	—	2	—	—	—	—
	359	0	1	—	—	3	6	0	—	—	0
	360	0	—	—	—	1	2	—	—	—	0
	362	0	3	—	—	—	8	0	—	—	—
	363	0	2	—	—	1	5	0	—	—	0
	365	0	1	—	—	2	6	0	—	—	0
	370	0	3	1	—	—	3	0	0	—	—
	371	**1**	4	—	—	1	6	0	—	—	0
	372	0	3	—	—	—	3	0	—	—	—
	374	0	4	2	—	—	8	0	0	—	—
B	320	8	**1**	—	—	—	**1**	4	—	—	—
	335	8	0	—	—	—	**1**	2	—	—	—
	348	1	0	—	—	1	0	2	—	—	0
	351	9	0	—	—	2	0	4	—	—	0
	352	3	0	—	—	—	0	1	—	—	—
	367	5	**1**	0	—	—	0	4	**1**	—	—
	368	8	0	—	—	1	0	6	—	—	0
	373	5	**1**	2	—	—	0	4	**1**	—	—
	381	11	**1**	4	—	2	**1**	6	0	—	0
	382	2	0	1	—	—	0	4	0	—	—
	383	—	0	3	—	—	—	1	0	—	—
C	378	2	3	0	—	—	0	**1**	3	—	—
	379*	2	3	0	—	—	**1**	**1**	1	—	—
	384	—	2	0	—	—	—	0	1	—	—
	385	—	2	0	—	—	—	0	1	—	—
D	338	3	—	—	0	1	0	—	—	1	0
	339	6	—	—	0	—	0	—	—	1	—
Ind.	325	4	—	—	—	—	0	—	—	—	—
	333	1	—	—	—	—	0	—	—	—	—
	341	5	—	—	—	—	0	—	—	—	—
	347	8	1	—	—	—	0	0	—	—	—
	355	4	2	—	—	—	0	0	—	—	—
	366	6	2	—	—	—	0	0	—	—	—

* Probably not really a member of group C.

sterile reciprocal, plus the 56 self-combinations. The probable total sterility in the population is 54.0 percent ± 1.4 percent, therefore, which makes it unlikely that more than 3 or 4 intra-sterile classes are present. These matings are shown in table 28.

The individuals are grouped with reference to their behavior in intercrosses in table 29. This table appears to reveal 4 classes containing 34, 11, 4 and 2 plants, respectively, in addition to 6 indeterminate individuals. Let us see what it really shows.

In the first place, there are 8 exceptions—fertility where there should be sterility—in the fertility columns. They are as follows, each mating being made but *once*.

Class A 316 × 324
" " 318 × 328
" " 324 × 342
" " 328 × 337
" " 336 × 328
" " 354 × 371
Class B 320 × 381
" " 373 × 367

There are also 6 exceptions—sterility where there should be fertility—in the sterile columns, and here one mating (No. 4) was made twice and one mating (No. 6) three times. These exceptions are as follows:

1. B × A 319 × 381
2. B × A 320 × 342
3. B × A 335 × 336
4. C × A 379 × 354
5. B × C 367 × 378
6. C × B 379 × 373

These exceptions are no more than were to have been expected from the predictions made above from *a priori* calculations. Of the fertile exceptions, at least 5 were made at the last of the season. No data regarding percentage of seed obtained to seed expected in full capsules were recorded, unfortunately, but it is probable from our other experiences that the majority of them produced only partly filled capsules, and would have proved sterile had they been made earlier. The sterile exceptions 379 × 354 and 379 × 373, made twice and thrice respectively are of little consequence because 379 falls into class C only through the single sterile mating 378 × 379 (made twice). Thus we could just as reasonably call 379 an indeterminate,—that is a plant fertile in all combinations tried,—and have but the sterile exception 378 × 379 for which to account. It could not go into groups A or B, though sterile with one plant of each of those groups because it also was fertile with 2 members of group A and with 3 members of group B.

This interpretation may be made either way without affecting the chief point the table was designed to show. No indeterminate individual and neither plant of the very uncertain class D, which was based on the single case of sterility 339 × 338, were crossed with plants of class C. Therefore the 3 classes A, B and C are the only ones for which we can claim independence.

A meaning can now be given to the results of the back-crosses which were listed in table 27. 38 plants were crossed with pollen from one or both parents. Out of the 23 plants crossed with No. 44 just 1 was sterile,—a single pollination of 366 × 44. It is possible that this mating also might have shown fertility if tested further, but it may show that 366 is the only plant among those tested that belongs to the same intra-sterile class as 44.

Plant 10 was used as pollen parent with 29 plants, of which 10 produced some seed. Plant 342 produced a few seeds which seemed to be parthenocarpic out of 4 tests, and plant 362 yielded 8 seeds in 1 of the 4 tests made. Therefore we have no hesitancy in classifying them as sterile. Plant 314, which was fertile to plant 10 pollen, was discarded early and is not classified in table 29. For this reason it may be left out of consideration. Plants 335 and 367 were fertile in one pollination each, and sterile in one pollination each. Since they gave full capsules in each of the successful pollinations, however, let us record them as fertile. Now what is the result? *Out of 20 sterile matings 18 are with plants belonging to class A.* The first exception is with the plant 379 which behaved so irregularly—as shown by table 29—that it is just as likely to be a member of class A as class C. The second exception is a single pollination with plant 385 of class C. *Fertility is shown in 7 cases, all of which are with class B.* Furthermore, the 3 sterile matings made with pollen from plant 34, a member of the same F_1 class as plant 10, are with plants of class A of family H. And the 1 sterile mating made with plant 18, a plant of F_1 class B, is with plant 339, a member of class D of family H. Therefore, it seems unquestionable that Plant 44 (and thus class A of F_1) belongs to the class A of family H.

Family I. Record of cross pollinations on progeny of plant 44 (F_1, cross No. 3, class C) × plant 34 (F_1, cross No. 2, class A) outside family I.

Ped. No. ♀	Fertile with parents ♂	Sterile with parents ♂	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
387	44			
391	44	34_4		
392				372_6 fam. H
394	44_2			
395	44			
396	44			315 fam. H, 317 fam. H
398	44, 34_3			
400	44	34_4		
401	44	34_6		10_3 F_1, 354 fam. H, 374 fam. H
405	44_2		351 fam. H	354 fam. H, 374 fam. H
408	44		337 fam. H, 477 fam. J, 524 fam. K	
409	44	34_4		
412	44, 34_2 late	34_2		
413	44		374 fam. H	
415	44	34_4		354 fam. H, 374 fam. H
421			490 fam. J	
425	34			
426	44_2	34_2		
430	44	34_5		
431	44, 34_2			377 fam. H
432			377_3 fam. H	
433	44			
440	44_2		381 fam. H	
442	44			
444	44_2	34		
446	44			
448			474 fam. J, 475 fam. J	
451	44_2	34_2		
455	44_4	34_2		
456	44_2	34_6		
457	44			
458		34_2	320 fam. H, 381 fam H	
460				380 fam. H
463	44			
465	44			
467	44		278_4, fam. G, 320 fam. H, 381 fam. H, 489 fam. J	374_8 fam. H
468		34_2		
470		34_4		

TABLE 31

Family I.—Record of cross-pollinations on progeny of plant 44 (F_1, cross No. 3, class C) × plant 34 (F_1, cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
387	395, 396	
390		396_2
391		396_2
392		395, 444_3, 468_2
394	390, 396_2, 398, 400, 405	
395		400, 405_2
396	413	400_4, 401_4, 405_2, 415
398	396, 400	413
400	401	396_2
401		405_2, 415_2, 426, 467
405	398_2, 413_2	401_3, 408, 415, 467_2
408	413	405_2, 409, 415, 426
409		408_3
412	420	
413	396, 401, 405_5, 408, 415, 418, 420	
414	425_2	415_2
415	413, 425	401_2, 405_2, 412, 414, 420_2, 426, 458
418	431	412_2
420	431, 425	401_2, 405, 415_2, 425_2, 426_2, 458
421		467
425		431
426	425_3, 433	405, 420_3, 440_2, 445, 458, 464_2
430	426_2, 433_3	431, 458
431	401_2, 426_4, 433, 439, 455	430, 440
432	431_3	
433	405, 426, 431, 439, 440_3, 451, 458	
439	433	440, 444
440	433	415, 426_2, 439_2, 444_2, 451_2, 457
442	439, 446	444_2, 451
444	431, 456, 458_2	440_3, 451
445		
446	442	430_2, 431
448		421_2
451		442, 444_3, 455_2, 467
455		415, 426_2, 440, 451_4, 456_2
456	444	455_2, 457_5, 458_2, 467_2
457	463_2	455, 456_4, 458, 467
458	413	405, 420, 451, 455_4, 456_2, 467
460		392_4, 468_3
463	456_2, 457_2, 465	
464		
465	456, 463	457_2
467		455, 456_2
468		
470		465_4

Family I.—Plant 44 of class C, cross No. 3 × plant 34 of class A, cross No. 2

Family I was produced from seed obtained by pollinating plant 44 of class C, cross No. 3, with pollen of plant 34 of class A, cross No. 2. It is therefore a test of the similarity of constitution of plants of class A of F_1, since plant 44 was crossed first with plant 10 of class A to produce family H and then with plant 34 of class A to produce family I.

83 greenhouse plants were grown; but the task of manipulating that number proved too great and very nearly one-half of them were discarded after several weeks of work, permitting our efforts to be more concentrated. We have not thought it necessary to report any of the pollinations made on the rejects.

Of the plants remaining, 25 were selfed from 1 to 6 times between the first and the middle of the reproductive period without obtaining a single seed. Somewhat contrary to what might have been expected, 6 of these same plants were again selfed several times during the latter part of the season with the same result. This does not prove that no seed could have been obtained at that time if further pollinations had been made, however, as a few seeds were produced in a part of the pollinations of 22 cross-matings made during the waning of the flowering period, where continued pollinations made before had left no doubt as to the sterility of the combination. In 9 other matings, 1 pollination each produced no capsule, but in each case other matings—usually several—giving full capsules, proved them to be fertile. They were therefore so recorded.

Table 30 shows the record of back-crosses with pollen of the parents, and also the crosses made with plants outside of the family. It will be discussed after making the usual classification.

The inter-crosses in this family are shown in table 31. About one-sixth of the 2025 different combinations possible with 45 plants were accomplished. The table shows 61 fertile and 97 sterile matings, including 13 pairs of fertile reciprocals and 20 pairs of sterile reciprocals. The total number of different cross-combinations, therefore, is 250, made up of 96 fertile and 154 sterile combinations. Adding the 45 self-combinations, we have 199 steriles out of a total of 295 combinations. The probable sterility in the population is thus 67.5 percent ± 1.8 percent, and we should scarcely expect more than 3 or at most 4 intra-sterile classes even if a Mendelian dominant type $(3 + 1)$ of distribution in the classes be assumed.

The grouping actually obtained is set forth in table 32. Three classes containing 34, 4 and 2 individuals, respectively, and 5 unplaced plants, appear. There are 6 fertile exceptions:

400 × 401
412 × 420
442 × 439
444 × 456
444 × 458
465 × 456

TABLE 32

Family I.—Progeny of plant 44 (F_1, cross No. 3, class C) × plant 34 (F_1, cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group				No. cases sterile within group			
		A	B	C	Ind.	A	B	C	Ind.
A	390	0	—	—	1	1	—	—	0
	391	0	—	—	—	1	—	—	—
	392	0	—	—	—	4	—	—	—
	395	0	—	—	1	3	—	—	0
	396	0	—	2	2	6	—	0	0
	400	**1**	—	1	1	2	—	0	0
	401	**1**	1	1	—	6	0	0	—
	405	0	—	2	2	10	—	0	0
	408	0	—	1	—	4	—	0	—
	409	0	—	—	—	1	—	—	—
	412	**1**	—	—	—	2	—	—	—
	414	0	1	—	—	1	0	—	—
	415	0	1	1	—	10	0	0	—
	418	0	1	1	—	1	0	0	—
	420	**1**	1	—	—	5	0	—	—
	421	0	—	—	—	2	—	—	—
	426	0	3	—	1	10	0	—	0
	439	**1**	1	—	1	2	0	—	0
	440	0	0	—	1	7	**1**	—	0
	442	**1**	1	—	—	2	0	—	—
	444	**2**	2	—	—	5	0	—	—
	445	0	—	—	—	1	—	—	—
	448	0	—	—	—	1	—	—	—
	451	0	—	—	1	6	—	—	0
	455	0	1	—	—	7	0	—	—
	456	**2**	—	—	1	4	—	—	0
	457	0	—	—	1	6	—	—	0
	458	**1**	0	1	1	9	**1**	0	0
	460	0	—	—	—	2	—	—	—
	464	0	—	—	—	1	—	—	—
	465	**1**	—	—	1	2	—	—	0
	467	0	—	—	—	8	—	—	—
	468	0	—	—	—	2	—	—	—
	470	0	—	—	—	1	—	—	—
B	425	4	0	—	—	0	1	—	—
	430	1	0	—	1	**1**	2	—	0
	431	6	0	—	2	**1**	3	—	0
	446	2	0	—	—	0	2	—	—
C	398	3	—	0	1	0	—	1	0
	413	8	—	0	—	0	—	1	—
Ind.	387	2	—	—	—	0	—	—	—
	394	4	—	1	—	0	—	0	—
	432	—	1	—	—	—	0	—	—
	433	6	2	—	—	0	0	—	—
	463	3	—	—	—	0	—	—	—

TABLE 33

The behavior of individuals of the various groups of family I toward individuals of the various groups of family H.

Class of fam. I	Ped. No. of fam. I	Fertility with individuals of family H				Sterility with individuals of family H			
		Class A	Class B	Class C	Ind.	Class A	Class B	Class C	Ind.
A	392					372			
	396					315, 317			
	401					354 recip., 374 recip.			
	405		351, 381			354, 374			
	408	337							
	415		381			354, 374			
	440		381						
	458		320, 381						
	460					342			380
	467	337, 371	320, 368, 381			374 reciprocal			
B	431								377
C	413	374							
Ind.	432				377				

Four of these matings were made but once, 1 was made twice and 1 was made reciprocally. The last 2 and 1 other were end-season matings, the others were mid-season matings. There are 2 sterile exceptions, 431 × 440 and 430 × 458, each tried but once. The number of combinations that form the basis of our grouping is so large, that there is little danger in accepting the classification as given, however, since these errors might have crept in in various other ways, as has been shown before. But it should be mentioned that plant 430 falls just as readily into group A as it does into group B.

The evidence in this table does not support the idea of more than 3 classes. A and B are well established. But C may be B, since neither members of the class were crossed with any B individuals. Of the indeterminates, 387, 394 and 463 may be B and 432 may be A. The sole positive evidence of a third class, therefore, rests upon plant 433, which is not A (6 matings in evidence) nor B (2 matings in evidence).

Let us now consider the back-crosses shown in table 30. Every cross made with the pollen of plant 44, 29 in number, was fertile. On the other hand 15 back-crosses with pollen from plant 34 were sterile, though an average of over 3 pollinations per plant was made. Seed was obtained in only 1 instance: 4 pollinations were made on plant 412, and 2 made late in the season gave some seeds. The interesting feature in these 15 sterile matings is that 14 of them were made on plants of class A, and the fifteenth on plant 430, which, though tabled in class B may just as readily be placed in class A.

But 3 plants were fertile to pollen of plant 34,—plants 425 and 431 of class B and plant 398 of class C.

A single mating of plant 10 on plant 401 of class A was sterile. Since plant 10 and plant 34 belong to the same class of the F_1 generation, this mating may be compared with the 3 sterile matings of class A plants of family H with pollen from plant 34.

Note then the similarity between families H and I. Each has 3 independent inter-fertile, intra-sterile groups with almost the same distribution of individuals within the classes; each behaves similarly in back-crosses. With the exception of a single unclassified plant of family H, all of the plants tested of both families were fertile with plant 44 of class C of the F_1 generation, the female parent of both. With regard to plants 10 and 34, the male parents of families H and I respectively, both of which belonged to class A of the F_1 generation, each was sterile with class A plants of both families and each fertile with other plants of their respective families. The conclusion is unavoidable, therefore, that class

A of the F_1 generation, class A of family H, and class A of family I, are identical.

This is not the only evidence that can be brought forward in favor of the similarity of these two families. A sufficient number of crosses (table 33) was made between the two populations to prove that class A of family H and class A of family I are the same. Ten members of class A of family I were crossed with plants from family H. Three pairs of reciprocals were made with like results for each pair. Counting these pairs as but 1 mating each, members of class A of family I were crossed 14 different ways with members of class A of family H. Of these matings 11 were sterile, and 3 fertile. But of the fertile matings, 2 were with 337 and did not give full capsules. These same class A plants of family I were also mated 9 times with members of class B of family H, and all matings were fertile. Bearing these results in mind, the single sterile mating of 460,—family I, class A,—with 380,—unplaced member of family H,—is pretty good evidence for placing 380 in class A of family H. Likewise, the sterility between 431 and 377 is evidence that 377 of family H is not a member of that family's class A, a conclusion supported by its fertility with unplaced 432 of family I. The remaining cross, plant 413 of class C of family I with plant 374 of class A of family H, was fertile.

We do not believe it rash to assert that this makes a complete case. There can be no doubt that families H and I are practically duplicates of each other. *In this instance, then, two plants belonging to a single class in which all of the individuals were cross-sterile with each other, when crossed with the same individual have produced populations as similar to each other in their behavior in crossing as if they were samples of the same population.*

This does not prove that all members of an intra-sterile class crossed with the same individual would produce identical populations. No such claim is made. It does indicate very strongly, however, that in this particular case, these 2 plants of the F_1 class A (10 and 34) are identical in that part of their constitution which affects self- and cross-sterility. The criticism may be offered that these results show merely a kind of dominance exhibited by plant 44, but if this be true, it is a dominance of a strikingly perfect kind.

Family J.—Plant 52 of class B, cross No. 3 × plant 23 of class A, cross No. 2

As has just been shown, F_1 plants of class C when crossed with their

TABLE 34

Family J.—Record of cross-pollinations on progeny of plant 52 (F_1, cross No. 3, class B) × plant 23 (F_1, cross No. 2, class A) outside family J.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
475	524 fam. K	
477	377 fam. H, 467 fam. I	
487	512 fam. K	
489	467_2 fam. I	
490	421 fam. I	
495	18 F_1	
499	18_2 F_1	
502	18 F_1, 512 fam. K	

sisters of class A give populations having a high percentage of cross-sterility and by the same token a small number—2 or 3—of intra-sterile groups. Family J tests the behavior of an F_1 plant of class B with a class A sister.

30 plants of this family were grown in the greenhouse, 6 dying or being discarded. They were all selfed from 1 to 12 times with no production of seed except on plants 473 and 489. These 2 individuals produced seed the latter part of the flowering season. No. 473 was selfed 7 times at various periods. The first 2 pollinations yielded no seed, the third and fourth a few seeds, and the last 3 half-filled capsules. No. 489 was selfed 9 times. The first 3 were failures; the remainder induced capsules, the last 3 pollinations producing a full quota of seed.

Only 1 back-cross was made. No. 474 was fertile with No. 52.

The few other crosses made with plants outside the family are recorded in table 34. All were successful. It should be noted that 3 of these successes were with plant 18, another member of class B of the F_1 generation.

As usual only a comparatively few of the 576 combinations possible between 24 plants were made. The record of cross-pollinations listed in table 35 are sufficient, however, to show the striking difference in percentage of cross-sterility between this family and the 2 families just described. There are 65 fertile matings including 14 pairs of fertile reciprocals, making 102 fertile combinations in all. Since there are no sterile reciprocals, the 13 sterile matings are equivalent to 26 sterile combinations. Adding the 24 self-combinations, gives a ratio of sterility to total combinations of 50 : 152. The probable sterility in this family is therefore 32.9 percent ± 2.6 percent, which leads us to expect about 5 intra-sterile groups.

The grouping made possible by the sterile matings is shown in table 36. There are no exceptions. Each individual in every group shows perfect inter-class fertility and intra-class sterility as far as they were tested. Apparently there are 4 classes containing 7, 4, 2 and 2 individuals, respectively, together with 9 plants which showed no cross-sterility and are unplaced.

TABLE 35

Family J.—Record of cross-pollinations on progeny of plant 52 (F_1, cross No. 3, class B) × plant 23 (F_1, cross No. 2, class A).

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
473	474, 475_6, 485_3	480
474	475_3, 480_2, 482, 485	
475	474, 477, 480, 482, 485_4	
477	473, 475_3, 482, 485_6	
478	484, 485	
480	474, 475_3, 482, 486, 487_2, 491	
482	474, 484, 485_2	
484	474, 480, 482, 487_2	485_3
485	474, 475, 482_5, 492	484
486	485, 492_3	474, 495
487	474, 482, 484, 486, 492, 499	
488	482, 487,	484
489	477, 492	486
490	489	
491	480	484
492	484, 487_2, 493, 495_2	
493		502
494		486, 502
495	499	
496		492
499	502_4, 503	
500	486, 493, 499, 502, 503	
502	499	495
503	499_2, 500, 502_2	

Table 37 shows the evidence for independence between these groups more clearly. A, B and C or D must be independent, but C and D may belong to one class since they were not crossed together. In addition 475, 477 and 482 are independent of each other and of A, B and C. Thus there are apparently 6 independent classes with frequencies of 7, 4, 2, 1, 1 and 1, these frequencies being subject to change of course given the data necessary to fit the remaining individuals into their proper niches. Before accepting this classification at its face value, however, we ought

TABLE 36

Family J.—Progeny of plant 52 (F_1, cross No. 3, class B) × plant 23 (F_1, cross No. 2, class A) grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group					No. cases sterile within group				
		A	B	C	D	Ind.	A	B	C	D	Ind.
A	474	0	2	2	—	3	1	0	0	—	0
	486	0	1	1	1	2	4	0	0	0	0
	489	0	—	—	1	2	1	—	—	0	0
	493	0	—	—	1	1	1	—	—	0	0
	494	0	—	—	—	—	2	—	—	—	—
	495	0	—	—	1	1	2	—	—	0	0
	502	0	—	—	—	3	3	—	—	—	0
B	484	1	0	1	1	3	0	3	0	0	0
	485	1	0	1	1	4	0	1	0	0	0
	488	—	0	—	—	2	—	1	—	—	0
	491	—	0	1	—	—	—	1	0	—	—
C	473	1	1	0	—	2	0	0	1	—	0
	480	2	2	0	—	3	0	0	1	—	0
D	492	4	2	—	0	1	0	0	—	1	0
	496	—	—	—	0	—	—	—	—	1	—
Ind.	475	1	1	2	—	2	0	0	0	—	0
	477	1	1	1	—	2	0	0	0	—	0
	478	—	2	—	—	—	—	0	—	—	—
	482	1	3	1	—	3	0	0	0	—	0
	487	2	2	1	1	2	0	0	0	0	0
	490	1	—	—	—	—	0	—	—	—	—
	499	2	—	—	—	3	0	—	—	—	0
	500	3	—	—	—	2	0	—	—	—	0
	503	1	—	—	—	2	0	—	—	—	0

TABLE 37

Family J.—Progeny of plant 52 (F_1, cross No. 3, class B) × plant 23 (F_1, cross No. 2, class A) grouped to show inter-class fertility.

	A	B	C	D	475	477	478	482	487	490	499	500	503
A		3	3	4	1	1		1	2	1	2	3	1
B	2		3	2	1	1	2	3	2				
C	3	3			2	1		1	1				
D	4	2							1				
475	1	1	2			1		1					
477	1	1	1		1			1					
478		2											
482	1	3	1		1	1			1				
487	2	2	1	1				1			1		
490	1												
499	2								1			1	1
500	3										1		1
503	1										1	1	

to see whether the independence of any of the 3 single plants is based upon a single pollination. Plants 475 and 477 were fertile reciprocally, 4 pollinations being made in all, but plants 475 and 482, and plants 477 and 482 were crossed but once. This is also true of the basis of independence between 477 and A, 477 and C, and 482 and C. It depends on 1 pollination in each case.

For these reasons it is hardly likely that more than 6 independent classes exist in this population, and the chances are perhaps even that there are only 5. Nevertheless, family J unquestionably contains 2 or 3 more intra-sterile classes than family H or family I.

TABLE 38

Family K.—Record of cross-pollinations on progeny of plant 52 (F_1, cross No. 3, class B) × plant 44 (F_1, cross No. 3, class C).

Ped. No. ♀	Fertile with parents ♂	Fertile with Ped. No. outside family ♂	Fertile with Ped. No. within family ♂	Sterile with parents ♂	Sterile with Ped. No. outside family ♂	Sterile with Ped. No. within family ♂
505						508
507			515			
508						505
509						
511	44, 52_2		508, 509			512_3
512	52			44		520
515			524	44		
517				44		524
520	52			44_3		512_2
521	44, 52		512			
524	44, 52	58 *N. alata*				
525			520_2			
527			505_2, 509			
528	52_3		58_2 *N. alata*			

Family K.—Plant 52 of class B, cross No. 3 × plant 44 of class C, cross No. 3

Very little was done upon family K, as table 38 shows, though this family resulting from crossing a plant of class B (52) with our much used plant 44 of class C, might have proved very interesting. The plants would possibly all have shown fertility in back-crosses with 52, while only a part would have proved fertile with the other parent. This is the indication of the few matings made. There were 6 cases of fertility and none of sterility with No. 52, and 3 cases of fertility and 4 of sterility with 44.

2 plants were crossed with *N. alata* plant No. 58; both were successful. These were the only crosses made outside of the family with K plants

used as females. But K pollen was fertile on several plants of other families; viz., 524 on 337 of family H, on 408 of family I, and on 475 of family J; 512 on 487 and 502 of family J.

The 14 matings made within the family, including as they do 2 pairs of sterile reciprocals, are hardly a sufficient basis for even a guess as to the amount of cross-sterility present potentially. We can only say that the number of intra-sterile classes would not have been large, the percentage of sterility probably lying between 35 and 50.

Argument on cross No. 2 and cross No. 3

If further evidence of the beautiful regularity with which plants belonging to the same intra-sterile class behave in crosses be desired, it is found in the crosses between families cited in tables 13, 18, 22, 27, 30, 33 and 34.

Plants 152 and 153 of class A, family D, were both sterile with family E pollen which is presumably of one kind. The mating 152 D × 204 E was even made reciprocally. Plants 167 and 171 of family D, which were discarded after a few matings had been made and were therefore undetermined as to class, were fertile to pollen of family E.

In family F, plants 216, 239 and 243, all of class B were each sterile with the pollen from the unplaced plant 247 of family G. Plant 244, an unplaced plant of family F was fertile with the pollen of 247, however. On the other hand, plants 216 and 241 of family F, class B were fertile with the pollen of plants 278 of class C, family G and 250 of class A, family G, respectively. Plant 278 of class C, family G, was also fertile with the pollen of plant 219 of class A, family F, although plant 219 was sterile with the pollen of plant 250 of class A, family G.

If we may say that sterility shows likeness of constitution and fertility unlikeness of constitution, these results show: (1) that class A of family F and class A of family G are alike; (2) that class A of family F and class C of family G are unlike; (3) that class B of family F and classes A and C of family G are unlike, as they should be since classes A of both families are alike; and (4) that the unplaced plant 247 of family G belongs in with class B of family F, as might very well be the case.

In the remaining matings between plants belonging to different families there was no sterility, except among those matings between families H and I already discussed. They are none the less interesting, however, because they show that once fertility has been found between classes belonging to different families, all matings between plants belonging to these classes will prove fertile barring experimental error.

In family G, unplaced plant 249 was fertile with plant 351 of class B, family H and with plant 467 of class A, family I. Plant 278 of class C was fertile with pollen from plant 374 of class A, family H. Plants 278 and 281, both members of class A, were also fertile with plants 467 and 405 of class A, family I, respectively. Thus 2 combinations between the classes A of families H and I proved to be fertile.

Likewise, 3 plants of class A, family H, 317, 319 and 321, proved to be fertile with the pollen of plant 311 of class F, family G. Another plant of class A, 337, also proved to be fertile with the unplaced plants 477 of family J and 524 of family K.

Fertile matings were made as follows between 4 plants of class A, family I, and plants of families G and J; 408 with 477, of family J unplaced; 421 with 490, of family J unplaced; 448 with 474 of family J, class A, and with 475 of family J unplaced; 467 with 278 of family G, class C, and with 489 family J, class A.

Fertile matings were also made with the pollen of 3 family I, class A plants on plants of family J. Pollen of 467 was fertile on 477 unplaced and on 489, class A of family J, and pollen of 421 was fertile on 490 unplaced of family J.

Thus plants of class A of family I were fertile once with a plant of class C, family G, 4 times including a reciprocal with unplaced plants of family J, and 3 times including a reciprocal with plants of class A, family J.

In these matings between families, then, not a single one militates against our conception of inter-fertile, intra-sterile groups. We believe, therefore, that the fundamental basis of this grouping is established beyond doubt, and that the actual groups as submitted in the foregoing pages are sufficiently exact to be made the foundation of a theoretical interpretation of the behavior of self-sterile plants among themselves.

Undoubtedly there will come the critic who will say we have been at some pains to make out a case for the presence of inter-fertile, intra-sterile classes in this family. He will point out that some of the exceptions among the matings may not have been due to experimental errors and hence must have subtle meanings other than those given, that our phrase "pseudo-fertility due to environment" veils the real facts. Let us forestall him.

Of course *some* of the matings which form exceptions to the rule of inter-fertile, intra-sterile classes may be the effect of an unknown biological cause; certainly factors other than environmental may be the basis of a portion of the change from sterility to partial fertility in certain matings as the flowering season wanes.

The first thing to establish, however, was a broad general rule for the behavior of self-sterile populations. This has been done by the work on these 2 crosses. *The members of any population of the self-sterile species under consideration fall naturally into a relatively small number of groups, each individual being cross-sterile reciprocally with every member of the same group and cross-fertile reciprocally with every other individual.* The sum total of the exceptions to this rule is well within the limits of experimental error, even though the question is one in which every bit of evidence, like pieces of a jig-saw puzzle, must fit, if a solution is to be obtained. The exceptions to the rule, in fact are of another order of magnitude than the confirmations. If, therefore, true exceptions do occur, they are so rare that the usefulness of the rule is not in the least impaired. Other general matters must be settled before it is even desirable to endeavor to inquire into them.

Lest there be some difficulty in carrying in mind the essential facts regarding the grouping of the plants of this series, let us summarize them here.

The two self-sterile species *N. Forgetiana* and *N. alata* were crossed reciprocally. The progeny of these two crosses behaved so similarly that collectively the 53 individuals studied could be placed in 6 intra-sterile classes 5 of which were proved to be independent. The remaining questionable group consisted of one plant.

From this population 8 families were raised which were characterized as follows:

D = *N. alata* plant 53 × plant 44, class C; probably consisted of 4-6 classes, 3 being established.

E = *N. alata* plant 58 × plant 44, class C; probably consisted of 1 class.

F = plant 34, class A × plant AA, *N. Forgetiana;* probably consisted of 5-6 classes, 4 being established.

G = plant 44, class C × plant AA, *N. Forgetiana;* probably consisted of 4-6 classes, 3 being established.

H = plant 44, class C × plant 10, class A; probably consisted of 3 classes, 3 being established.

I = plant 44, class C × plant 34, class A; probably consisted of 3 classes, 3 being established.

J = plant 52, class B × plant 23, class A; probably consisted of 5-6 classes, 5-6 being established.

K = plant 52, class B × plant 44, class A; probably consisted of 4-6 classes.

It was also determined that class A of the F_1 generation, class A of family H, and class A of family I are identical.

Cross No. 4. N. commutata × N. Forgetiana (self-sterile × self-sterile)

The race used here with the pollen of *N. Forgetiana* was received from Italy under the name *N. commutata* Fisch. and Meyer. It is the plant called *N. Langsdorffii* Weinm. variety *grandiflora* by COMES (1899). Of it he says: "Elle est connue depuis 1835 dans les jardins européens, mais on en ignorait la patrie." It has been duplicated in our experiments by crosses between *N. alata* and *N. Langsdorffii.* It is an additional argument in favor of such an origin, that it is self-sterile, since *N. Langsdorffii* is always self-fertile. When crossed with *N. Langsdorffii* the F_1 plants are self-fertile. The behavior of this race when crossed with *N. Forgetiana* is interesting, therefore, whether it be a true wild species or was produced by hybridization. In the first case, a new species cross is reported, in the second case, a self-sterile race extracted from a cross between a truly self-fertile species and a self-sterile species, is crossed again with a different self-sterile species.

The F_1 plants were highly fertile, in the sense that 90-100 percent of the pollen was normal in nearly every plant, and that "proper" combinations yielded full capsules.

A rather small number, 12, field-grown F_1 plants were used in our experiments. These were selfed from 3-10 times, an average of over 4 pollinations per plant. 11 were completely self-sterile, yielding not a single seed. Plant No. 3, however, produced 4 good capsules out of 4 pollinations. This plant behaved like a real self-fertile. Crossed as a female with each of the other 11 individuals it was fertile; crossed as a male with all but plants 5 and 11, it was also fertile. Further, it was fertile as a female with *N. Forgetiana.* The meaning of this behavior has not been determined conclusively. Two interpretations are possible. Owing either to its hybrid origin (self-fertile × self-sterile) or to a recent introduction of *N. Langsdorffii* "blood," the race is a mixture of self-fertile and self-sterile plants; or, by reason of its having been grown near *N. Langsdorffii* the preceding generation, the seed from which this plant came was produced by a stray pollen grain of that species. The second interpretation seems more probable, since we have corroborated

TABLE 39

Result of matings on F_1 plants of cross No. 4, N. commutata × N. Forgetiana.

Ped. No. ♀	Fertile with Ped. No. ♂	Sterile with Ped. No. ♂
1	3_3	2_9, 4_5,
2	3_2	1_3, 4_4
3	1_3, 2_5, 4_3, 5_5, 6_3, 7_3, 8_5, 9_4, 10_4, 11_2, 12_3	
4	3_2, 5_2, 6_3	
5	8_2, 10_4	6_4, 7_5
6	1_4, 3, 4_4, 8_4, 10_4, 12_4	5_5, 7_4, 9_4, 11_5
7	3_4, 4_5, 12_4	5_2, 11_3
8	1_4, 2_4, 3_5, 4_3	9_4, 10_2
9	1_4, 2_2, 3, 4_4, 12_4	7_2, 8_3
10	1_3, 2_4, 3_3, 4_3, 12_4	7_2
11	1_4, 2_4, 8_5, 10_6	5_5, 9_5
12	3_3, 7_3, 11_3	1_3, 2_2, 4_3

TABLE 40

Plants of F_1 generation, cross No. 4, grouped in accordance with their behavior in inter-crosses.

Group	Ped. No.	No. cases fertile within group			No. cases sterile within group		
		A	B	C	A	B	C
A	1	0	3	2	3	0	0
	2	0	2	2	3	0	0
	4	0	4	2	3	0	0
	12	0	4	1	3	0	0
B	5	1	0	2	0	3	0
	6	3	0	2	0	4	0
	7	2	0	0	0	4	1
	9	4	0	0	0	3	1
	11	3	0	2	0	4	0
C	8	3	3	0	0	1	1
	10	4	3	0	0	1	1

COMPTON's conclusion that true self-fertility is completely dominant over self-sterility.[16]

In this family 70 cross-matings were made, of which 48 were fertile and 22 sterile. These matings were each made more than once, as is shown by the subscripts in table 39. There were 22 pairs of fertile reciprocals and 4 pairs of sterile reciprocals. By multiplying the sterile and the fertile matings each by 2 and subtracting in each case the proper

---

[16] The relation between self-fertile and self-sterile plants is to be made the subject of a later paper.

TABLE 41

Intercrosses between progeny of pseudo self-fertile N. alata plant used in cross No. 2. Compare with table 1.

Ped. No.	Plants with which fertile		Plants with which sterile	
	as ♂	as ♀	as ♂	as ♀
53	57	58	54_2	54_2, 56, 59_4
54			53_2 57_2, 58_2	53_2, 59
56			53, 57, 58, 59	59_3
57		53	58	54_2, 56, 59_3
58	53, 59			54_2, 56, 57, 62, 64, 66, 71, 79
59		58	53_4, 54, 56_3, 57_3	56
62			58, 79	66
64			58	
65			79	
66			58, 62, 71, 79	76, 78, 79
71			58	66
76			66	
78			66	
79			58, 66	62, 65, 66

number to allow for the reciprocals, we find that there were 52 fertile combinations and 36 sterile combinations.

If the self-fertile plant is omitted, there are 66 cross-combinations, each well established by more than 1 pollination through which one may group the remaining 11 individuals in intra-sterile classes. This grouping is shown in table 40. The 11 plants fall into 3 classes consisting of 5, 4 and 2 individuals. There is not a single case of intra-class fertility and but 2 instances of inter-class sterility. Matings 10 × 7 and 9 × 8 show sterility where fertility is to be expected.

Argument on cross No. 4

Outside of the fact that a plant which seems to be a true self-fertile appeared in this family and was tested with 11 self-sterile plants, no new phenomena are found in cross No. 4. The same cross-sterility, the same small number of inter-fertile, intra-sterile classes is found here that is found in crosses No. 2 and No. 3. Cross No. 4 merely furnishes corroboratory evidence of facts discussed earlier in the paper. It does show, however, that the facts discovered in crosses 1, 2 and 3, are not peculiar to a single hybrid.

INTRA-SPECIFIC PEDIGREE CULTURE EXPERIMENTS

Our experiments within each of these species can be described very briefly for they have been confined largely to self-sterility tests. Not a single thorough inquiry into the cross-mating proclivities of the plants of a pure (?) species has been made. This may seem very odd when so much time has been spent on inter-specific crosses. But our resolution to favor the wider crosses is not without reason. We have satisfied ourselves that the crosses within a species behave in a manner similar to that of the crosses already described. It seems probable, therefore, that intra-specific crosses would provide no data that could not be obtained from inter-specific crosses, although the converse might not be true.

N. Forgetiana. Between 200 and 300 plants of *N. Forgetiana* have been selfed under various environmental conditions, with pseudo-fertility in only 3 instances, as has already been described. *N. Forgetiana* is therefore a species on which environmental variations have little effect. It is a species in which, if one could measure accurately the intensity of the particular environmental factors that affect the full production of self-sterility, either the norm for a standard average environment would stand markedly toward the *sterile* end of the scale, or the dispersion coefficient would be small. The environmental complex that tends towards the *greatest* amount of pseudo self-fertility is necessary for any visible effect on the plants.

A small number of intra-sterile classes has been shown to exist in *N. Forgetiana*. Judging from cross-sterility percentages, the probable maximum is between 5 and 8 groups, but no accurate classification has been made.

N. angustifolia. Between 80 and 100 plants of *N. angustifolia* have been tested for self-sterility without the production of a single seed. This work was done during three summer seasons on field-grown plants. A certain environmental variation obtained of course, but since no pollinations were made at the extreme end of a flowering season, one cannot maintain that no pseudo-fertility exists. We are only justified in stating that *N. angustifolia* is similar to *N. Forgetiana* in being difficult to influence by environmental changes.

Intra-sterile groups have also been demonstrated in this species. Their number has not been determined but is probably no greater than in *N. Forgetiana.*

N. alata. We have shown earlier that *N. alata* is a self-sterile species in which a considerable amount of pseudo self-fertility appears at the end of the flowering season under adverse conditions. In other words if the environmental factors affecting self-sterility could be measured as suggested in the case of *N. Forgetiana,* either the norm for a standard average environment would be further toward the *fertile* end of the scale than in the latter species, or the dispersion coefficient would be larger.

As in the other two species, intra-sterile classes have been proved to exist, the maximum number probably being smaller than in *N. Forgetiana* or *N. angustifolia*.

The most important new fact discovered in *N. alata* is the probability that a population may exist consisting of only one intra-sterile class (compare family E). Recall that self-sterility is a sporophytic character, that inbreeding decreases the number of intra-sterile classes, and that there is no physiological or morphological obstacle to the fusion of any two complemental gametes provided they meet. All of these facts favor the idea that the behavior of self-sterile plants among themselves,—given the presence of the character self-sterility through the presence of a homozygous factor *X*,—is due to underlying causes which may be pictured as follows. A certain number of factors which affect self-sterility exist. The action of these factors is not cumulative. Mating is possible normally only to plants which differ in at least one of these factors.

If these premises be correct, after a very few generations of self-sterile plants raised from selfed seed by taking advantage of the phenomenon of pseudo self-fertility, one should find a population resulting from a single capsule which is homozygous for these effective factors and which is therefore wholly cross-sterile under normal conditions.

These conditions are very nearly met by the behavior of the grand-progeny of the original pseudo self-fertile *N. alata* plant that is recorded in table 1. Table 41 is made up from table 1 by tabling the cross-matings both ways when only made one way because of our belief that reciprocal crosses are always identical. By this table it appears that the 3 matings 53 × 57, 58 × 53, and 58 × 59 are fertile. Tabled both ways there are 6 fertile combinations. But let it be recalled that these matings were made during a long flowering season, and that during its wane several of the self-pollinations produced seed. What is more likely than that some sterile cross-matings should show pseudo-fertility at the same time? Our evidence is this. Of these matings 1 was made the middle of the season and did not give a full capsule, the other two were made at the end of the season. But this is not all. Our demonstration that every member of an intra-sterile class should be sterile with every other member is the result of an experience with nearly 10,000 cross-pollinations. The exceptions which have been met are very infrequent and are well within the expected experimental error. Now if table 41 be examined carefully, it is seen that there is every indication that all of the 14 plants listed belong to *one class* and that the 3 apparently fertile matings are due to pseudo cross-fertility.

N. glutinosa. Not over a dozen plants of *N. glutinosa* have been tested for self-sterility. It appears to behave like *N. alata.* Cross-fertility has been demonstrated, but the number of cross-matings made is not sufficient to prove the existence of intra-sterile groups. The above statement also holds for the race described as *N. commutata.*

SUMMARY AND INTERPRETATION OF THE RESULTS

The experiments on the self-sterile species *Nicotiana Forgetiana, N. alata, N. glutinosa* and *N. angustifolia* described in the foregoing pages, concern only the behavior of self-sterile plants when bred *inter se.* All questions connected with the relation between true self-fertility and self-sterility have been omitted designedly as pertaining to a distinct problem. The inquiry thus limited is believed to have established the following points:

1. Self-sterility is inherited.

2. The four species *N. Forgetiana, N. alata, N. glutinosa* and *N. angustifolia* breed true to the tendency toward self-sterility.

3. Self-sterility is fully expressed in these species from the beginning to the middle of the flowering season. Toward the close of the flowering season, especially in plants exhibiting the effect of adverse environmental conditions, some self-fertility may be shown. That this phenomenon is simply a non-inherited fluctuation is confirmed in four ways: (a) the graduated character of the increased fertility as the flowering season wanes, (b) the return to complete self-sterility at the beginning of a second flowering season, (c) the sterility of all progeny raised from selfed seed, and (d) the failure to obtain an increased tendency toward self fertility after three successive generations had been raised from selfed seed of the most extreme variants. It has been called pseudo self-fertility.

This fact naturally shows that self-sterility, whatever its nature, is only a physiological impediment to self-fertilization.

4. Other environmental factors appear to have little or no influence on self-fertility.

5. The waning of the reproductive period affects *N. alata* and *N. glutinosa* more markedly than it does *N. Forgetiana* or *N. angustifolia.* This indicates multiple allelomorphism in a fundamental factor the presence of which is necessary for the development of self-sterility.

(N.B. This factor should not be confused with any of those assumed in the interpretation of the behavior of self-sterile plants among themselves).

6. Cross-sterility in its nature identical with self-sterility was found in every population of self-sterile plants tested. The percentage of cross-sterility in different populations, based in each case on numerous cross-matings, varied from 2.4 percent to 100 percent.

7. Omitting fluctuations toward self-fertility correlated with a waning flowering period and a few cases of true sterility as indicated by microscopical examinations of the pollen, no variability in fruitfulness was noticed in "fertile" combinations. Fertile matings always resulted in full capsules.

8. Self-sterility behaves as a sporophytic character. This is demonstrated by the behavior of reciprocal matings,—pairs of reciprocals always giving like results either when fertile or sterile. It follows from this fact that no selective fertilization occurs.

9. The F_2 generation of a cross between *N. Forgetiana* and *N. alata* showed a low percentage of cross-sterility, 2.4 percent. This cross was followed to the F_5 generation by means of successive sib matings. The F_5 generation showed 21.6 percent cross-sterility.

In a repetition of this cross made with different plants, several F_2 populations studied each showed much higher percentages of cross-sterility.

10. All of the individuals of a family arising from one mating may be fertile with both parents, but a part of the individuals may be sterile with one or with both parents.

11. Cross-sterility exhibits a regularity of behavior such that if A is sterile with B and with C, it may be predicted that B will be sterile with C. On the basis of this cross-sterility the plants in each family may be divided into a relatively small number of groups in which each member of a class is sterile with every other member of that class and fertile with every member of every other class.

12. The distribution of the individuals within each class in several of the families studied was such that the classes may not be assumed to be of the same size. In certain cases this distribution rather resembled that of the coefficients of a point binomial.

13 Assuming a point binomial distribution of individuals within the classes as a limiting type, the number of intra-sterile classes necessary to account for the highest percentage of cross-fertility found is estimated to be less than 25. In most of the families tested the number of intra-

sterile classes varied from 1 to 6. In a cross between *N. alata* and *N. Forgetiana* in which 53 F_1 plants were tested rather thoroughly, 5 (or 6) such classes were found.

14. In those instances where a part of the individuals of a family were sterile to one or to both parents, only the members of a single class behaved in that manner.

15. Individuals belonging to different families as well as to different generations may belong to a single intra-sterile class.

16. Individuals belonging to different intra-sterile classes of the F_1 generation when mated with the same individual, produced populations varying in the number of intra-sterile classes.

17. Individuals belonging to a single intra-sterile F_1 class when mated with the same individual, sometimes produced populations having the same number of intra-sterile classes, a similar distribution of individuals within the classes, and possibly the same classes (see families H and I). It is not established that this behavior is universal, however. In the one case where the status of both the parents and the progeny as regards cross-sterility was established very definitely (families H and I), the two populations behaved in this manner; but in a case where the status of neither the parents nor their progenies (families D and E) was quite so clear, the two populations appeared to behave differently.

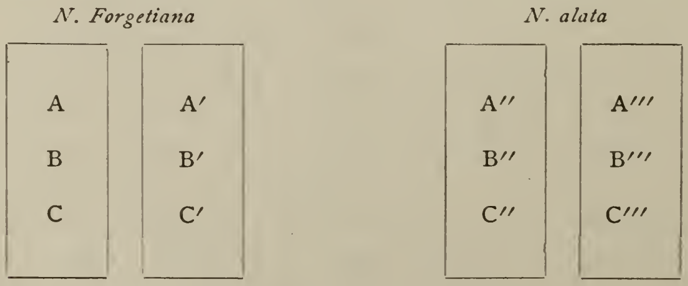
This rather varied series of facts can be given a very simple interpretation in keeping with recent interpretations of other inheritance phenomena provided judgment be suspended on one or two obscure points.

Let us assume first that a self-sterile species is self-sterile because it is homozygous for a fundamental self-sterility factor. Second, let us assume that a series of partially coupled factors affect the behavior of self-sterile plants among themselves. The action of these factors is on the sporophyte, and the nature of this action is such that two plants are not fertile together unless they differ by at least one of these factors.

It is not necessary to define the action of these factors more specifically, although this will be attempted in a subsequent publication. It may make matters somewhat clearer, however, to state that the immediate difference between a fertile and a sterile combination is in the rate of pollen-tube growth. If at the height of the season a series of self-pollinations and a series of cross-pollinations are made on a single plant and the pistils fixed, sectioned and stained at intervals of 12 hours, it is found by plotting the average length of the pollen tubes in each pistil against time in 12 hour periods that the growth curve of selfed pollen tubes is a straight line which reaches less than half the distance to the ovary during the life of the flower, while the curve of crossed pollen tubes resembles that of an autocatalysis and reaches the ovary in less than 96 hours. Further, it is unnecessary to know why gametes, which themselves bear various factors effective on the behavior of self-sterile plants, should act during the process preliminary to fertilization as if each bore the factors characteristic of the plant on which they were produced. Attention is called, however, to the fact that modern discoveries tend more and more to show that the sole function of the gametophytes of the Angiosperms is to produce sporophytes. The characters which they possess appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization. In other words, the hereditary genes carried by pollen grains—and probably by eggcells—may be thought of as being dormant until the appropriate time comes for them to play their proper parts.

It may be helpful to draw a picture of what may be expected to happen under the assumptions which have been made and to see how closely the actual facts are paralleled. First, it should be stated that no interpretation of the fact that within a family the intra-sterile classes are often of unequal size can be made without assuming linkage except by a number of awkward subsidiary assumptions. Second, our picture is as simple as possible in view of the facts at hand, but it may be extended *ad libitum* as far as number of factors is concerned. Third, since all of the facts of Mendelism are merely those to be expected from the known behavior of the chromosomes as carrying bodies for our hypothetical genes, chromosome diagrams are used without apology.

Assume first then that a plant of *N. Forgetiana* is heterozygous for 3 linked factors effective on the behavior of self-sterile plants, and that the homologous chromosomes of an *N. alata* plant are heterozygous for different multiple allelomorphs of the same factors. The two plants may be represented thus.



These plants cannot be self-fertilized because all of their gametes are influenced by their sporophytic constitution ABC.A′B′C′ and A″B″C″. A‴B‴C‴, respectively, nor can either be fertilized by gametes borne on a plant of like constitution.

Now each of these plants of *N. Forgetiana* and of *N. alata* produces 8 types of gametes. *N. Forgetiana,* for example, produces great numbers of ABC and A′B′C′, medium numbers of A′BC, AB′C′, ABC′ and A′B′C by one crossover or linkage break, and small numbers of AB′C and A′BC′ by double crossing over. *N. alata* behaves in a similar manner. Thus the progeny of this cross will consist of $8^2 = 64$ intra-sterile, inter-fertile groups of individuals, the groups being of various sizes. Further, since no individuals with constitutions ABC.A′B′C′ or A″B″C″. A‴B‴C‴ are produced in the F_1 generation, every F_1 class will be fertile with both of its parents.

Since by hypothesis two plants need differ by but one effective factor in order to be fertile in inter-crosses, it is clear that matings may occur in which certain of these factors are homozygous. To illustrate, it is possible to obtain two plants of constitutions ABC.A′B′C and A″B″C. A‴B‴C among the grandchildren of this generation. The factor C is homozygous and can be left out of consideration since the two plants form only 4 different types of gametes each. The first forms gametes AB and A′B′ in large numbers, and A′B and AB′ in small numbers; likewise the second forms gametes A″B″ and A‴B‴ in large numbers, and A″B‴ and A‴B″ in small numbers. Even with the elimination of the C allelomorphs as effective differences, therefore, it is possible to obtain a family having 16 intra-sterile classes by crossing two such plants. Of these classes 4 will be large, 8 medium and 4 small.

It is not unlikely that 16 classes is the maximum that need be considered, but what of the smaller number of groups usually found? The answer is that simplification can go on and on until very few intra-sterile classes are formed.

Suppose, for example, that AB.AB′ is crossed with AB.A′B; 4 classes will be formed AB.AB, AB.A′B, AB′.AB and AB′.A′B, of which the third class will be sterile with the female parent and the second class sterile with the male parent. Or, suppose that AA′ is crossed with AA″. Again 4 classes will be formed, AA, AA′, AA″ and A′A″. AA may then be crossed with AA′, and only 2 intra-sterile classes formed.

This may be assumed to be the simplest form in which a natural population of self-sterile plants may exist, but theoretically it is possible by taking advantage of the phenomenon of pseudo self-fertility or pseudo cross-fertility to obtain a family consisting of but 1 group. In such a family every plant would be sterile with every other plant. It is possible that the two families met in the course of our experiments in which cross-sterility appeared to be universal, were of this kind.

This hypothesis fits perfectly what to us seem the important experimental facts. One may have F_1 generations of various types of complexity, with an increasing simplicity in succeeding generations through inbreeding; or, the F_1 generation may be less complex than the F_2 generation,—the effect of inbreeding first becoming apparent in the F_3 generation. Cross-sterility with resultant intra-sterile classes in single or in different families is explained. Both sterility and fertility in back-crosses is clear. The similar behavior of reciprocal crosses is reasonable. Perfect intra-sterility in the asexual progeny of a self-sterile plant is what is to be expected. The facts established by DARWIN and by CORRENS when viewed with due consideration for pseudo-fertility become orderly. And yet this is but hypothesis, to be modified, extended, restricted or superseded as becomes necessary. If it proves useful for a time it will have served its purpose. Even now there are points upon which other heredity phenomena throw no light. We will devote a concluding paragraph to their discussion.

In our experimental work the number of intra-sterile classes and the number of individuals within each class were determined as definitely as possible. But these experiments have been too much of the pioneer type not to be rough in many ways. With our present experience the same facts could be determined more accurately and on much larger populations with less work than the original determinations demanded, and this appears to be a requisite for further advance. According to our hypothesis, accepting it without subsidiary refinements, the number of classes should always be even, and the classes should be equal in size when only 2 or 4 make up the population. Furthermore there should always be pairs of classes containing the same number of individuals. Now in making some of our calculations we have assumed that the individuals are distributed within the classes in numbers corresponding to the frequencies of the point binomial. Such a distribution was assumed only as a limiting type of unequal grouping, however, there being scarcely any evidence that such a distribution is characteristic. As a matter of fact only in the F_1 of cross No. 2 and No. 3 and its descendants, families H and I, is it possible to say that the number of individuals within the various classes may not be approximately equal. But in these cases we stumble upon an obstacle that cannot be cleared away with our present knowledge. The distributions found in these families are such that larger samples of the populations could not give us classes of equal size. For the present we must accept the conception of a small number of intra-sterile groups in certain families with all that this involves. We might explain them by subsidiary hypotheses of differential vitality or by reduplication in the sense of Bateson, but since there is no other good reason for such assumptions we prefer to leave these matters in abeyance.

LITERATURE CITED

Bateson, W., and Gregory, R. P., 1905 On the inheritance of heterostylism in Primula. Proc. Roy. Soc. B **76**:581-586.

Baur, E., 1911 Einführung in die experimentelle Vererbungslehre. Ed. 2, 1914, pp. viii + 401. Berlin: Borntraeger.

Beaton, D., 1850 On Amaryllids. Jour. Hort. Soc. **5**: 132-136.

Burck, W., 1908 Darwin's Kreuzungsgesetz und die Grundlagen der Blütenbiologie. Rec. Trav. Bot. Néerl. **4**: 17-118.

Castle, W. E., 1896 The early embryology of *Ciona intestinalis* Flemming (L.). Bull. Mus. Comp. Zoöl., Harvard University **27**: 201-280.

Comes, O., 1899 Monographie du genre Nicotiana. pp. 1-80. Naples: Typographie Coöpèrative.

Compton, R. H., 1912 Preliminary note on the inheritance of sterility in *Reseda odorata*. Proc. Phil. Soc. Cambridge **17**: 7.

1913 Phenomena and problems of self-sterility. New Phytologist **12**: 197-206.

Correns, C., 1912 Selbststerilität und Individualstoffe. Festschr. d. mat.-nat. Gesell. zur 84. Versamml. deutsch. Naturfoscher u. Ärzte, Münster i. W. pp. 1-32.

Darwin, Chas., 1859 Origin of species. Ed. 6, 1882, 2 vols. New York: D. Appleton.

1862 The various contrivances by which Orchids are fertilised by insects. Ed. 2, 1877. New York: D. Appleton.

1868 Animals and plants under domestication. Ed. 2, 1875, 2 vols. New York: D. Appleton.

1876 Effects of cross and self fertilisation in the vegetable kingdom. Ed. 2, 1878. New York: D. Appleton.

1877 Different forms of flowers on plants of the same species. Ed. 2, 1880. New York: D. Appleton.

[illegible] 1913 Inheritance of flower size in crosses between species of Nicotiana. [illegible] Gaz. **55**: 177-188.

[illegible] phenomenon of self-sterility. Amer. Nat. **49**: 77-87.

[illegible] eritance in crosses between *Nicotiana Langsdorffii* and *Nicotiana alata*. [illegible] ics **1**: 311-333.

[illegible] and Hayes, H. K., 1912 Heterozygosis in evolution and in plant breed- [illegible] U. S. Dept. Agr., Bur. Plant Ind. Bull. 243, 58 pp.

[illegible] 1881 Die Pflanzen-Mischlinge. pp. iv + 569. Berlin: Borntraeger.

[illegible] rsuche und Beobachtungen über Kreuzung und Fruchtansatz bei Blüten- [illegible] zen. Abh. nat. Ver. Bremen **11**: 413-421.

[illegible] er Unfruchtbarkeit bei Bestäubung mit eigenem Pollen. Abh. nat. Ver. Bremen **12**: 409-416, 495, 496.

Fuchs, H. M., 1914 a On the conditions of self-fertilization in Ciona. Arch. f. Entwicklungsmech. d. Organ. **40**: 157-204.

1914 b The action of egg-secretions on the fertilizing power of sperm. Arch. f. Entwicklungsmech. d. Organ. **40**: 205-252.

Gärtner, K. F., 1844 Versuche und Beobactungen über die Befruchtungsorgane der vollkommeneren Gewächse und über die natürliche und künstliche Befruchtung durch den eigenen Pollen. pp. x + [2] + 644. Stuttgart E. Schweizerbart'sche Verlagshandlung.

1849 Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. pp. xiv + 790. Stuttgart: Hering.

Gregory, R. P., 1911 Experiments with *Primula sinensis*. Jour. Genetics **1**: 73-132.

Herbert, Wm., 1837 Amaryllidaceæ. pp. vi + 428. London: Ridgway & Sons.

Hildebrand, F., 1865 Bastardirungsversuche an Orchideen. Bot. Ztg. **23**: 245-249.

1866 Über die Nothwendigkeit der Insektenhilfe bei der Befruchtung von *Corydalis cava.* Jahrb. wiss. Bot. **5**: 359-363.

1869 Über die Bestäubungsvorrichtungen bei den Fumariaceen. Jahrb. wiss. Bot. **7**: 423.

1896 Über Selbststerilität bei einigen Cruciferen. Ber. d. deutsch. bot. Gesell. **14**: 324-331.

Jennings, H. S., 1916 The numerical results of diverse systems of breeding. Genetics **1**: 53-89.

Jost, L., 1905 Zur Physiologie des Pollens. Ber. d. deutsch. bot. Gesell. **23**: 504-515.

1907 Über die Selbststerilität einiger Blüten. Bot. Ztg. **65**: 77-117.

Kirchner, O., 1905 Über die Wirkung der Selbstbestäubung bei den Papilionaceen. Nat. Zeitschr. f. Land.- u. Forstwirtsch. **3**: 1-16, 49-64, 47-111. A long list of legumes investigated.

Knuth, P., 1898 Handbuch der Blütenbiologie. Band I, pp. 400. Leipzig: Engelmann.

Kölreuter, J. G., 1761-6 Vorlaüfige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, nebst Fortsetzungen 1, 2 u. 3. pp. 266. Ostwald's Klassiker, Nr. 41. Leipzig: Engelmann.

Kraus, E. J., 1915 The self-sterility problem. Jour. Heredity **6**: 549-557.

Lecoq, H., 1862 De la fécondation naturelle et artificielle des végétaux et de l'hybridation. pp. 17-425. Paris: Maison rustique. Quotes M. Rivière on *Oncidium Cavendishianum.*

Lewis, C. I., and Vincent, C. C., 1909 Pollination of the apple. Ore. Agr. Exp. Sta. Bull. 104. 40 pp.

Lotsy, J. P., 1913 Hybrides entre espèces d'Antirrhinum. IV^{me} Conférence Internationale de Génétique. pp. 416-428.

Morgan, T. H., 1904 Some further experiments on self fertilization in Ciona. Biol. Bull. **8**: 313-330.

1910 Cross and self fertilization in *Ciona intestinalis.* Arch. f. Entwicklungsmech. d. Organ. **30**: 206-234.

1913 Heredity and sex. pp. ix + 282. New York: Columbia University Press.

Mowbray, Wm., 1830 Trans. Hort. Soc. A letter to the editor.

Müller, Fritz, 1868 Notizen über die Geschlechtsverhältnisse brasilianischer Pflanzen. Bot. Ztg. **26**: 113-116. A letter to Hildebrand.

1873 Bestäubungsversuche an Abutilon-Arten. Jenaische Zeitschr. f. Naturwiss. **7**: 22-45, 441-450. Partial translation in Amer. Nat. **8**: 223-227.

1893 See Focke, W. O.

Munro, R., 1868 On the reproduction and cross-fertilization of Passifloras. Bot. Soc. Edinburgh **9**: 399-402.

Rimpau, W., 1877 Die Selbststerilität des Roggens. Landw. Jahrb. **6**: 1073-1076.

SCHACHT, H., 1858 Über Pflanzen-Befruchtung. Jahrb. wiss. Bot. **1** : 193-232.

SCOTT, JOHN, 1865 On the individual sterility and cross-impregnation of certain species of Oncidium. Jour. Linn. Soc. London **8** : 163-167.

SETCHELL, W. A., 1912 Studies in Nicotiana. Univ. California Pub. Bot. **5** : 1-28.

SPRENGEL, C. K., 1793 Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung. Ostwald's Klassiker, Nr. 48, 49, 50, 51. Leipzig: Engelmann.

STOUT, A. B., 1916 Self- and cross-pollinations in *Cichorium intybus* with reference to sterility. Mem. N. Y. Bot. Gard. **6** : 333-354.

WAITE, M. B., 1895 The pollination of pear flowers. U. S. Dept. Agr. Div. Veg. Path. Bull. **5** : 1-86.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, NOVEMBER 1917

TABLE OF CONTENTS

STUDIES ON SELF-STERILITY. II. POLLEN-TUBE GROWTH

E. M. EAST and J. B. PARK
Harvard University, Bussey Institution, Forest Hills, Massachusetts

Reprinted from GENETICS **3**: 353-366, July 1918

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SELF-STERILITY II. POLLEN-TUBE GROWTH

E. M. EAST and J. B. PARK
Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received November 23, 1917]

TABLE OF CONTENTS

INTRODUCTION

In the first paper of this series (EAST and PARK 1917), various pedigree culture experiments involving the behavior of self-sterile Nicotianas when crossed or selfed were described in considerable detail. Among the points there established are the following:

1. The four species *N. Forgetiana, N. alata, N. glutinosa* and *N. angustifolia* are truly self-sterile, but the character is affected by attendant conditions in rather a peculiar way. The plants are completely self-sterile during the active part of the flowering season, but toward the close of this period, especially under adverse conditions, some self-fertility may be shown. *N. alata* and *N. glutinosa* are influenced thus more markedly than *N. Forgetiana* and *N. angustifolia.* As a direct corollary of this fact it follows that self-sterility is only a physiological impediment to self-fertilization.

2. Cross-sterility, apparently of the same nature as self-sterility, exists.

3. Cross-sterility exhibits a regularity in its behavior such that if plant A is sterile with plant B and with plant C, it may be predicted that plant B will be sterile with plant C. On the basis of this cross-sterility the plants within a family or even within a series of families may be divided into a comparatively small number of groups in which each member of a group is sterile with every other member of that group and fertile with every member of every other group.

4. Excluding the pseudo-fertility sometimes manifested during the wane of the flowering season and true sterility which is due to non-functional gametes, there is no fluctuation in fertility in compatible combinations. Incompatible combinations produce no seed, compatible combinations are fully fertile.

5. Reciprocal crosses always behave in the same manner; from which it follows that the effective hereditary factors controlling compatibility partake of the nature of the sporophyte rather than the gametophyte generation.

The immediate cause of these peculiar manifestations is the varied rate of pollen-tube growth characteristic of compatible and incompatible combinations. It is with these phenomena the present paper is concerned.

HISTORICAL

Numerous researches on pollen-tube growth have been made during the last three or four decades, but owing to conflicting results, comparatively few contributions to knowledge have resulted.

Van Tieghem (1869) appears to have been the first investigator to demonstrate pollen germination. He also showed that certain pollen grains contain enzymes which invert cane sugar. This conclusion was corroborated by Strasburger in 1886, who found also that starch could be transformed into sugar, an indication of diastase. Green (1894) succeeded in isolating both of these substances, but could not demonstrate the presence of cytolase, an enzyme he believed must be concerned in pollen-tube growth from the fact that growth is intercellular. Green concluded that the reserve foods of the pollen grain are starch, dextrin, cane sugar, maltose and glucose, the style containing the same substances with the exception of dextrin. These conclusions, however, can hardly be accepted without question.

Several authors have assumed that the pollen grains of certain species have developed specific chemical requirements for germination, thus accounting for their failure to obtain growth on artificial media; but this can hardly be true since pollen grains will so often germinate on stigmas of plants belonging to a different species or even to another genus, to say nothing of the successes that have been obtained on artificial media varying from comparatively pure water to the pure (?) agar agar of the trade. (Cf. Strasburger 1886; Rittinghaus 1887; Molisch 1893; Lidforss 1896, 1899; Jost 1905, 1907; Tokugawa 1914). Questioning this conclusion, however, does not imply a denial that in certain cases a preference may have been developed for particular substances. In other words, pollen grains may germinate and grow on a variety of media, but the rate of growth may be much greater in some cases than in others. No other conclusion seems to interpret appropriately the results of MOLISCH (1893), MIYOSHI (1894), LIDFORSS (1896), JOST (1907) and ourselves, even though we agree with STOUT (1916) that experiments on artificial media are rather unsatisfactory.

MOLISCH (1893) believed he had demonstrated both anaerotropism and chemotropism for acids and for secretions of the gynæcium, especially those of the stigma. He did not assume chemotropism to be a general phenomenon, for there are pollen tubes (e.g. *Orobus vernus*) which neither shun the air nor are attracted by the stigmas; nevertheless he did feel that chemotropism plays an important rôle in the passage of the pollen tube to the egg cell. MOLISCH unquestionably made a serious attack on the problem, for he investigated over 100 species.

LIDFORSS (1899) confirmed MOLISCH'S observation that the pollen tubes of *Narcissus tazetta* grow toward their own stigmas in a gelatin medium, but his endeavors to imitate the effect of the stigmas with various sugars, organic acids, amides and tannins were without success. On the other hand, he did succeed in attracting the pollen tubes by the use of pieces of onion bulb and by granules of a commercial preparation of diastase. He believed that this success was due to certain proteins, since the diastase still attracted the tubes after the ferment was killed by heat, and since egg albumen washed free of mineral salts exerted the same effect. Casein and "taka" diastase were without effect, but this was thought to be dependent upon the presence in them of mineral salts.

He states that pollen tubes of *Fritillaria imperialis* are more sensitive to salts than Narcissus. The former were killed by the same diastase preparation that had attracted the Narcissus tubes. On the other hand, dialyzed egg albumen exerted a strong attraction for the Fritillaria pollen tubes. Numerous other experiments were carried out in which the effect of proteins on various species of Choripetalæ was tested. No tendency to attract was discovered, but this he believed to be due to their great sensitiveness to small amounts of salts.

MIYOSHI (1894) found that the stigma and style of many angiosperms contained reducing sugars. Chemotropic effects on their pollen tubes were obtained by the use of several different sugars and dextrins in a gelatin medium. Meat extract, asparagin, glycerine and gum arabic had no effect, and alcohol and certain salts excited more or less repulsion.

Perhaps the most general conclusion of MIYOSHI was that pollen tubes could be turned from one solution to another if the concentration of the second be increased as demanded by WEBER's law.

These experiments, as well as the later ones along the same lines made by MARTIN (1913), TOKUGAWA (1914), ANDRONESCU (1915), ADAMS (1916) and others, must be accepted with some reservation. There is certainly a probability that pollen tubes show chemotropism, but it must be admitted, as STOUT (1916) maintains, that the amount of pollen-tube growth observed in artificial media is small, probably never over 1.5 mm. This being the case, one is likely to be over-influenced by working hypotheses, and to conclude in favor of chemotropism without due evidence. At the same time, these investigators must be thanked for having given us a general idea, though perhaps somewhat superficial, of the physiology of the pollen tube.

The only data on pollen-tube growth bearing directly on the problem of self-sterility are those of JOST (1907) and of CORRENS (1912). They found that when a self-sterile plant is pollinated with its own pollen, the tubes are emitted freely but grow extremely slowly. Since a cross-pollination on the same plant results in rapidly growing tubes, the hypothesis was advanced, somewhat differently by each, that special substances in each plant inhibit the growth of pollen tubes from pollen of that plant.

POLLEN-TUBE GROWTH IN ARTIFICIAL MEDIA

Our own experiments on pollen physiology through the use of artificial media were made on *N. angustifolia* and *N. Forgetiana*. The medium usually employed was 2 percent agar agar to which various nutrients were added, although pure agar was used successfully. As nutrients different percentages (1-20) of cane sugar, glucose, levulose and sodium malate were used. The tubes grew well on all of these media, the best development being obtained on 2 percent agar plus 20 percent cane sugar. The maximum growth in this medium was about .6 mm. This length of pollen-tube is almost negligible when compared with the 3 cm to 7 cm necessary for the sperm nucleus to reach the ovule. Nevertheless, there seems to be no question but that there is a true germination and a real growth on artificial media. If the pollen grains are perfect morphologically, that is if no true pollen sterility is present, pollen tubes are formed in nearly every case. Owing to the comparatively short length to which they grow, one is hardly justified in plotting a growth curve, but there is no doubt but that the rate of growth from germination onward is either progressively slower, or that it starts slowly, reaches a maximum in from 12 to 24 hours and then falls off. This fact should not be overlooked, as it is not what occurs when a natural compatible mating is made, and shows clearly the great difference between pollen-tube growth in a natural and in an artificial medium.

In over 100 experiments of this type a high percentage of pollen germination (70-80 percent) was obtained, and the pollen tubes grew well no matter what medium was used. The tubes were emitted in all directions, but in general the growth of an individual tube was in one direction, though there was considerable variation from a straight line.

Since the experiments of MOLISCH, LIDFORSS, MIYOSHI and others all indicated that pollen tubes are attracted toward certain substances, it was thought that possibly the same phenomenon might occur if portions of the gynæcium of flowers of the same species were placed in the media. Many experiments were tried therefore in which parts of stigmas, styles and ovaries (both crushed and uncrushed) or of their extracts were placed in the media and pollen scattered near them at variious distances (.5 to 3 cm). In some cases gynæcium parts from the same self-sterile plant which furnished the pollen were used, in other instances the gynæcium parts came from one plant and the pollen from a plant cross-sterile with the first. The tendency of the pollen tubes in these tests was compared with that of pollen from the same plants when placed near gynæcium parts of plants with which the pollen was known to be compatible. We were not able to discover any difference in the behavior of the pollen tubes in these trials. Occasionally, perhaps in 10 percent of the cases, the pollen tubes seemed to be attracted by the gynæcium parts, but the percentage was about the same in all cases. If there was really any attraction at all, which is doubtful, it was no greater between plant parts from plants known to be capable of effecting mutual cross-fertilization than it was from plant parts taken from plants which were cross-sterile together, or even when taken from the same plant. Notwithstanding the fact that there was no decided turning of the tubes toward any object or substance placed in the medium, there was some evidence that the presence of gynæcium parts promoted growth. On a number of occasions data were secured such as are shown in table 1.

The evidence of stimulation from the presence of ovules and more particularly of stigmas is unmistakable but whether the presence of "compatible" stigmas or ovules shows an additional stimulation over that due to "incompatible" stigmas and ovules is doubtful.

TABLE I

Growth of pollen tubes in a 2 percent agar medium in VAN TIEGHEM *cells. Plants A and B are both self-sterile, but are cross-fertile.*

Exp.	Materials used	Ave. length tubes in μ
1	Pollen A + ovary B crushed	24
	Pollen A + stigma B crushed	24
	Pollen B + ovary A crushed	18
	Pollen B + ovary B crushed	8
	Pollen B + stigma B crushed	20
	Pollen A only	8
	Pollen B only	14
2	Pollen A + stigma A	120
	Pollen A + stigma B	170
	Pollen A	40
	Pollen B + stigma B	100
	Pollen B + ovary B	88
	Pollen B + ovary A	100
	Pollen B	50
3	Pollen B + stigma B	60
	Pollen B + stigma A	100
	Pollen B + ovary B	30
	Pollen B + ovary A	50
	Pollen B only	30
	Pollen A only	10

Note: Data taken after 24 hours in exp. 1, after 48 hours in exp. 2, and after 24 hours in exp. 3.

These results do not corroborate the work of the earlier writers mentioned above, but neither do they prove there is no such thing as pollen-tube chemotropism. They indicate some sort of nutritive value or stimulative effect of substances contained in gynæcium parts, but there is no evidence that gynæcium parts are more nutritive than other plant parts nor that "compatible" plant parts are better than "incompatible" plant parts. Experiments of this kind are unsatisfactory. They may not be useless, but it seems improbable that any notable increase in knowledge will be obtained by their use until the technique is so improved that the growth curve in artificial media compares favorably with the natural growth curve.

ATTEMPTS TO SELF-POLLINATE MUTILATED PISTILS

In the early part of our work numerous attempts were made to obtain selfed seed on self-sterile plants by endeavoring to force pollen tubes to grow in shortened styles. The experiments were of two types. Various methods of obtaining temporary unions between stigma and style after excising portions of the latter were tried by means of wax and glass envelopes. All of these attempts were unsuccessful. Pollinations of decapitated pistils were also made using stigmatic fluid and various sugars as germination media. In two cases, seed was obtained where stigmatic fluid was used. The matter is merely mentioned to show the possibility of developing a successful technique. The experiments were discontinued as soon as it had been proved by end-season self-pollinations that self-fertilization of self-sterile plants is possible, and that for this reason self-sterility is no true impediment to the fusion of an egg with a sperm nucleus which is the product of the same plant.

POLLEN-TUBE GROWTH IN THE PISTIL

The most gratifying experiments along these lines were those concerned with the rate of growth of pollen tubes in the pistils of self-pollinated and of cross-pollinated plants. Studies were made on pistils of *N. Forgetiana, N. alata* and *N. angustifolia*. The technique consisted of making series of self-pollinations and of cross-pollinations, both compatible and incompatible, on a single plant, collecting the pistils thus treated on successive days, and fixing, dehydrating, imbedding and sectioning them in the usual manner. Longitudinal sections about 10μ thick were used. Triple staining with safranin, gentian violet and orange G gave the best results, although safranin alone was almost as satisfactory.

About 400 slides each containing from 10 to 30 serial sections were prepared in this manner.

The germination of the pollen was found to be just as high in the selfed as in the crossed pistils, and the number of pollen tubes in a single pistil was very large. By actual count it was determined that single pistils may contain from 1200 to 2000 tubes, a number sufficient to fertilize from 4 to 6 times the number of ovules in the ovary.

The distribution of pollen tubes in the selfed pistils was always minus skew as is shown by the following sample frequencies.

Distance from stigma mm	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5
1 section after 6 days	1	43	30	30	20	13	7	7	5	2	1	1	
1 section after 7 days				4	20	24	18	9	7	2	2	1	

The large number of short pollen tubes and the few greatly in the lead raise the important question: Do some pollen tubes grow faster than others because they have different genetic constitutions? Should this be so, selective fertilization would result. We have good evidence, however, that this is not the case.[1] The difference in length of the various pollen tubes is probably due largely to variation in the time of germination. Those pollen grains which are in intimate contact with the moist stigma absorb its secretions and put forth their tubes more quickly than do those less favorably situated. If, therefore, a flower be pollinated at a particular time, one may accept the mode of the frequency distribution of the pollen tubes within the pistil as a proper measure of pollen-tube growth for a given period.

A considerable amount of data of this kind has been collected for the purpose of comparing the rate of pollen-tube growth in selfings, and in cross-fertile and cross-sterile matings. Figures 1, 2 and 3 are graphs made from a random sample of the results secured. Each point represents the estimated modal length of the pollen tubes in a pistil collected at the indicated length of time after pollination. Ordinates to the various broken lines at the top of the figure represent the total length of the pistil of the respective plants. Figures 1 and 2 are from studies on *Nicotiana Forgetiana*. The rate of growth of selfed pistils in figure 1 and of the composite of selfed pistils in figure 2 are typical of selfed plants during the active part of the flowering season. The growth curve is practically a straight line. The pollen tubes grow well; as far as one may judge visually there is no difference between them and tubes from cross-pollinations. But they grow so slowly that even after the extraordinary flower life attained on plant 3 where a 14-day point is recorded, the pollen tubes are only half way to the ovary.

In crossed pistils, on the other hand, if the mating is compatible, growth curves are produced which are of a very different character. The pollen tubes start to grow at about the same rate as in selfed pistils, but the speed continually increases until fertilization ensues,—usually after from 3 to 5 days. The curve simulates that of an autocatalytic reaction.

The points plotted for selfings on plants 6 and 7, shown in figure 2 produce curves intermediate between the true "self" curves and the "cross" curves. This is the type of change that is brought about late in the flowering season and which when carried to an extreme produces pseudo self-fertility.

Figure 3 represents curves similar to those just described, but com-

---

[1] For a preliminary report on this subject see Jour. Heredity **8**: 382, 1917. Further details will be published later.

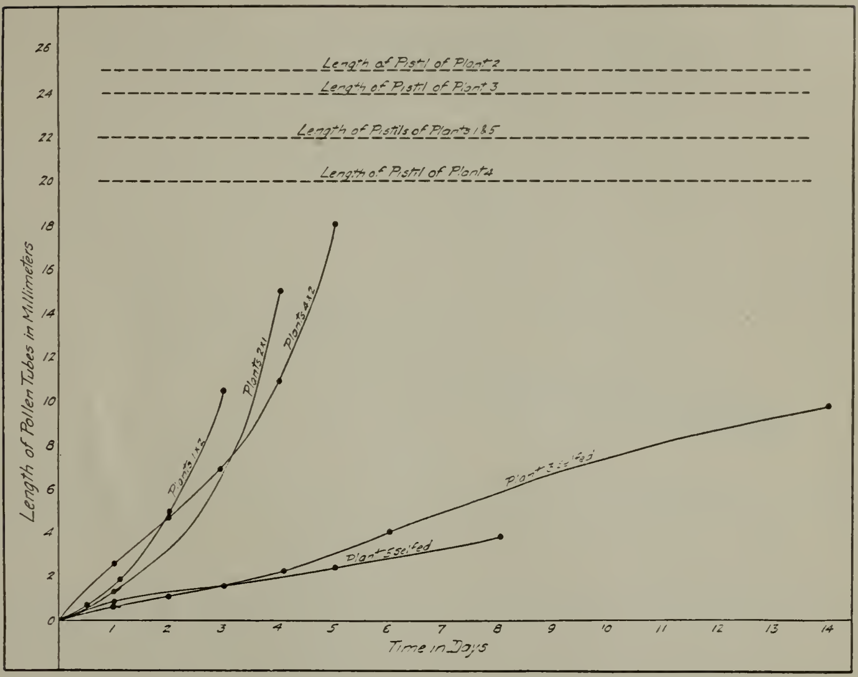


FIGURE 1.—Growth curves of pollen tubes from selfed and from crossed pistils of plants of *Nicotiana Forgetiana.*

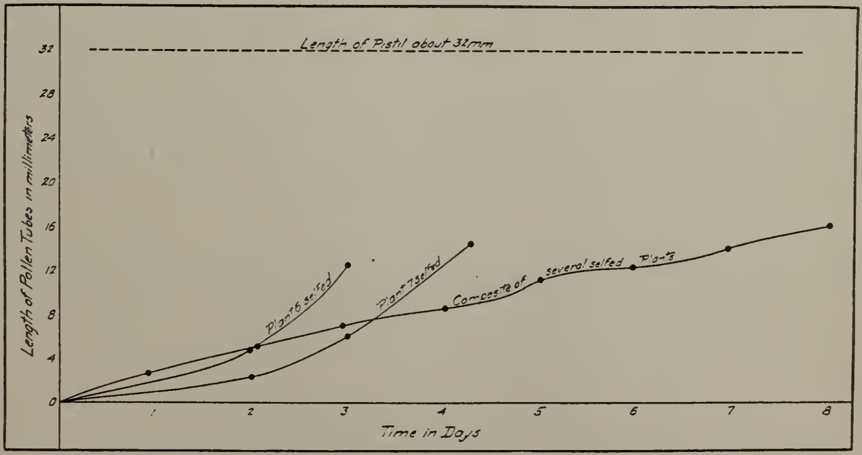


FIGURE 2.—A composite growth curve of pollen tubes from normal selfed pistils of two plants of *Nicotiana Forgetiana.* End-season growth curves from selfed pistils of plants of the same species.

piled from data upon *N. angustifolia.* The selfings produce straight lines and the compatible crosses produce curves in which pollen-tube

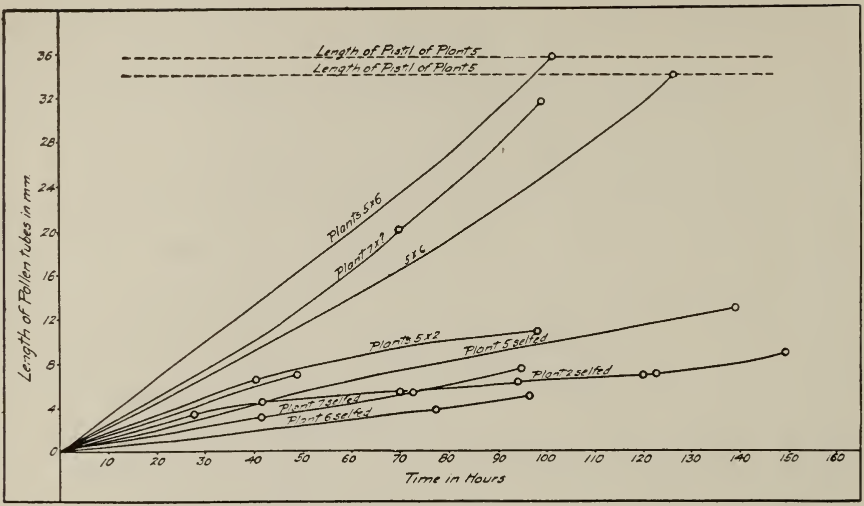


FIGURE 3.—Growth curves of pollen tubes from pistils of plants of *Nicotiana angustifolia.* Plants 5 and 2 are cross-sterile with each other.

growth becomes faster and faster as they approach the ovary. Since no points were noted on the crossed pistils during the early part of the progress of the tubes, the curves as drawn are not exactly like those of figure 1, but this difference has no real basis.

One of the curves of figure 3 is from an incompatible cross. It is practically the same as the self upon the same plant.

Many other curves have been made, but these are fair samples. All show the same type of growth. Selfs made during the active part of the flowering season always produce straight-line growth curves. The growth of the tubes is at a steady rate throughout the length of the style traversed. The same is true of incompatible crosses. Toward the wane of the flowering season, however, the type of curve always changes until it resembles that of a compatible cross, though there remains a slight difference. The growth is more rapid than that from mid-season selfings, but the velocity in these cases is almost constant while in compatible crosses there is an acceleration.

SUMMARY AND DISCUSSION

The following general conclusions may be drawn from the data reported in this paper.

1. Pollen grains of the four species of Nicotiana used in these investigations germinate on many artificial media as well as on the stigmas of the plants themselves, but the length of pollen tube obtained is never over .6 mm and usually is from .1 mm to .2 mm.

2. Though pollen tubes are emitted freely on artificial media, their growth is unlike that obtaining under natural conditions. There the growth either remains constant or becomes more rapid, but on artificial media the latter part of the growth is markedly retarded.

3. Pollen-tube chemotropism was not observed, but since the presence of gynæcium parts in the medium caused a longer tube to be produced, this negative result may have been due to rapid diffusion of the chemical stimulants.

4. It is possible to obtain pollen-tube penetration followed by fertilization in a decapitated style by the use of a proper germinating medium.

5. Pollen grains germinate as well on the stigmas of flowers of the same plant as they do on the stigmas of flowers of other plants with which they are compatible.

6. From 5 to 10 times as many pollen tubes are produced as are necessary to fecundate the ovules.

7. The pollen tubes produced after a selfing are indistinguishable in size from the pollen tubes produced after a cross, when pollen tubes of the same length are measured.

8. Though there is variation in the length of the pollen tubes both after a self-pollination and after a cross-pollination, this variation seems to be due wholly to differences in the rate of germination of the pollen grains or to other causes which are environmental in nature and not to any differences in gametic constitution between the pollen grains themselves.

9. Pollen tubes produced after self-pollinations grow steadily and apparently normally, but do not reach the ovary before the flower decays because this growth is slow. Length plotted against time is a straight line.

10. Pollen tubes produced after a compatible cross start their growth at about the same rate as the pollen tubes produced after selfing; but the growth becomes constantly more and more rapid. Length plotted against time produces a curve that resembles that of an autocatalytic reaction.

11. Cross-sterile combinations resemble selfings in the rate of pollen-tube growth.

12. At the wane of the flowering season rate of growth of self pollen tubes becomes more rapid, though there is little evidence of acceleration during their passage down the style.

These results appear to us to show that the pollen tubes in a selfed pistil are not inhibited in their growth by substances secreted in that pistil, but rather that a substance or substances are secreted in the pistil after a compatible cross which accelerate growth, and that the direct cause of this secretion is a catalyser which the pollen-tube nucleus is able to produce because the zygotic constitution of the plant producing it is different in certain particular hereditary factors from that of the plant on which it is placed. Since pollen-tube growth is intercellular, it may be that some cytolysis occurs, but in the main there appears to be some local reaction between the pollen-tube nucleus and the contiguous cells of the style which produces or makes serviceable the nutrients necessary for tube growth. The action must be local because the presence of compatible pollen tubes does not accelerate the growth of self pollen tubes. The reaction must be mutual because one cannot account for the peculiar behavior of self-sterile plants in crosses if one interprets pollen-tube growth as a simple parasitism.

The action in the case of self pollen tubes or where incompatible crosses are made, is accounted for by the likeness of the parents in the effective hereditary factors postulated. Some action must take place in these cases because growth occurs but this is the action on which the other phenomenon is built. It does not seem to be in the nature of an inhibition because the growth of self pollen tubes is constant from the beginning to the end of the growth. If any change in rate of growth occurs it is a slight acceleration. Nor does this growth appear at all analogous to immunity phenomena as has been suggested by COMPTON (1913) and STOUT (1916). At least if there is similarity, the current theories of immunity do not serve to make the matter any clearer.

The change in rate of tube growth in selfed pistils toward the end of the flowering season we hold to be a phenomenon apart from those just discussed. Here instead of a mutual reaction between active cells, there seems to be more of a parasitism. The pollen tube is active, but the style cells are inactive. The active pollen tube, then, feeds on the broken down cells of the style. Our evidence of this is not conclusive, but it is very suggestive that the pollen-tube growth in this pseudo-fertility, as we have called it, seems to be merely faster throughout the whole period of its growth rather than increasingly rapid. It would seem that if this were the case, then where there is pseudo cross-fertility between a plant in active flower and a plant at the wane of the flowering period, reciprocal crosses would not give the same result as was maintained in our earlier paper. But our contention there was that plants in the height of their flowering period give like results in reciprocal crosses.

Moreover in cases where pseudo cross-fertility was noted, with perhaps a very few doubtful ones, the plants used in reciprocal crosses were at about the same flowering stage. We have since made a few incompatible crosses (10), however, between plants at the most active part of their flowering season and plants at the extreme end of their flowering season. There was, and we may admit we expected it, a difference between the reciprocals. Some fertility was shown when the old plants were used as pistillate parents, there was none in the reciprocals.

LITERATURE CITED

Adams, J., 1916 On the germination of the pollen grains of apple and other fruit trees. Bot. Gaz. **61**: 131-147.

Amici, G. B., 1830 Note sur la mode d'action du pollen sur la stigmate. Ann. sci. nat. **21**: 329-332.

Andronescu, D. I., 1915 The physiology of the pollen of *Zea mays* with special reference to vitality. Thesis: Univ. of Illinois. pp. 1-36. Champaign: Pub. by author.

Correns, C., 1889 Culturversuche mit dem Pollen von *Primula acaulis* Lam. Ber. d. d. bot. Gesell. **7**: 265-272.

1912 Selbststerilität und Individualstoffe. Festschr. d. math.-nat. Gesell. zur 84. Versamml. deutsch. Naturforscher u. Ärzte Münster i. W. pp. 1-32.

Coupin, Henri, 1906 Sur l'action de quelques alcaloïdes à l'égard des tubes polliniques. Compt. rend. Acad. Sci. Paris **142**: 841-843.

Degagny, Charles, 1886 Sur le tube pollinique, son rôle physiologique. Compt. rend. Acad. Sci. Paris **102**: 230-231.

East, E. M., and Park, J. B., 1917 Studies on self-sterility I. The behavior of self-sterile plants. Genetics **2**: 505-609.

Green, J. R., 1894 Researches on the germination of the pollen grain and the nutrition of the pollen tube. Phil. Trans. Roy. Soc. London B **185**: 385-409.

Hansgirg, A., 1897 Beiträge zur Biologie und Morphologie des Pollens. Sitzber. kgl. Ges. d. Wiss. Prague **23**: 1-76.

Jost, L., 1905 Zur Physiologie des Pollens. Ber. d.d. bot. Gesell. **23**: 504-515.

1907 Über die Selbststerilität einiger Blüten. Bot. Ztg. **65**: 77-117.

Lidforss, Bengt, 1896 Zur Biologie des Pollens. Jahrb. f. wiss. Bot. **29**: 1-38.

1899 Über den Chemotropismus der Pollenschläuche. Ber. d. d. bot. Gesell. **17**: 236-242.

Mangin, Louis, 1890 Sur la callose, nouvelle substance fondamentale existant dans la membrane. Compt. rend. Acad. Sci. Paris **110**: 644-647.

Martin, J. N., 1913 The physiology of the pollen of *Trifolium pratense*. Bot. Gaz. **56**: 112-156.

Miyoshi, Manabu, 1894 Über Reizbewegungen der Pollenschläuche. Flora **78**: 76-93.

Molisch, Hans, 1893 Zur Physiologie des Pollens. Sitzungsber. Weiner Akad. Wiss., math.-naturw. Kl. **102**: 423-448.

Rittinghaus, P., 1887 Einige Beobachtungen über das Eindringen der Pollenschläuche ins Leitgewebe. Verh. nat. Vereines Rheinland **43**: 105-122.

Stout, A. B., 1916 Self- and cross-pollinations in *Cichorium intybus* with reference to sterility. Mem. N. Y. Bot. Gard. **6**: 333-454.

STRASBURGER, E., 1886 Über fremdartige Bestäubung. Jahrb. f. wiss. Bot. **17** : 50-98.

VAN TIEGHEM, PH., 1869 Recherches sur la végétation libre du pollen et de l'ovule. Ann. sc. nat. V, **12** : 312.

TOKUGAWA, Y., 1914 Zur Physologie des Pollens. Jour. Coll. Sci. Tokyo **35** : 1-35.

TOMASCHEK, ANTON, 1882 Das Bewegungsvermögen der Pollenschläuche und Pollenpflanzen. Sitzber. Wien. Akad. Wiss. **84** (1881) : 612-615.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JULY 1918

TABLE OF CONTENTS

STUDIES ON SELF-STERILITY. III. THE RELATION BETWEEN SELF-FERTILE AND SELF-STERILE PLANTS

E M. EAST
Bussey Institution, Harvard University, Forest Hills, Massachusetts

Reprinted from Genetics: **4** 341-345, July, 1919

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SELF-STERILITY. III. THE RELATION BETWEEN SELF-FERTILE AND SELF-STERILE PLANTS

E. M. EAST

Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received March 14, 1919]

TABLE OF CONTENTS

INTRODUCTION

In the first paper of this series (EAST and PARK 1917), where the behavior of self-sterile plants was described in some detail, it was pointed out that the difference between self-fertile and self-sterile plants might prove to be a wholly different problem. This statement has been overlooked by several reviewers who criticized the interpretation of the behavior of self-sterile plants proposed because it failed to take into account the phenomenon of self-fertility. The prediction was not made at random, however. Even at that time various data had been gathered indicating a simple one-factor difference between self-fertile and self-sterile plants in keeping with COMPTON'S previous work (1912) on *Reseda odorata*. It can now be stated unequivocally that the position then taken is correct. In the material investigated self-fertile plants differ from self-sterile plants by a single essential Mendelian factor. Self-fertility is dominant. Adopting a presence-and-absence mode of expression, a plant is self-fertile because of the presence of a determiner for self-fertility; when this determiner is absent, the individual is self-sterile.

COMPTON'S WORK ON RESEDA

The only investigation in which crosses between self-fertile and self-sterile plants have been studied is that of COMPTON (1912, 1913) on the mignonette, *Reseda odorata*. Having had his attention directed to the species by the observations of Darwin, a number of experiments were made with the following results:

(1) Self-sterile plants intercrossed produced only self-sterile offspring. (2) Certain self-fertile plants when self-fertilized threw approximately 3 self-fertile to 1 self-sterile offspring. (3) These same plants when crossed with self-sterile individuals, produced self-fertiles and self-steriles in the ratio one to one. (4) Other self-fertile plants yielded none but self-fertile offspring from selfed seed.

These facts are satisfactorily interpreted by assuming a single factor difference with complete dominance. The recessives produced only recessives. The dominants in part produced only dominants and in part produced both types in the usual ratio of 3 to 1. He was dealing, therefore, in part with homozygous and in part with heterozygous plants, and the behavior of the heterozygous individuals was checked by the back cross with the recessive.

CORROBORATION OF COMPTON'S RESULTS BY EXPERIMENTS ON NICOTIANA

These experiments of COMPTON have been corroborated by crossing two of the self-sterile species used in our previous work, *Nicotiana Forgetiana* and *Nicotiana alata,* with a third species *Nicotiana Langsdorffii,* which is consistently self-fertile.

Nicotiana Forgetiana and *Nicotiana Langsdorffii* were crossed reciprocally. In each case the plants were very vigorous, exceeding both parents somewhat in height. They grew quickly, matured rapidly, and produced a profusion of fertile flowers. The flowers were somewhat intermediate in size but resembled the larger-flowered parent, *Nicotiana Forgetiana,* in form. No difference could be discerned in the reciprocals either in the first or second hybrid generation in appearance or behavior. The two experiments may therefore be considered as one.

About 400 plants were grown and selfed by hand with the usual precautions against cross-pollination. In each case, from 6 to 20 blossoms were operated on. *Every plant was self-fertile.* Seed set in abundance, filling the capsules. Not every flower pollinated produced seed, of course, but the percentage was practically the same as that obtained in check experiments on pure *Nicotiana Langsdorffii,* 85 percent. The work was completed as early in the season as possible in order not to be disturbed by the pseudo self-fertility which is sometimes present in self-sterile plants at the close of the flowering season.

From selfed seed of the cross *N. Forgetiana* × *N. Langsdorffii,* 89 plants were grown and tested for self-fertility by guarded hand-pollinations such as were made in the first hybrid generation. Of them 70 proved to be self-fertile and 19 self-sterile.

From selfed seed of the reciprocal cross, 92 plants were tested. Of this lot 74 showed self-fertility and 18 self-sterility. There was a sum total, therefore, of 144 self-fertile and 37 self-sterile plants in F_2, a ratio 3.8 to 1.

If the hypothesis of a one-factor difference is correct the deficiency of recessives is somewhat greater than is to be expected in a population of this size. Nevertheless this failure to measure up to expectation need not disturb us. About one-fourth of the bags used in protecting the flowers were torn by wind, and the plants had to be tested a second time. This unfortunate occurrence prolonged the experiment until well into September when the plants were past their prime. It is not unexpected therefore that some truly self-sterile plants should have been listed as self-fertile because of "end-season" pseudo-fertility. In fact a slight fertility was shown by about 30 percent of the plants classed as self-sterile; i.e., they produced partially filled capsules in about 15 percent of the pollinations.

These plants were tested further by taking them into the greenhouse and bringing them into a second season of flowering. Pollinations were then made at the beginning of the season, and the plants proved to be fully self-sterile.

If this be not sufficient evidence to prove the case, there is the behavior of the third hybrid generation to be relied upon. *All progeny of the recessive (self-sterile) segregates of F_2 were again self-sterile.* About 200 were tested.

The cross between *N. Langsdorffii* and *N. alata* yield results similar to those just described. The plants of the first hybrid generation were all self-fertile; those of the second hybrid generation were partly self-fertile and partly self-sterile. About 200 F_2 plants were tested, of which 38 were self-sterile. Again there was a deficiency of recessives. The progeny of the self-steriles were all self-sterile, but no investigation of the amount of pseudo self-fertility was made. The matter of particular interest in this cross was the cross-fertility of F_2 plants having flowers of very different corolla lengths. Flowers were obtained as short as 2.0 cm and as long as 6.0 cm, yet reciprocal crosses were very easy to make.

It will be remembered that KÖLREUTER was unable to fertilize *Mirabilis longiflora* with pollen from *Mirabilis Jalapa* although the reverse cross could be carried out without difficulty. In interpreting these facts it has been customary to assume that *M. Jalapa* pollen tubes are short and thus unable to reach the micropyles of the ovaries of *M. longiflora.* From work on pollen-tube growth (EAST and PARK 1918) and observations on the F_2 individuals of the cross between *N. Langsdorffii* and *N. alata,* we believe this assumption to be incorrect. Pollen tubes of all species observed by us have continued to grow as long as the flowers remained unwithered even in many generic crosses. The real cause of the occasional lack of success when a long-flowered plant is pollinated with pollen from a short-flowered plant, therefore, is in the "death" of the flower *before* the pollen tube has had time to reach the micropyle.

Though we may conclude that lack of a particular factor F results in self-sterility, there are some other factors to be considered in the behavior of crosses between self-fertile and self-sterile plants. When the self-sterile segregates of the cross between *N. Forgetiana* and *N. Langsdorffii* were examined carefully throughout the second flowering season, the type of self-sterility present did not seem to be the same in all cases. A majority of the plants exhibited a much greater amount of pseudo self-fertility than had ever been found in *N. Forgetiana.* In that species only an occasional plant produced a few selfed seeds and then only at the extreme end of the flowering season. Among the F_2 individuals of the cross, however, pseudo-fertility set in about the middle of the season and from then on it was very easy to get capsules which on casual examination would be said to be full of seed. As a matter of record only about 30 percent of such pollinations were successful and the capsules on the average had only about 70 percent of the normal complement of seed. Nevertheless, some 60 to 75 percent of the F_2 segregates classified as self-sterile showed at least 100 times the pseudo-fertility of the parent species, *N. Forgetiana.* The remaining plants were comparable to the latter in self-sterility.

It was also noticeable that the progeny of the most self-sterile of the F_2 plants were similar to them, while the progeny of the others were in part like their mother plants and in part like *N. Forgetiana.*

The simplest explanation of this state of affairs is that there is really a two-factor difference as regards self-sterility and self-fertility between *N. Forgetiana* and *N. Langsdorffii. N. Langsdorffii* is homozygous for a factor F; when this factor is absent the plants are self-sterile. It is also homozygous for a dilution factor D. The constitution of *N. Forgetiana* is $dd\ ff$. The F_1 individuals, having the constitution $Ff\ Dd$, are all self-fertile. In the F_2 generation a ratio of $9\ FD : 3\ Fd : 3fD : 1\ fd$ is obtained. There are 3 self-fertile to 1 self-sterile because of the distribution of the allelomorphic pair *F* and *f*. But of the self-steriles, those having the constitution *fD* show a great deal more pseudo self-fertility than those having the constitution *fd*. Only the *fd* plants are wholly comparable to *N. Forgetiana*.

In describing the behavior of self-sterile plants this statement was made (EAST and PARK 1917):

> "The waning of the reproductive period affects *N. alata* and *N. glutinosa* more markedly than it does *N. Forgetiana* or *N. angustifolia.* This indicates multiple allelomorphism in a fundamental factor the presence [or absence] of which is necessary for the development of self-sterility. This factor should not be confused with any of those assumed in the interpretation of the behavior of self-sterile plants among themselves."

The peculiarities of the cross between *N. Forgetiana* and *N. Langsdorffii* show that subsidiary factors affecting the manifestation of self-sterility, given homozygosity in *ff*, are as likely to be the interpretation of the differences shown in these four species as is multiple allelomorphism.

SUMMARY

Data are reported showing that in Nicotiana self-sterility is due to the presence of the allelomorph of a dominant fertility factor, *F*. When a population is homozygous for this factor, *ff*, it is self-sterile.

The factors which control the peculiar and systematic behavior of self-sterile plants when intercrossed among themselves are wholly independent of this factor and the latter does not need to be considered in an interpretation of their expression.

The manifestation of self-sterility as evinced by the degree to which pseudo-fertility shows, is due to a subsidiary inherited factor (or factors), but without the presence of the principal factor *ff* there is no evidence that it functions.

LITERATURE CITED

COMPTON, R. H., 1912 Preliminary note on the inheritance of sterility in *Reseda odorata*. Proc. Phil. Soc. Cambridge **17**: 7.

1913 Phenomena and problems of self-sterility. New Phytologist **12**: 197-206.

EAST, E. M., and PARK, J. B., 1917 Studies on self-sterility. I. The behavior of self-sterile plants. Genetics **2**: 505-609.

1918 Studies on self-sterility. II. Pollen-tube growth. Genetics **3**: 353-366.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JULY 1919

TABLE OF CONTENTS

STUDIES ON SELF-STERILITY. IV. SELECTIVE FERTILIZATION

E. M. EAST
Bussey Institution, Harvard University, Forest Hills, Massachusetts

Reprinted from GENETICS **4**: 346-355, July, 1919

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SELF-STERILITY. IV. SELECTIVE FERTILIZATION

E. M. EAST
Bussey Institution, Harvard University, Forest Hills, Massachusetts

Reprinted from GENETICS **4**: 346-355, July, 1919

STUDIES ON SELF-STERILITY. IV. SELECTIVE FERTILIZATION

E. M. EAST

Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received March 31, 1919]

TABLE OF CONTENTS

INTRODUCTION

Selective fertilization has been evoked many times as a means of accounting for peculiar or unusual breeding results. CASTLE'S (1903) original theory of sex-determination, and CUÉNOT'S (1908) interpretation of the non-appearance of homozygous yellow mice, are examples. Fortunately, it has always been possible to explain matters without retaining the hypothesis; in many cases, in fact, direct proof has been available that selective fertilization does not occur. Nevertheless, selective fertilization as a contingency has remained a sort of nightmare to investigators in genetics. Such antipathy is not unnatural, but one must have in mind the changes which have taken place in the subject during the last decade, to understand clearly the reason.

MENDEL'S discoveries, the Laws of Segregation and of Recombination, made heredity enticingly simple. All extensions, additions and exceptions have tended toward complexity. In this genetics has but repeated the history of chemistry and physics, yet it is to be expected, perhaps, that any suggested change in genetic conceptions savoring of increased complexity should find favor slowly. And selective fertilization is a tenet which would increase the difficulties of the subject a hundredfold.

The outgrowth of Mendelism has been a theory of inheritance founded on the conception of specific character determiners, genes, located in the chromatin. In the sense that the central problem of heredity is clearly one of chromosome, or at least of chromatin, distribution, the modern generalization has a simple grandeur not found in early Mendelism; but this simplicity is quite delusive, as a short consideration shows.

The conception of the gene is unquestionably the foundation of genetics. Students of heredity have submitted good evidence that *characters* are the product of many relatively *stable* genes which have a real basis in the germplasm, and that each of these genes may be the cause of various effects in different parts of the organism. They have shown that while the effects of a particular gene may not be wholly the same under different environmental conditions, nevertheless neither changes in the factors of environment nor association in particular combinations in the germplasm serves to change their individuality or constitution with a *significant* frequency.

Heredity, then, is the distribution of genes, and the genes have been located definitely in the chromosomes. Fortunately, chromosome distribution has been standardized in a remarkable manner in the majority of plants and animals; hence, the greater part of the phenomena found in breeding experiments may be described by a comparatively few simple mathematical formulae. It is to this orderly chromosome distribution that one must impute the utility of the Mendelian nomenclature, for to it in large measure is due the regularity with which certain ratios recur. There are irregularities in chromosome distribution, it is true. They have even furnished some of the critical tests of the modern theory of heredity taken as a whole. But because they curtail the practical value of the theory through limiting the possibilities of prediction, it is well that they are rare.

The standard chromosome mechanism for distribution of genes is that in which homologous chromosomes mate at synapsis, and homologous genes, *one* from either parent, pass by chance to either pole of the mitotic figure, in the formation of the mature gametes. The chromosomes may separate without having exchanged genes, presumably; or, genes may be exchanged. Just how this interchange occurs is not wholly clear. MORGAN has assumed that the genes have a linear arrangement, and that there must be transverse breaks in the chromosomes. CASTLE (1918) believes the arrangement is not linear, and that breaks may occur in many ways. It is possible that neither assumption is correct. The writer has felt for some time that possibly the genes are arranged spatially in a manner somewhat analogous to that assumed by chemists for organic molecules, though perhaps it might be better to say in a manner analogous to certain crystals, for there certainly is no evidence that the genes are radicles belonging to single molecules. But the point is that with a spatial arrangement similar to that assumed for the radicles of molecules, with the homologous chromosomes mirror images of each other, with homologous genes interchanging by a definite mechanism, a more delicate system of action is possible than with mere chromosome breaks.

However this may be, the hinge on which the usefulness of this whole scheme turns is that *the genes pass to either daughter cell by chance,* and that the gametes thus formed *mate by chance.*

Even when such inheritance obtains, selective elimination of both gametes and zygotes is somewhat common, and causes rather chaotic conditions wherever it occurs. For example, the difficulties which characterize all endeavor to analyze inheritance in the Oenotheras are probably due in large measure to this cause. The additional difficulties which would arise should it be found that there is *selection of genes* in gamete formation, and *selection of gametes* at fertilization are so great as to be hardly imaginable.

DISCUSSION OF THE PROBLEM

Particularly suitable material with which to test the second possibility is found in those plants which are self-sterile. Since the direct cause of self-sterility is the slowness of growth of *self* pollen tubes as compared with *cross* pollen tubes, it would seem as if selective fertilization would have a better opportunity to manifest itself under such circumstances than under those which obtain in self-fertile plants and in animals.

Experiments with the self-sterile species *Nicotiana Forgetiana, N. alata* and *N. angustifolia* have shown that in self-pollinations and in incompatible cross-pollinations the pollen grains germinate as well as in compatible cross-pollinations. No differences are to be found between the two types either as to the percentage of grains germinating, the length of time required for germination, or the size of the tubes after germination, provided pollen tubes of the same length are measured. Pollen tubes produced after self-pollination or after incompatible cross-pollination grow so steadily that length plotted against time is a straight line; but pollen tubes produced after a compatible cross grow at such a constantly increasing rate that the growth curve resembles that of an autocatalytic reaction. As the flowering season is about to come to an end, more rapid pollen-tube growth occurs after a self-pollination or an incompatible cross-pollination, though there is little evidence of the accelerated growth characteristic of compatible combinations. The pollen tubes grow more rapidly, but the curve by its constant velocity still resembles the curve of a "normal" self-pollination.

These facts are the basis of our problem, and naturally they suggest the possibility of selective fertilization. Part of the work reported in the first of these studies (East and Park 1917) was done upon a cross between *N. Forgetiana* and *N. alata.* The segregating generations naturally contained numerous individuals heterozygous for a large number of hereditary factors. There were differences in height of plant, size of leaf, color of flower, and size of flower, differences which could hardly be interpreted as the result of less than twenty or thirty determiners unless a great many of the variations shown in different organs were due to the activity of a single gene. Similar hereditary differences were marked even in the so-called pure species. This being true, it is important to know whether pollen tubes whose nuclei carry certain determiners grow faster than those which carry other determiners.

POLLEN-TUBE FREQUENCY DISTRIBUTIONS

One method which throws some light on the probability of selective fertilization is that of studying the frequency distribution of the pollen tubes after pollination. When applications of pollen are made, and the pistils prepared, sectioned and stained at varying periods of time after pollination, similar results are obtained no matter what the type of combination has been. In table 1, for example, a few frequency distributions of pollen-tubes after self-pollinating self-sterile plants during the height of the flowering season, are given. In general they are minus skew, and show that the greater number of pollen tubes are grouped at points from 3.5 mm to 7.5 mm from the end of the stigma at the expiration of from 5 to 7 days after pollination. A number of tubes have pushed out ahead of the majority, and a great many pollen grains—from 5 to 25 percent—have not germinated at all.

Distribution of pollen tubes in sections of pistils from self-sterile plants which had been pollinated at the end of the flowering season, show practically the same thing (table 2). The pollen tubes have reached distances comparable to those shown in table 1 in a shorter period of time, but otherwise no marked difference can be seen.

These two tables are presented merely for comparison with tables 3 and 4.

TABLE 1

Frequency distribution of pollen tubes after self-pollinating self-sterile plants during the height of the flowering season.

Source of data	Distance from the stigma in millimeters													
	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5
1 section after 5 days......	2	20	25	20	14	6	5	2						
1 section after 6 days......		1	43	30	30	20	13	7	7	5	2	2	1	
1 section after 6 days......	2	2	50	41	40	16	17	6	5	2	3	1	1	
1 section after 7 days......					4	20	24	18	9	7	2	2	1	
1 section after 7 days......			1	6	20	25	21	16	16	8	6	2	1	1

TABLE 2

Frequency distribution of pollen tubes after self-pollinating self-sterile plants at the end of the flowering season

Source of data	Distance from the stigma in millimeters													
	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5
1 section after 3 days......	3	3	20	30	16	6	2	1	1	1				
1 section after 3 days......		6	30	21	20	18	6	2	2	1				
1 section after 4 days......		1	6	20	28	16	8	4	5	2	1			
1 section after 4 days......			2	6	18	25	26	24	20	16	8	2	1	
1 section after 4 days......						2	18	20	18	8	6	4	3	1

In table 3 some distributions of pollen tubes from the F_2 generation of a cross between *N. Forgetiana* and *N. alata* are given. The cross is compatible, and since the individuals are unquestionably heterozygous in a large number of factors, they should show a marked tendency to vary if there is selective fertilization. The frequency distributions shown in table 4, on the other hand, where *sib* matings for three generations ought

TABLE 3

Frequency distribution of pollen tubes after cross-pollinating compatible plants of F_2 generation N. Forgetiana × N. alata.

Source of data	Distance from the stigma in millimeters											
	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5
1 section after 2 days......	3	16	26	28	24	21	16	12	8	2	1	1
1 section after 2 days......	6	20	21	16	8	3	1					
1 section after 2 days......			1	16	20	18	16	8	3	3	1	
1 section after 3 days......				1	16	15	14	8	4	2	2	2
1 section after 3 days......			1	6	40	28	20	16	3	1	1	

TABLE 4

Frequency distribution of pollen tubes after cross-pollinating compatible plants of F_5 generation (sib matings) N. Forgetiana × N. alata

Source of data	Distance from the stigma in millimeters											
	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5
1 section after 2 days......		6	18	24	20	18	7	2	4	2		
1 section after 2 days......			2	36	30	20	18	7	6	5		1
1 section after 3 days......			1	16	26	21	17	5	5	2	1	
1 section after 3 days......				2	24	21	18	3	8	1	2	
1 section after 3 days......					1	16	26	21	20	14	10	4

to have brought about a considerable degree of homozygosis, should be less variable. As a matter of fact, however, there seems to be no significant difference in the two cases.

There is no evidence that variability in gametic constitution is the cause of variability in rate of pollen-tube growth. In fact, there is no positive proof that there is a measurable variability in pollen-tube growth.

In both of these types of pollination and in all similar cases examined, percentages of ungerminated pollen grains comparable to those determined for incompatible matings were found. The actual percentages have little meaning, for ungerminated pollen grains are loosely held by the stigmas and the correct number of grains which do not germinate is not likely to be obtained. But the fact that a considerable percentage of grains which contain protoplasm and in every respect seem to be normal, remain as long as 6 days without germinating, leads one to believe that difference in the rate of germination is largely responsible for the varied length of the pollen tubes measured. The pollen grains may differ among themselves in the thickness of their walls or the composition of the protoplasm outside the nuclei, thus accounting in some measure for rapidity of germination, without it being necessary to assume gametic differentiation as a cause. Furthermore the entire series of results on the behavior of self-sterile plants reported in the first paper of this series (EAST and PARK 1917), makes it unlikely that differences in gametic composition show themselves in any way *before fertilization.* The factorial composition of the mother plant controls the behavior of self-sterile plants, and all the pollen grains of a single plant may be taken to have the same factorial composition as far as any functions to be performed *before* fertilization are concerned.

It is not to be supposed that the variability in length of pollen tube shown in tables 3 and 4 really represents the difference of time at fertilization. In compatible matings the pollen tubes grow faster and faster so that the variability shown in a frequency distribution of pollen tubes determined at 1 day or 2 days after pollination may be quite different at a later date. It has not been found possible to obtain satisfactory measurements of pollen tubes as they approach the micropyles, but it may be assumed that at this time the rate of growth is so fast that practically all of the ovules are fertilized within a few hours. Selective fertilization is hardly probable therefore for this additional reason.

INFLUENCE OF THE GROWTH OF COMPATIBLE POLLEN TUBES UPON INCOMPATIBLE POLLEN TUBES

In interpreting the results of our experiments on pollen-tube growth (EAST and PARK 1918), it was assumed that after a compatible cross substances are secreted in the pistil which accelerate the elongation of the tube, and that the immediate cause of this secretion is a catalyser which the pollen-tube nucleus is able to produce because the hereditary constitution of the plant producing it is different from that of the plant on which it is placed. Superficial consideration might lead one to suppose that if this were true, incompatible pollen tubes would be accelerated by the growth of compatible pollen tubes if a mixture of the two kinds of pollen were placed on the stigma. Second thought, however, shows that this is probably not the case. Plant enzymes are colloids having large molecules, hence they do not pass freely through cell membranes. Their actions are largely local; where they do not seem to be local, the direct cause of the reaction is more likely to be a crystalloid produced by action of the colloid.

The writer has been able to devise no experiment to measure absolutely such possible stimulation, but two experiments have shown that when mixtures of compatible and incompatible pollen are applied to a single stigma, only the compatible pollen produces seed.

In the first experiment a number of pistils were pollinated with a definite number of compatible pollen grains. The work was done under a binocular, and the count is thought to be accurate within an experimental error of ±2 grains. The pistils were then carefully covered with incompatible pollen. Eight capsules matured with the results shown in table 5.

TABLE 5

The effect of compatible pollen on the growth of incompatible pollen tubes.

Pistil No.	Number of compatible pollen grains	Number of seeds produced
1	51	46
2	48	42
3	50	41
4	62	49
5	32	23
6	67	58
7	61	54
8	46	40

The indications from this experiment are that no incompatible pollen tubes contributed to the production of the seeds obtained; but of course it is impossible to maintain that these tubes were not accelerated in their growth to some degree.

In the second experiment, a more critical test of the matter was made. Three pistils of a white-flowered self-sterile plant coming from a line of plants homozygous for this color were selfed. Five or six hours after these plants were covered with pollen from a self-sterile family bearing red flowers. Capsules full of seed were obtained. If these seeds were produced by the compatible pollen only, the resulting progeny should be red-flowered for red is dominant; if incompatible pollen has functioned, white-flowered plants should be obtained. Three hundred plants have been grown with *not a single* white-flowered individual.

SUMMARY AND DISCUSSION

The experiments described in this paper were designed to test the possibility of selective fertilization occurring in self-sterile Nicotianas, it being assumed that from the nature of the material the phenomenon might here be possible. (1) Comparisons were made between the pollen-tube frequency distributions of highly heterozygous and of comparatively homozygous plants. (2) The influence of compatible matings on incompatible matings was investigated. In neither case was there any indication of selective fertilization.

Though it is impossible to prove a negative, there is so much circumstantial evidence against selection both in the formation of gametes and zygotes, the probability that it ever occurs is very remote. In the first place gametes are formed in many animals and plants, particularly in species crosses, which can never function. If the mechanism of gamete formation were such as to make it necessary to assume a selection of genes, a low frequency of non-functional gametes would be expected. Similarly zygotes are produced in the numbers to be expected by chance mating of gametes, even though these zygotes have no possibility of passing through a complete life cycle. There are two cases in mice, eight in Drosophila, and four in plants where the evidence of lethal factors is too complete to be disregarded. In reality there are probably hundreds of such instances in plants and animals which have been investigated during recent years that ought to be interpreted in the same manner.

Again, pollen grains show no tendency to behave as if the genes which they carry function before fertilization. It will be recalled that BATESON (1909) found pollen shape and color in the sweet pea to be inherited as a maternal character. The writer (EAST 1916) has corroborated this discovery for color of Nicotiana pollen. It may be claimed, however, that these facts are just what is to be expected because of the morphogenesis of the outer characters of the pollen grain. This is true; but the criticism does not apply to the phenomena found in the behavior of self-sterile plants in cross matings where cross-sterility of groups of plants exists *presumably because of genes possessed by the mother plants.* In fact the only activity shown by a male gametophyte which seems to be due to the factors it is carrying over into the next generation, is a lack of any activity. In BELLING'S (1914) work on the velvet bean, he found 50 percent of the F_1 pollen was abortive in a certain cross. It appears then that in this instance the presence or absence of a gene of the generation which would ordinarily function after fertilization, has caused the pollen grain to abort. This lack of ability to function does not necessarily mean the actual activity of the genes of this generation however; the machine has simply remained uncompleted, so to speak. For this reason, there seems to be no wisdom in even suspecting selective fertilization; unless mixtures of pollen (or spermatozoa even) from different individuals should be used. If pollen grains from a single plant are alike as far as their activities before fertilization are concerned, there is no basis for selection.

May we not extend this conception to animals for the present and accept as a fundamental genetic hypothesis the tenet of chance segregation in the germ cells and chance mating of these germ cells?

LITERATURE CITED

BATESON, W., 1909 Mendel's principles of heredity. pp. 396. Cambridge, England: Cambridge University Press.
BELLING, J., 1914 The mode of inheritance of semi-sterility in the offspring of certain hybrid plants. Zeitschr. f. ind. Abstamm. u. Vererb. **12**: 303-342.
CASTLE, W. E., 1903 The heredity of sex. Mus. Comp. Zoöl. Bull. **40**: 189-218.
CASTLE, W. E., 1919 Is the arrangement of the genes in the chromosome linear? Proc. Nat. Acad. Sci. **5**: 25-32.
CUÉNOT, L., 1908 Sur quelques anomalies apparentes des proportions Mendéliennes (6^e note). Arch. Zoöl. Exp. et Gén. **9**: 7-15.
EAST, E. M., 1916 Inheritance in crosses between *Nicotiana Langsdorffii* and *Nicotiana alata.* Genetics **1**: 311-333.
EAST, E. M., and PARK, J. B., 1917 Studies on self-sterility. I. The behavior of self-sterile plants. Genetics **2**: 505-609.
1918 Studies on sterility. II. Pollen-tube growth. Genetics **3**: 353-366.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JULY 1919

TABLE OF CONTENTS

STUDIES ON SELF-STERILITY. V. A FAMILY OF SELF-STERILE PLANTS WHOLLY CROSS-STERILE *INTER SE*

E. M. EAST
Bussey Institution, Harvard University, Forest Hills, Massachusetts

Reprinted from GENETICS **4**: 356-363, 1919

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

---

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

STUDIES ON SELF-STERILITY. V. A FAMILY OF SELF-STERILE PLANTS WHOLLY CROSS-STERILE *INTER SE*

E. M. EAST

Bussey Institution, Harvard University, Forest Hills, Massachusetts

Reprinted from GENETICS **4**: 356-363, 1919

STUDIES ON SELF-STERILITY V. A FAMILY OF SELF-STERILE PLANTS WHOLLY CROSS-STERILE *INTER SE*

E. M. EAST
Harvard University, Bussey Institution, Forest Hills, Massachusetts

[Received June 26, 1919]

In the first paper of this series (EAST and PARK 1917),[1] the behavior of a number of families of self-sterile plants under various schemes of mating was described. In one cross between the two species *Nicotiana Forgetiana* and *Nicotiana alata,* fifty-three plants of the F_1 generation could be separated into not less than four groups in which each member of every group was cross-sterile with every other member of that group, although showing cross-fertility with every member of every other group. The interpretation given of these and other similar facts was in brief as follows: (1) a self-sterile species exhibits this peculiarity because homozygous for a basic self-sterility factor; (2) a series of partially coupled factors affects the behavior of sterile plants among themselves; (3) these secondary factors act as if sporophytic in nature, so that all gametes produced by a single individual are identical in this regard with the plant on which they originated; (4) the nature of the action of these secondary factors is such that two plants are not fertile together unless they differ by at least one of these factors.

Though the self-sterility and the cross-sterility existent in these plants is fully expressed at the beginning and height of the flowering season, toward the close of the flowering season, particularly in plants exhibiting the effect of adverse environmental conditions, occasionally some fertility is shown. It is possible therefore to obtain seed from truly self-sterile plants and from combinations that are fundamentally incompatible. By taking advantage of this pseudo-fertility it should be possible to obtain families of plants wholly cross-sterile *inter se*. Such a family, apparently, is family E described on pages 565 to 567 of the paper we are discussing. Unfortunately very little work had been done on this family when that paper was written. Since a reserve supply of the seed

---

[1] EAST, E. M., and PARK, J. B. Studies on self-sterility I. The behavior of self-sterile plants. Genetics **2**: 505-609, 1917.

from which the family came had been preserved, however, it has been possible to make a more extended study of the case.

In table 1 are recorded the infertile crosses made upon 54 plants of

TABLE 1

Record of infertile crosses made on 54 plants of family E(2). Number of pollinations is shown by subscripts.

Ped. No.	Sterile with Ped. No. ♂	Sterile with Ped. No. ♀
1	$3_3, 5_3, 10_3, 50_3, 75$	$44_4, 57_3, 59_3, 61_3, 72_4, 73_3, 74_3$
3	$5_5, 8_3, 14_6, 23_2, 50_3$	$1_3, 5_3, 69_3$
5	$3_3, 9_4, 10_5, 14_3, 16_3, 23_3, 50_3, 74_2$	$1_3, 3_5, 54_3, 55_3, 56_7, 57_3, 59_4, 60_3, 61, 74_7$
8	$9_3, 10_3, 14_3, 16_3, 17_3, 50_6$	3_3
9	$10_3, 14_3, 16_3, 17_3, 23_3, 50_3$	$5_4, 8_3, 61_3$
10	$14_3, 17_3, 44_3, 50_3$	$1_3, 5_5, 8_3, 9_3, 45_3, 58_3, 61_3, 67_3, 68_6$
14	$16_3, 17_3, 19_3, 26_3, 43_3, 50_9, 75_3$	$3_6, 5_3, 8_3, 9_3, 10_3, 50_2, 73_4$
16	$17_2, 19_3, 41_3, 42_3, 44_3, 50_8$	$5_3, 8_3, 9_3, 14_3$
17	$22_3, 23_3, 43_3, 44_3, 50_3, 55_3$	$8_3, 9_3, 10_3, 14_3, 16_2$
19	$23_4, 26_4, 29_3, 50_3, 61_3, 62_3, 69_4, 75_3$	$14_3, 16_3$
22	$26_3, 27_3, 31_4, 50_3, 61_3, 62_3, 69_3$	17_3
23	$26_4, 41_6, 42_6, 44_2, 50_3, 56_3$	$3_2, 5_3, 9_3, 17_3, 19_4, 53_3, 54_4, 56_8, 63_3, 64_3, 66_6, 72_3, 73_3$
26	$31_4, 35_4, 38_3, 50_3, 61_3, 62_3$	$14_3, 19_4, 22_3, 23_4, 42_3, 44_3, 49_3, 55_3$
27	$29_3, 35_3, 50_3, 61_4, 62_3, 75_3$	22_3
29	$31_3, 33_3, 38_3, 50_3\ 61_4, 62_3, 68_3$	$19_3, 27_3, 75_4$
31	$33_3, 35_4, 38_3, 50_3, 61_4, 62_3, 73_3$	$22_4, 26_4, 29_3, 42_3, 43_3, 75_3$
33	$35_3, 38_6, 39_7, 40_7, 41_7, 50_3$	$29_3, 31_3, 38_4, 75_3$
35	$38_3, 39_3, 40_4, 42_3, 50_3, 61_3, 69_3, 75_3$	$26_4, 27_3, 31_4, 33_3, 68_3, 70_3, 71_3, 73_3$
38	$33_4, 39_3, 40_4, 42_3, 44_3, 50_4, 61,_3, 62_4, 73_4$	$26_3, 29_3, 31_3, 33_3, 33_6, 35_3, 52_3, 75_3$
39	$40_4, 42_3, 43_3, 50_7, 60_3, 61_3, 62_3, 75_4$	$33_7, 35_3, 38_3, 44_3, 49_3, 50_3, 52_3, 63_3, 64_3$
40	$42_3, 44_4, 45_3, 50_3, 52_4, 61_4, 62_3, 63_4$	$33_7, 35_4, 38_4, 39_4$

TABLE 1 (continued)

Record of infertile crosses made on 54 plants of family E (2). Number of pollinations is shown by subscripts.

Ped. No	Sterile with Ped. No. ♂	Sterile with Ped No. ♀
41	$44_3, 46_3, 52_3, 53_3, 54_3, 74_3$	$16_3, 23_6, 33_7, 43_3$
42	$26_3, 31_3, 44_3, 50_3, 75_3$	$16_3, 23_6, 35_3, 38_3, 39_3, 40_3, 43_4$
43	$31_3, 41_3, 44_3, 50_3, 59_6$	$14_3, 17_3, 39_3, 61_4$
44	$1_4, 26_3, 39_3, 46_3, 49_3, 50_6, 52_5, 53_3, 54_4$	$10_3, 16_3, 17_3, 23_2, 38_3, 40_4, 41_3, 42_3, 43_3, 45_3, 50_{13}, 52_3$
45	$10_3, 44_3, 46_3, 50_3, 61_4$	$40_3, 49_3$
46		$41_3, 44_3, 45_3$
49	$26_3, 39_3, 45_3, 50_4, 51_3, 62_3$	44_3
50	$14_2, 39_3, 44_{13}, 52_3, 53_4$ $54_3, 56_3$	$1_3, 3_3, 5_3, 8_6, 9_3, 10_3, 14_9, 16_8, 17_3, 19_3, 22_3, 23_3, 26_3, 27_3, 29_3, 31_3, 33_3, 35_3, 38_4, 39_7, 40_3, 42_3, 43_3, 44_6, 45_3, 49_4, 52_3, 53_3, 54_6, 55_3, 56_3, 57_4, 58_3, 59_3, 60_3, 61_3, 63_3, 64_3, 65_3, 66_3, 67_3, 68_3, 69_3, 70_3, 71_3, 72_3, 74_3, 75_3$
51		49_3
52	$38_3, 39_3, 44_3, 50_3, 53_4, 54_5, 55_4, 56_3, 57_3, 58_3, 59_3, 68_4$	$40_4, 41_3, 44_5, 50_3$
53	$23_3, 50_3, 54_4, 55_3, 56_3, 57_3, 58_4, 62_3, 64_3$	$41_3, 44_3, 50_4, 52_4$
54	$5_3, 23_4, 50_6, 55_3, 56_4, 57_3, 58_3, 64_5$	$41_3, 44_4, 50_3, 52_5, 53_4$
55	$5_3, 26_3, 50_3, 56_3, 57_3, 58_4, 59_3, 62_4$	$17_3, 52_4, 53_3, 54_3$
56	$5_7, 23_8, 50_3, 57_3, 58_3, 59_3, 60_3, 61_3, 63_4, 64_2$	$23_3, 50_3, 52_3, 53_3, 54_4, 55_3$
57	$1_3, 5_3, 50_4, 58_3, 59_4, 60_3, 61_3, 69_4$	$52_3, 53_3, 54_3, 55_3, 56_3$
58	$10_3, 50_3, 59_3, 60_5, 61_3, 65_4, 73_3, 74_4$	$52_3, 53_4, 54_3, 55_4, 56_3, 57_3$
59	$1_3, 5_4, 50_3, 60_3, 61_3, 71_3, 73_3, 75_3$	$43_6, 52_3, 55_3, 56_3, 57_4, 58_3$
60	$5_3, 50_3, 61_3, 69_3, 71_3, 75_4$	$39_3, 56_3, 57_3, 58_5, 59_3$
61	1_3, 5, $9_3, 10_3, 43_4, 50_3, 69_3, 71_4$	$19_3, 22_3, 26_3, 27_4, 29_4, 31_4, 35_3, 38_3, 39_3, 40_4, 45_4, 56_3, 57_3, 58_3, 59_3, 60_3, 63_3, 64_3, 65_3, 66_3, 74_3, 75_4$
62		$19_3, 22_3, 26_3, 27_3, 29_3, 31_3, 38_4, 39_3, 40_3, 49_3, 53_3, 55_4, 63_3, 64_3, 69_3, 71_4, 72_3, 73_3, 75_4$

TABLE 1 (continued)

Record of infertile crosses made on 54 plants of family E (2). Number of pollinations is shown by subscripts.

Ped. No	Sterile with Ped. No. ♂	Sterile with Ped No. ♀
63	$23_3, 39_3, 50_3, 61_3, 62_3, 64_3, 65_3, 74_3, 75_3$	$40_4, 56_4, 73_3, 74_4$
64	$23_3, 39_3, 50_3, 61_3, 62_3, 67_3, 68_3, 73_4, 75_3$	$53_3, 54_5, 56_2, 63_3, 65_3, 66_3, 69_3, 70_3, 71_4, 73_3$
65	$1_3, 50_3, 61_3, 64_3, 68_3, 69_3, 70_2$	$58_4, 63_3$
66	$23_6, 50_3, 61_3, 64_3, 71_3, 73_3, 74_4$	$67_2, 68_3$
67	$10_3, 50_3, 67_2, 69_3, 70_3, 71_3$	64_3
68	$10_6, 35_3, 50_3, 66_3, 69_3, 70_3$	$29_3, 52_4, 64_3, 65_3, 69_3$
69	$3_3, 50_3, 62_3, 64_3, 68_3, 73_3, 74_3, 75_3$	$19_4, 22_3, 35_3, 57_4, 60_3, 61_3, 65_3, 67_3, 68_3, 70_4, 71_6, 75_3$
70	$35_3, 50_3, 64_3, 69_4, 71_3, 72_3, 73_4, 74_3$	$65_2, 67_3, 68_3$
71	$35_3, 50_3, 62_4, 64_4, 69_6, 72_3, 73_3, 74_3$	$59_3, 60_3, 61_4, 66_3, 67_3, 70_3, 72_4$
72	$1_4, 23_3, 50_3, 62_3, 71_4, 73_3, 74_6$	$70_3, 71_3, 73_4$
73	$1_3, 14_4, 23_3, 35_3, 62_3, 63_3, 64_3, 72_4$	$31_3, 38_4, 58_3, 59_3, 64_4, 66_3, 69_3, 70_4, 71_3, 72_3, 74_4$
74	$1_3, 5_7, 50_3, 61_3, 63_4, 73_4, 75_3$	$5_2, 41_3, 58_4, 63_3, 66_4, 69_3, 70_3, 71_3, 72_6$
75	$29_4, 31_3, 33_3, 38_3, 50_3, 61_4, 62_4, 69_3$	$1, 14_3, 19_3, 27_3, 35_3, 39_4, 42_3, 59_3, 60_4, 63_3, 64_3, 69_3, 74_3$

this family, the subscripts showing the number of attempts made for each combination. The table was constructed by assuming that if a combination had been made one way, the reciprocal had also been made, as explained in our former study (EAST and PARK 1917). Thus it can be seen that while only a fraction of the possible combinations were made, nevertheless the plants were linked together in an unbroken chain. In other words, if it be true that when A is sterile with B and with C, B is sterile with C, then each of these 54 plants is sterile with the other.

It is not true however that no seed at all was obtained in the numerous attempts to combine plants of this family. Table 2 shows that 13 combinations produced capsules. From the number of sterile pollinations made with the same plants and from the fact that nearly all of the fertility appeared at the end of the flowering season, it would seem that

TABLE 2

Record of fertile crosses made on 54 plants of family E (2),—presumably pseudo-fertility. First number is female.

Combination	Number of fertile pollinations	Number of sterile pollinations	Number of sterile reciprocal pollinations
3 × 5	1	5	3
5 × 10	1	5	–
5 × 74	1	2	See 74 × 5
16 × 50	1	8	–
17 × 22	1	3	–
23 × 44	1	2	–
33 × 38	2	6	4
39 × 50	4	7	3
44 × 50	1	6	See 50 × 44
44 × 52	1	5	3
50 × 44	1	13	See 44 × 50
56 × 23	1	8	3
74 × 5	1	7	See 5 × 74

these apparent exceptions are all illustrations of fluctuating pseudo-fertility. There is the whole of our experience with this type of fertility back of such an assertion, but there is also some specific evidence on the case in point.

The number of seeds produced by these plants when crossed with compatible pollen is in general from 300 to 600 per capsule (table 3), while the number of seeds in the presumably pseudo-fertile combinations is usually much less. At the same time 4 of the latter combinations produced what seemed to be full capsules. Combination 16×50 produced a full capsule at the seventh attempt, although eight out of nine attempts were failures, and combination 50 × 44 produced a full capsule at the twelfth attempt although thirteen out of fourteen attempts were failures. On the other hand plant 23 gave a full capsule with pollen of plant 44 on the first attempt, plant 33 gave two capsules out of eight attempts with pollen of plant 38, and plant 39 gave four capsules out of eleven attempts with pollen of plant 50. Now combination 33 × 38 was about 50 percent fertile, and combination 39 × 50 became progressively more fertile as shown by the number of seeds produced. These three plants, 23, 39, and 50 were crossed with a large number of other plants, nevertheless, and showed cross-sterility. Further, at the beginning of another flowering season crosses 23 × 44 and 39 × 50 were impossible. At the same time it is not without the bounds of probability that combination 39 × 50

TABLE 3

Comparison of the number of seeds in capsules of the presumably pseudo-fertile combinations in family E(2) with the number of seeds in the capsules of the same plants when pollinated with pollen from the plant of the F_2 generation of the cross between N. Forgetiana and N. Langsdorffii.

Combination	Number of seeds in capsules	Number of seeds in capsules when pollinated with (314 × 328)
3 × 5	28	
5 × 10	115	365, 382, 421
5 × 74	127	365, 382, 421
16 × 50	418	
17 × 22	27	370
23 × 44	436	
33 × 38	124, 131	
39 × 50	151, 255, 289, 352	
44 × 50	128	
44 × 52	191	
50 × 44	427	
56 × 23	82	
74 × 5	185	

was for some unknown reason more easy to make than other combinations in this family. We have no theory to offer at present as to why this may be true. It may stand as an open question. The general conclusion from all the evidence is that family E (2) may be considered to consist of plants wholly cross-sterile *inter se.*

The question then arises: Is the origin of family E (2) compatible with our previous conclusions as to the behavior of self-sterile plants when crossed *inter se.* First, it must be emphasized that the cross-sterility found has nothing to do with true sterility. A random sample of 25 plants was used in a test with the pollen a single plant coming from the F_2 generation of a cross between *Nicotiana Forgetiana* and *Nicotiana Langsdorffii.* Out of 64 pollinations there were only 2 failures (table 4). Again, out of 51 attempts to use the pollen of these plants in crosses thought to be compatible, there was only 1 failure. The sterility found, therefore, is wholly of the nature termed "self-sterility," or "incompatibility," and must be interpreted as such.

The origin of a family consisting of one class of plants cross-sterile with each other was to have been predicted on the basis of the interpre-

TABLE 4

Record of pollinations made on a random sample of 25 plants of family E(2) with pollen from a single self-sterile plant of the F_2 generation of a cross between Nicotiana Forgetiana and Nicotiana Langsdorffii (814 × 328).

Plant No.	Successful pollinations	Unsuccessful pollinations	Number of seeds in each mature capsule
5	3	0	365, 382, 421
6	3	0	360, 330, 515
9	4	1	390, 500, 400, 370
10	1	0	631
17	1	0	370
22	3	0	358, 405, 230
25	1	0	377
26	2	0	630, 425
31	3	0	481, 404, 470
36	5	0	453, 350, 405, 372, 340
38	2	0	432, 192
40	3	0	271, 195, 317
46	1	1	185
51	4	0	225, 252, 382, 384
53	1	0	157
54	2	0	420, 177
57	4	0	295, 650, 250, 462
58	3	0	700, 618, 902
59	1	0	327
60	1	0	330
61	5	0	635, 588, 580, 468, 678
64	3	0	338, 230, 376
70	2	0	230, 176
71	2	0	480, 240
73	2	0	291, 358
Total	62	2	

tations we have used, by taking advantage of the phenomenon of pseudo self-fertility. Continued self-fertilization is possible by persistent efforts at self-pollination carried to the very end of the flowering season. And continued self-fertilization should bring about homozygosis in the secondary factors affecting the behavior of self-sterile plants among themselves. When such a point is reached, the resulting population should not only be self-sterile but should belong to a single class all members of which are cross-sterile with each other.

Family E (2) was not the result of continued self-pollination and pseudo self-fertility, however. It was produced as follows: The female parent was No. 58, a plant of *N. alata,* the result of three generations of selfing a self-sterile strain *at the end of the season.* The behavior of No. 58 and of its sister plants when crossed with each other leads one to believe they were all members of one intra-sterile class, but the evidence is hardly sufficient to establish the point. The male parent was a member of the F_1 population (plant 44, *loc. cit.,* p. 559) produced by crossing a self-sterile plant of *N. Forgetiana* with a sister plant of the mother of the *N. alata* plant just described (No. 58).

Now it is obvious that the female parent of this family may have come from a fraternity homozygous for the secondary factors effective on compatibility *inter se.* They may have been, for example, plants with the composition *AABB.* It is possible also that the male parent, though originating from a cross, might have had the formula *AABB,* since its parents might have been *AABB* and *AaBB.* But a whole population having a single formula could not have arisen through a cross except through an illegitimate mating (pseudo-fertility). If then the two parents of the population had the same constitution and produced seed through pseudo-fertility, then family D (*loc. cit.,* p. 563), coming from the same male crossed on a sister of plant 58, ought to be a duplicate of family E (2). This however does not appear to be the case. Family D consisted of at least two intra-sterile classes, unless a good deal of unrecognized pseudo-sterility was present. On the other hand both of the parents, in the few tests made on family E (2), were sterile with their progeny,—a result to be expected on the theory of homozygosis. It seems, then, that the unsettled question, a question which must await further investigation, is, why family D and family E (2) are not similar in composition and behavior.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JULY 1919

TABLE OF CONTENTS

[Reprinted from THE AMERICAN NATURALIST, Vol. LII., June–July, 1918.]

THE RÔLE OF REPRODUCTION IN EVOLUTION[1]

PROFESSOR E. M. EAST

BUSSEY INSTITUTION, HARVARD UNIVERSITY

THE establishment of methods of reproduction which maintain variation and inheritance mechanisms on a high plane of efficiency is naturally a fundamental requirement in organic evolution. Since, however, inheritance mechanisms presumably equivalent are common to every method of reproduction, one should be able to interpret the evolutionary tendencies in the matter by comparing their effectiveness in offering selective agencies their raw material. Some will hold this statement to be a self-evident truth; others may maintain as strongly either that the premises are wrong or that the conclusion is not justified even if the premises be granted. Perhaps it is safer to ply the middle course; if the case is not so obvious as a Euclidian axiom, as a compensation rigorous proof may be less difficult.

As a basis for argument, let us sketch the general trend of reproductive evolution in plants and animals.

Ordinarily, one speaks of two types of reproduction among organisms, asexual and sexual. This is a convention that has taken on the dignity of a "folkway" among biologists. Its employment should imply assent to the proposition that the varied forms in which each of these classes presents itself are inherently equivalent, and that

---

[1] Read by title at the Symposium of the American Society of Naturalists on the subject "Factors of Organic Evolution," Jan. 5, 1918.

the groups considered as units are fundamentally distinct, but it is doubtful whether any such implication would be admitted by the majority of its users. In fact one could hardly maintain that simple division, sporification, the production of gemmules, true budding, fragmentation with regeneration of parts, and the various kinds of apogamy and parthenogenesis on the one hand, and all nuclear fusions on the other, can be grouped together as if they are of the same evolutionary value, if this term be used in any narrow or special sense; but from a broader viewpoint, the conventional classification has a real and deep meaning which perhaps the biologist has grasped instinctively.

There are both asexual and sexual methods of reproduction in nearly all groups of animals and plants; among animals the second has almost supplanted the first, among plants the two have continued side by side. In neither kingdom was sex developed as a more rapid means of multiplication, since, as Maupas showed, a single infusorian may become the progenitor of some 50,000 individuals during the time necessary for one pair to conjugate. Some other requirement was fulfilled; and fulfilled adequately if we may judge by the number of times sexual differentiation arose and the tenacity with which it was retained.

Just when sexual reproduction first originated in the vegetable kingdom is still a question. Among the lower forms only the schizophytes, flagellates and myxomycetes have passed it by. Perhaps it is for this reason that these forms have remained the submerged tenth of the plant world. It is tempting, as Coulter (1914) says, to see sex origin in the Green Algæ. There, in certain species, of which *Ulothrix* is a good example, spores of different sizes are produced. Those largest in size germinate immediately under favorable conditions and produce new individuals. Those smaller in size also germinate and produce new individuals, but these are small and their growth slow. Only the smallest are incapable of carrying on their vegetative functions. These come together in pairs. Two individuals become one as a prerequisite to renewed vigor. Vegetative spores become gametes. Something valuable—speed of multiplication—is given up for a time that something more valuable in the general scheme of evolution may be attained.

This is indeed an alluring genesis of sex. Let us use the indefinite article, however; no doubt it is *a* genesis of sex, but it can hardly be *the* genesis of sex. Various manifestations of sex are present in other widely separated groups of unicellular plants, the Peridineæ, the Conjugatæ and the Diotomeæ—the Conjugatæ being indeed the only great group of plants in which there is no asexual reproduction. In these forms one can not make out such a good case of actual gametic origin, but the circumstantial evidence of sex development in parallel lines is witness of its paramount importance.

After the origin of sex, many changes in reproductive mechanisms occurred in plants, but almost all of them resulted merely in greater protection of the gametes, in increased assurance of fertilization, or in provision for better distribution. First there was a visible morphological differentiation of gametes, the one becoming a large inactive cell stored with food, the other becoming small and mobile. Then came the evolution of various sex organs, and finally the alternation of generations. In the higher plants a long line of changes have occurred connected with the alternation of generations; the spore-producing type has developed from a form of little importance to that which dominates the vegetable world, the gamete-producing type has degenerated until it consists of but two or three cell divisions. In these variations there is reproductive insurance, something which also may be said of those manifold adaptations which provide zygotic protection either in the seed or the adult plant, but they are no more direct changes in reproductive mechanism than are the diverse means which arose to secure dispersal. In fact in all of these changes no new process of fundamental evolutionary significance occurred, unless it be the various mechanisms devised to promote or to insure cross-fertilization, and which may be interpreted as variations tending to perfect sexuality.

Coincident with the general trend of plant evolution just mentioned, two important changes in the nature of retrogressions occurred, which have persisted in many species. A new type of asexual propagation arose, apogamy, which though it appeared under several guises, apogamy in the narrow sense, parthenogenesis and polyembryony, is none the less asexual reproduction returned under another name and apparently with no particular advantages over the older types. Further, hermaphroditism was developed and has persisted in numerous lines. We may be wrong in calling hermaphroditism a retrogression, for it has the great advantage of a certain economy of effort in the production of gametes, but nevertheless it is certainly a change which *per se* is in the opposite direction from that established when sex was first evolved. A moment of consideration not only makes this clear, but gives us a pretty satisfactory proof that the gain made when continuous multiplication was halted for a time by the intervention of a fusion at the genesis of sexual reproduction was in some way connected with the mixture of dissimilar germplasms. This conclusion is hardly avoidable from the fact that although hermaphroditism retained the cell fusion mechanism of gonochorism it was still necessary for Nature to evolve means for cross-fertilization. And the multitude of ways in which she solved this problem must mean that an immense advantage was secured.

In spite of the great morphological differences between animals and plants, the essential evolutionary changes affecting reproduction in the two kingdoms have been so similar as to be almost uncanny. Accepting the division of animals into twelve phyla as recognized by many modern zoologists (Parker and Haswell), one finds the following facts regarding reproduction. Asexual reproduction in the narrow sense is common in Protozoa, Porifera, Cœlenterata and Platyhelminthes, and is sporadic in Molluscoida, Annulata, Arthropoda and Chordata. If fragmentation and regeneration be included, Echinodermata and possibly Nemathelminthes are added. If parthenogenesis is included, Trochelminthes is admitted. Thus only the Mollusca have no form of asexual reproduction, and zoologists would hardly feel safe in maintaining its absence there since the life history of so many forms is unknown. This being the case, one must admit that asexual reproduction has been found satisfactory for most of the great groups of animals as far as actual multiplication is concerned. For other reasons, however, it evidently did not fulfill all requirements, since sexual reproduction is established in every phylum. Further, omitting the Protozoa in which it is difficult to decide such sexual differences, gonochorism is present everywhere except in the Porifera, and hermaphroditism everywhere except in the Trochelminthes, although in Nemathelminthes, Echinodermata and Arthropoda it is rare.

Now if our conclusions regarding the true rôle played by sex in evolution are correct, hermaphroditism is a secondary and not a primitive phenomenon. In this we follow Delage, Montgomery and Caullery rather than the majority of zoologists. We believe it to be the only logical view in spite of the fact that the Porifera, usually considered so unspecialized, are all hermaphroditic. Perhaps the Porifera are farther along in specialization than is admitted, for to find the substance nearest chemically to the so-called skeleton of the sponges one must turn to the arthropods (the product of the spinning glands of certain insects). Hermaphroditism, therefore, as in plants, is from this viewpoint a regression. And as in plants it was not found adequate. In giving up diecism for monecism, something was lost, and this something had to be regained by further specialization. Hence, even as in the vegetable kingdom one finds the essential feature of bisexuality, mechanisms providing for mixtures of different germplasms, restored by means of protandry, protogyny or self-sterility.

In even such a brief consideration of the more important changes which have occurred in the reproductive mechanisms of animals and plants, one thing stands out impressively. Both animals and plants have adopted as the most acceptable and satisfactory modes of reproduction, methods which are identical in what we deem to be the essential features, something that can be said of no other life process. These significant features are the preparation of cells which in general contain but half of the nuclear material possessed by the cells from which they arise, which are differentiated into two general classes that show attraction toward each other, and which will fuse together in pairs to form the starting point of a new organism. This parallel evolution is of itself valid evidence of the importance of the process. Let us return to our original proposition for its interpretation.

First, is there any evidence that sexual reproduction differs from asexual reproduction in what may be called the heredity coefficient? In other words, does one method hold any advantage over the other as an actual means for the transmission of characters? I have answered this question in the negative, but it must be confessed that the basis for this answer is a long and intimate experience in handling pedigree cultures of plants rather than the study of a large amount of quantitative data bearing directly on the problem. Quantitative data are to be found, of course, and plants furnish the best material because of the ease in handling large numbers of both clons and seedlings side by side; but even with the best of plant material, several undesired variables are present. Practically the inquiry must take the form of a comparison between the variability of a homozygous race when propagated by seeds and when propagated by some asexual method. The first difficulty is that of obtaining a homozygous race and thus eliminating Mendelian recombination. The traditionally greater variability of seed-propagated strains is due wholly to this difficulty, I believe. It may be impossible to obtain a race homozygous in all factors. There may be a physiological limit to homozygosis even in hermaphroditic plants. The best one can do is to use a species which is naturally self-fertilized, relying on continued self-fertilization for the elimination of all the heterozygous characters possible. I have examined many populations of this character in the genus *Nicotiana* and have been astounded at the extremely narrow variability they exhibit. Even though one can not grow each member of such a population under identical conditions as to nutrition, the plants impress one as if each had been cut out with the same die. Qualitative characters such as color show no greater variation, as far as human vision may determine, than descendants of the same mother plant propagated by cuttings. Further, in certain characters affected but slightly by external conditions, such as flower size, the sexually produced population not only shows no greater variability than the asexually produced population, but it shows no more than is displayed by a single plant. Yet one must remember that in such a test the seeds necessarily contain but a small quantity of nutrients, and for this reason the individual plants are produced under somewhat more varied conditions than those resulting from cuttings, hence it would not have been unreasonable to have predicted a slightly greater variability for the sexually produced population even though the coefficient of heredity of both were the same.

I have made similar though less systematic observations on wheat—an autogamous plant almost as satisfactory for such a test as *Nicotiana*—with practically identical results. I do not know of any published data on the subject, however, taken either from these or any other plants. In fact, there are few other plants from which data could be obtained with so little likelihood of experimental error.

On the other hand, zoology has furnished a considerable amount of such evidence (*cf.* Casteel and Phillips, 1903; Kellogg, 1906; Wright, Lee and Pearson, 1907). One need only mention Kellogg's work on bees as a type. Kellogg assumed that if amphimixis were the principal cause of the continuous variations postulated by Darwin and Weismann as the most important source of material for the use of the natural selection,[2] parthenogenetically produced individuals should be less variable than those produced sexually. A statistical investigation showed, however, that the characters of drones probably are more variable than those of worker bees of the same race. Since Kellogg believes Darwin's judgment that "males vary more than females" to have been disapproved, he concludes that "amphimixis is not only not necessary in order to insure Darwinian variation, but there is no evidence (that I am aware of) to show that it increases variation."

It is hardly necessary to point out here the numerous mathematical and biological pitfalls which should be considered before one could accept as valid the statistical differences that appear to exist when coefficients of variation based on such data are examined. It should suffice to note that the researches of Wright, Lee and Pearson (1907) on wasps of the species *Vespa vulgaris* showed just as great a difference in variability between workers and drones in favor of the former. Apparently, the statistics in these two nearly related groups lead to opposite conclusions; in reality probably neither statistical difference is significant as far as the question we are discussing is concerned. The only conclusion justified by such data would seem to be that the coefficient of heredity is as high in the production of asexual as it is in the production of sexual forms.

Moreover, one can not expect anything more definite from this method of attack. Biologists may differ as to

---

[2] It should be noted here that all parthenogenetic eggs are not mere spores. Some preparation often occurs through the emission of one polar body. This may be merely a kind of recapitulation, a vestigial process no longer having any significance whatever, but since we are not certain it seems to the writer that the evidence from plants at present must be regarded as stronger.

the definition of fluctuation, mutation, etc., but they are generally agreed that germinal variations, be they great or small, are in most species so rare they can not be gauged by the use of ordinary statistical methods. For this reason, a comparison between the variability of the drones and of the workers of a pure race of bees is not likely to show any difference between these two modes of reproduction in the matter of the frequency or the type of the germinal variation produced, and can not answer the question as to whether sexual reproduction contributes more material for the use of natural selection than asexual reproduction. A study of variability in crossed races, where the effect of Mendelian recombination can be considered, would be a more logical attack upon the second problem, but is hardly necessary in view of the other evidence available.

One is then justified in claiming there is no experimental evidence to show that sexual reproduction in itself is not an exact equivalent of asexual reproduction in the matter of a heredity coefficient, but is this also true for germinal variation? We believe it is. Variations there are in both asexual and sexual reproduction, but it can not be maintained that they occur more frequently in the latter. There are insects in Oligocene amber apparently identical with those of to-day, proving that constancy of type is possible through long periods of time under sexual reproduction; yet germinal variations occur to-day in somewhat noteworthy numbers, as Morgan's work on *Drosophila* shows, although the proportion of these variations which show possibilities of having an evolutionary value, as evidenced by persistence in natural types, is probably small. On the other hand, the number of variations produced under the dominance of asexual reproduction can not be said to be less numerous, even among organisms of a relatively high specialization. If there are those who doubt this statement, let them refer to the immense list of bud-variations in the higher plants compiled by Cramer (1907).

There would be little reason in pushing the claims further, since even though there does not seem to be a sufficient difference between sexual and asexual reproduction in the matter of variation frequency to make it a subject of experimental proof, certain theoretical points raise the suspicion that there is such a difference. All we would maintain is that to account for the general persistence of sexual reproduction by such a cause, the difference in its favor should be so great that it could easily be determined experimentally. Since this is not true, we believe the hypothesis should be discarded.

The points of theory referred to are these. It will be allowed by all that there is some considerable evidence of the chromosomes being the most important conservators of hereditary factors—the physical bases of heredity in whatever form they may be. If it is assumed then that changes in constitution in these cell organoids are followed by changes in type, and that such changes in constitution are equally probable in all chromosomes, it follows that parthenogenetic individuals having the haploid number of chromosomes should show a larger proportion of germinal variations than members of the same species having the diploid number of chromosomes, because variations of all kinds should be recognizable in the former case, while in the latter, recessive variations could not be detected until the first or second filial generation, and then only when the proper mating was made. There is some evidence that this reasoning is not wholly improbable. But variations occur much more frequently in heterozygotes than in homozygotes. To me this simply means that bud-variations *are detected* more frequently in heterozygotes than in homozygotes: and an interpretation is not hard to find. Retrogressive variations are much more frequent than progressive variations, and a retrogressive variation in a particular character shows only when the organism is heterozygous for that character. If a retrogressive bud-variation arises in a homozygote and gametes are afterwards developed from the sporting branch it is not at all unlikely that the variation may show in the next generation, but it will be attributed then to gametic mutation. If one compares asexual and sexual reproduction from the standpoint of frequency of variation only, then sexual reproduction may seem to hold the advantage over asexual reproduction in the usual sense; but parthenogenesis, which is certainly a form of asexual reproduction, is in theory better adapted than sexual reproduction for giving large numbers of variations.

If, therefore, one is constrained to agree that the bulk of the evidence points to a practically identical coefficient of heredity for both forms of reproduction, and that variation in the sense of actual changes in germinal constitution *may* occur with greater frequency in asexual reproduction, if there is any difference at all between the two forms, he is driven either to the conclusion of Maupas that continued asexual reproduction is impossible through some protoplasmic limitation or to the conclusion of Weismann that a mixture of germplasms offers sufficient advantages to account for everything. This is the dilemma[3] unless one wishes to maintain that efficient mechanisms for nutrition, adaptation, protection and distribution could not be evolved or maintained under asexual reproduction.

The contention of Maupas can not be dealt with experimentally any more successfully than the question as to the inheritance of acquired characters since experimental time and evolutionary time are not of the same order of magnitude. The long-continued experiments of Woodruff in which vigorous strains of paramecium have been kept dividing asexually for several thousand generations, however, as well as the botanical evidence that numerous species having no sexual means of multiplication have continued to exist during long periods of time, weight the balance against him. One need not hesitate to concede that all of these organisms are rather low unspecialized types; the modern development of genetics has built up such a solid structure in favor of Weismann's view that there is little need of argument along the older line.

---

[3] Naturally another hypothesis wholly new to biology may be submitted at any time.

The main argument in favor of Weismann's viewpoint does not take long to state. It is this: Mendelian heredity is a manifestation of sexual reproduction. Wherever sexual reproduction occurs, there Mendelian heredity will be found. The very fact that it describes the sexual heredity of both animals and plants is sufficient proof of its generality in this regard. Now if N variations occur in the germplasm of an asexually reproducing organism, only N types can be formed to offer raw material to selective agencies. But if N variations occur in the germplasm of a sexually reproducing organism 2^n types can be formed. The advantage is almost incalculable. Ten variations in an asexual species mean simply 10 types, 10 variations in a sexual species mean the possibility of 1,024 types. Twenty variations in the one case is again only 20 types to survive or perish in the struggle for existence; 20 variations, in the other case, may present 1,032,576 types to compete in the struggle. It is necessary to hedge the argument by pointing out that these figures are the maximum possibilities in favor of sexual reproduction. It is improbable that they ever actually occur in nature, for 2^{20} types really to be found in the wild competing for place after only 20 germinal variations would mean an enormous number of individuals even if the 20 changes had taken place in different chromosomes, and if the variations were linked at all closely in inheritance the number required would be staggering. But there are breaks in linked inheritance, and the *possibility* is as stated.

These advantages remain even though it should be shown later that the more fundamental and generalized characters of an organism are not distributed by Mendelian heredity. Loeb (1916) believes that the cytoplasm of the egg is roughly the potential embryo and that the chromosomes, distributed as required by the breeding facts of Mendelian heredity, are the machinery for impressing the finer details. There is something to be said for this point of view, though at present it is but a working hypothesis. But granting its truth it does not detract from the advantages gained by sexual reproduction. Even the most strict mutationist would hardly maintain that evolution in general has come about through tremendous changes involving sterility between the mutant and the parent types. It seems unnecessary to deny such possibilities; but the weight of evidence is in favor of the majority of variations being comparatively small, changes in detail, the very kind which are known to be Mendelian in their inheritance.

Yet sexual reproduction in itself does not assure these advantages, though they are based upon it. There must be means for the mixture of germplasms. This opportunity was furnished originally by bisexuality. Then came hermaphroditism, manifestly an economic gain, yet on the whole unsuccessful except as functional bisexuality was restored by self-sterility, protandry, protogyny or mechanical devices which promoted cross-fertilization.

The prime reason for the success of sexual reproduction then, as Weismann maintained, is the opportunity it gives for mingling germplasms of different constitution and thereby furnishing many times the raw material to selective agencies that could possibly be produced through asexual reproduction. Further, there are three minor advantages which rest upon the same mechanism. They are minor advantages only when compared to the major, and should not be passed by.

Let us first consider heterosis, the vigor which accompanies hybridization. This phenomenon has long been known. It is characteristic of first generation hybrids both in the animal and vegetable kingdoms. It affects the characters of organisms in much the same manner as do the best environmental conditions. In other words, the majority of characters seem to reach the highest development in the first hybrid generation. The hybrid individual therefore holds some considerable superiority over the individuals of the pure races which entered into it, and is thereby the better enabled to survive and to produce the multiplicity of forms which its heterozygous factors make possible. The frequence of this phenomenon, for it is almost universal, together with the fact that it seems impossible to fix the condition, led Shull and the writer independently to the conclusion that certain factors in addition to their functions as transmitters of hereditary characters also had the faculty of carrying some sort of a developmental stimulus when in the heterozygous condition. The recent work of Morgan on linked characters, however, makes it possible to give another interpretation, as Jones (1917) has demonstrated. If it be assumed that several variations have occurred in each of one or more chromosomes, then it can be shown that the first-generation hybrid between such a variant and the race from which it arose will bring together all dominant or partially dominant characters. In the second hybrid generation, on the other hand, Mendelian recombination steps in and makes it improbable that many individuals shall have such a zygotic composition. And only in the rare cases where the proper breaks in linkage have occurred can a homozygous individual of this type be produced.

The latter hypothesis holds the advantage that it furnishes hope for a homozygous combination as valuable as that of the first hybrid generation no matter how rarely it may be assumed to occur, but whether it holds for the majority of organisms or not may depend on a future decision as to the frequency of side-by-side synapsis as compared to end-to-end synapsis. Our knowledge of linkage rests almost entirely on Morgan's work on *Drosophila* where side-by-side synapsis occurs at the maturation of the germ cells. If the break in linkage between groups of characters apparently carried by a single chromosome, which Morgan finds to be so exact in *Drosophila*, should actually depend on Jannsen's theory of chromosome, twisting at synapsis, then some other type of inheritance may be found in species having end-to-end synapsis. Perhaps this is the reason why the Œnotheras have such a peculiar heredity, for in them Davis (1909) thinks end-to-end synapsis prevails. But, be this as it may, the vigor of first generation hybrids is a fact and not a theory, and the advantage it brings to the heterozygotic individual in competition with its fellows can not be gainsaid.

The investigations of Shull and of the writer on the effects of cross- and self-fertilization have brought to light another series of facts with a bearing on the problem under discussion. It has been shown that the apparent deterioration of cross-bred species when self-fertilized is in large measure and perhaps wholly due to the loss of hybrid vigor[4] through the formation of homozygotic Mendelian recombinations and not an effect of inbreeding *per se* because of the union of like germplasms. This is a plausible argument against Darwin's idea that continued inbreeding is abhorrent to Nature. It may even be said to be a valid reason for declining to accept Maupas's belief in the impossibility of continued asexual reproduction, for there is no very good reason for distinguishing between continued asexual propagation and continued self-fertilization. Inbreeding simply brings about the opposite effect from crossing, and we can see no reason for the comparative failure of naturally inbred types in the wild other than the lack of chances for progress. The one is the conservative manufacturer who continues the original type of his article, the other is the progressive who makes changes here and there without discouragement until the acceptable improvement is found. In fact, if this argument be overlooked, the inbred types which have persisted hold some advantages over the cross-bred types. The self-fertilized species are inherently strong and vigorous, witness tobacco and wheat. They stand or fall on their own merits. They are unable, as are cross-bred species, to cover up inherent weakness by the vigor of heterozygosis. Cross-fertilized maize has become the king of cultivated plants because of its variability, but many of our best varieties carry recessive characters very disadvantageous to the species.

The next secondary advantage of sexual reproduction is

---

[4] Accepting the view that the vigor of the first hybrid generation is due to dominant characters meeting makes this argument even more forcible.

the division of labor made possible by secondary sexual characters, using the term very generally and including even such differences as those which separate the egg and the sperm. It is not known just how these differences arose or by what mechanism they are transmitted. The greatest hope of reading the riddle lies in an investigation of hermaphroditic plants, for there are technical difficulties which seem to preclude their solution in animals. For example, breaks in the linkage between sex-linked characters occur only in the female in *Drosophila,* and as the sex chromosome is double in the female, it can not be determined whether the differentiation between male and female is due to the whole chromosome or not. But this ignorance does not give reason for a denial of the great advantage which sexes bearing different characters hold over sexes alike in all characters except the primary sex organs.

The only glimpse of the truth we have on these matters comes from recent work on the effect of secretions of the sex organs on secondary sexual characters. The effect of removing the sex organs and the result of transplanting them to abnormal positions in the body have shown that in vertebrates the secretions of these organs themselves activate the production of the secondary sexual characters. This does not seem to be the case in arthropods, however, so one can not say that primary sexual differentiation and secondary sexual differentiation is one and the same thing.

Finally there is a presumable advantage in gonochoristic reproduction in having sex-linked characters. We say presumable advantages, for all of the relationships between sex and sex-linked characters are not clear. The facts are these: One sex is always heterozygous for the sex determiner and the factors linked with it. Now it may very well be that there is an actual advantage in the heterozygous condition, as we have seen above. But should the so-called vigor of heterozygosis prove to be only an expression of the meeting of dominant characters, still a possible advantage accrues to this phenomenon because the mechanism contributes toward mixing of germplasms. As an example, let us take the *Drosophila* type of sex determination. There the sperm is of two kinds: the one containing the sex chromosome and its sex-linked factors, the other lacking it. The eggs are all alike, each bearing the sex chromosome. It follows then that the male *always* receives this chromosome from his *mother*, who may have received it from *either* her *father* or *mother*. Moreover, further variability may be derived from the linkage breaks which occur always in the female. This last phenomenon is hardly worthy of special mention, however, until it is shown to be typical of such reproduction.

This short reconnaissance presents the pertinent facts in the situation as they appear to the writer. A very great number of interesting things connected with reproduction during the course of evolution have not been mentioned. This is because it is felt that the essential feature of the rôle of reproduction in evolution is the persistence of mechanisms in both the animal and plant kingdoms which offer selective agencies the greatest amount of raw material. Other phenomena are wholly secondary.

LITERATURE CITED

Casteel, D. B., and Phillips, E. F. 1903. Comparative Variability of Drones and Workers of the Honey Bee. *Biol. Bull.*, 6: 18–37.

Coulter, J. M. 1914. The Evolution of Sex in Plants. Chicago, University of Chicago Press. Pp. 1–140.

Cramer, P. J. S. 1907. Kritische Übersicht der bekannten Fälle von Knospenvariation. Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen. Derde Verzameling, Deel VI, Derde Stuk. Haarlem, De Erven Loosjes, pp. iii–xviii + 474.

Davis, B. M. 1909. Cytological Studies on *Œnothera*. I. *Ann. Bot.* 23: 551–571.

Jones, D. F. 1917. Dominance of Linked Factors as a Means of Accounting for Heterosis. *Genetics*, 2: 466–479.

Kellogg, V. L. 1906. Variation in Parthenogenetic Insects. *Science*, N. S., 24: 695–699.

Loeb, J. 1916. The Organism as a Whole. N. Y., Putnam. Pp. v–x + 379.

Wright, A., Lee, A., and Pearson, K. 1907. A Cooperative Study of Queens, Drones and Workers in *Vespa vulgaris*. *Biometrika*, 5: 407–422.

[Reprinted from BROOKLYN BOTANIC GARDEN MEMOIRS, 1: 141–153. 1918.]

INTERCROSSES BETWEEN SELF-STERILE PLANTS

E. M. EAST

Bussey Institution, Harvard University

The fact that self-fertilization is practically impossible in certain hermaphroditic plants, although both the pollen and the ovules are functional in crosses, has been known since the time of Kölreuter (1760–1765). The oddity of the phenomenon has been a lure for almost every hybridist from that time forward. As in the case of most other genetical problems, however, our knowledge of its cause and meaning remained in *status quo* from the time of Darwin until Mendelian days. Indeed when the writer began his investigations on the subject in 1910, the only considerable post-Darwinian work had been done by a zoologist (Morgan, 1904) on the self-sterile ascidian, *Ciona intestinalis*. Since 1910 botanical papers have appeared by Correns (1912), Compton (1913) and Stout (1916), but these investigations will not be discussed here, as it is proposed to treat in this paper only certain phases of the work carried on by the author and his associates[1] during the past seven years, leaving critical review for another place. For our purpose it seems essential only to present a hasty sketch of the subject as left by Darwin.

In addition to the utilization of most of the previous and the contemporaneous work, Darwin (1876) carried out several investigations of his own on the five self-sterile species, *Eschscholtzia californica*, *Abutilon darwinii*, *Senecio cruentus*, *Reseda odorata* and *Reseda lutea*.

Darwin's first important result was that the expression of self-sterility in *Eschscholtzia californica* and *Abutilon darwinii* was influenced by changes in external conditions. Six generations of *Eschscholtzia californica* had been found to be completely sterile in southern Brazil by Fritz Müller (1868, 1873). As English plants were self-fertile, Darwin obtained from Müller seed of Brazilian plants of known self-sterility. The plants which they produced in England, while not wholly self-fertile, tended toward self-fertility, which fact Darwin attributed to the lower English temperature. A second generation of seedlings proved to be still more self-fertile. Conversely, seed of English stock was somewhat self-sterile the first season and one plant

---

[1] The author desires to make grateful acknowledgment to Dr. O. E. White and Dr. J. B. Park for their painstaking aid in this work. Without it, the numerous experiments undertaken could not have been completed.

wholly self-sterile the second season, when grown in Brazil. One may assume, I think, arguing from data of similar character, that this progressive result was not due to actual inheritance of an acquired character but rather to the fact that the first generation in each case passed a portion of its life cycle in the original environment.

Similar results were obtained in the case of *Abutilon darwinii*, which though self-sterile in its native Brazil, *became moderately self-fertile late in the first flowering season in Darwin's greenhouse.*

Darwin made more detailed experiments on *Senecio cruentus*, *Reseda odorata* and *Reseda lutea* and found, as he believed, that each plant though self-sterile was cross-fertile with every other plant. His pollination experiments with *Senecio cruentus* and *Reseda lutea* were so inadequate that they may be omitted from consideration; it was really his experiments on *Reseda odorata* that were thought to establish the fact of complete cross-fertility.

DARWIN'S EXPERIMENTS ON *Reseda odorata* IN 1868

Male Parents

Female Parents	*A*	*B*	*C*	*D*	*E*	*F*	*G*
A	S.	F.	F.				
B	F.	S.	F.	F.			
C	F.	F.	S.	F.	F.		
D	F.	F.	F.	S.	F.		
E	F.		F.	F.	S.		
F						S.	
G							S.

Only sixteen cross matings were made, however, and this is not sufficient to prove the point, as is shown by one of our own experiments, where 131 cross-matings were made with only 4 cases of cross-sterility. From the fertile cross-pollinations Darwin raised four plants in 1869. Three of these proved to be self-fertile and one self-sterile. Six more plants were grown in 1870. Of these, two were almost self-sterile and four were almost completely self-fertile. The former produced altogether five seeds from self-pollinations, and the resulting plants proved to be self-sterile like their parents. These varied results Darwin attributed to a difference in inherited sexual constitution, but it seems to me that this conclusion should be questioned. Our own results have proved conclusively that toward the very last of the flowering season[2] self-sterile plants may sometimes become somewhat self-fertile.

Darwin's (1876, p. 346) general conclusions are as follows:

> "Finally, the most interesting point in regard to self-sterile plants is the evidence which they afford of the advantage, or rather the necessity, of some degree or kind of differentiation in the sexual elements, in order that they should unite and give birth to a new being. It was ascertained that the five plants of *Reseda odorata* which were selected by chance could be perfectly fertilised by pollen taken from any one of them, but not by their own pollen; and a few additional trials were made with some other individuals, which I have not thought worth recording. So again, Hildebrand and Fritz Müller frequently speak of self-sterile plants being fertile with the pollen of any other individual; and if there had been any exception to the rule, these could hardly have escaped their observation and my own. We may therefore confidently assert that a self-sterile plant can be fertilised by the pollen of any one out of a thousand or ten thousand individuals of the same species, but not by its own. Now it is obviously impossible that the sexual organs and elements of every individual can have been specialised with respect to every other individual. But there is no difficulty in believing that the sexual elements of each differ slightly in the same diversified manner as do their external characters; and it has often been remarked that no two individuals are absolutely alike. Therefore we can hardly avoid the conclusion that differences of an analogous and indefinite nature in the reproductive system are sufficient to excite the mutual action of the sexual elements, and that unless there be such differentiation fertility fails."

One cannot but admire these inductions Darwin has so cleverly drawn from such meager data, nevertheless one cannot accept them today just as they stand. The reasons for this statement will be seen more clearly when our own data have been presented, but a brief can be submitted with only the support of the work known to Darwin.

In the first place, the seemingly contradictory results that were obtained in the experiments on *Reseda odorata* are not necessarily confusing. As reported, self-sterile plants produced varying ratios of self-sterile and self-fertile plants. Unfortunately, the progeny of the self-fertile plants was not followed. If it has been, the problem might have been more easily solved, for, in all probability, the daughter plants would have been self-sterile. It is my own belief, however, that the answer can be read in the casual remarks dropped by Darwin in the midst of his careful descriptions, remarks to which he paid little attention. Darwin found that both *Eschscholtzia california* and *Abutilon darwinii*, though self-sterile in Brazil tended to become self-fertile in England,—especially late in the flowering season. Now

---

[2] Cf. Darwin's observation on *Abutilon darwinii.*

these facts together with that mentioned above regarding the inconstancy of the results obtained from planting the seed of self-sterile plants, may be interpreted by the assumption that he was dealing entirely with fluctuations in all of the five species investigated. These species genetically were wholly self-sterile. The tendency toward self-fertility was due to conditions. In other words, these plants genetically self-sterile needed conditions conducive to a fine healthy growth to bring out their self-sterility. In the lower temperature of England, at a time of decline (the last of the flowering season), they became phenotypically somewhat self-fertile. In the light of my own experiences, I believe we can reconstruct a picture of Darwin's experiments on *Reseda odorata* with considerable confidence. He isolated the plants that he desired to test under nets; then came pressure of other work, and the data were not collected until the plants had ceased flowering. At that time capsules were found beneath the nets, and this seemed to prove at least a partial self-fertility. But instead of this procedure, suppose that successive self-pollinations had been made throughout the season. The presumption is that the plants would have been declared to be self-sterile with the same remark added which he jotted down in the case of *Abutilon darwinii*, viz., they "became moderately self-fertile late in their flowering season."

Again, Darwin found no cross-sterility in the plants tested, and concluded that a self-sterile plant can be fertilized with the pollen of any one of a thousand or ten thousand individuals of the same species. Such a conclusion was less cautious than was Darwin's wont for it was made from a total personal experience of some twenty-odd cross-matings only, unless his records are extremely incomplete. Indeed this conclusion must have been somewhat of a surprise to himself since he states that "it is obvious impossible that the sexual organs and elements of every individual can have been specialized with respect to every other individual." He surmounted this difficulty by assuming that the sexual elements of each plant differ slightly in the same manner as their external characteristics, and that this slight difference is sufficient to excite the mutual action of the sex elements necessary in order to have fertilization ensue. The kernel in this conclusion, that differences in the reproductive systems of two self-sterile plants are necessary in order to promote cross-fertilization, is so similar to that to which the writer has been forced after seven years of rather intensive work as to be uncanny, for it seems to have been reached in spite of rather than because of the data at hand. This feeling of surprise at Darwin's clairvoyancy may seem affected, since he was usually in advance of his time, but it is a fact perhaps worth mentioning as a confession of omission that the writer reached his conclusions as the outgrowth of work on heterozygosis and did not refer to Darwin's view until recently. Be this as it may, a short comparison of Darwin's main induction with the facts from which it came will, I think, show a real reason for wonderment. He believed in universal cross-fertility of self-sterile plants, his basis being the small number of cross-fertilizations made by Hildebrand, Müller and himself; although Robertson Munro (1868), with whose work he was familiar, had found cross-sterility in *Passiflora alata*, and even the works of Hildebrand and Müller as published leave the matter in doubt. Now how much more reasonable the general induction mentioned above seems if one assumes (1) that self-sterile plants breed true for self-sterility but may show a slight degree of self-fertility as a fluctuation under certain conditions, (2) that a variable but limited number of germinal "factors" influence the success of matings, cross-fertilization being possible only when two plants differ in these effective factors, and (3) that when two plants have the same effective factorial composition, cross-sterility of the same type as self-sterility exists. This is what we believe our own work has shown, as we shall try to demonstrate.

Emphasis must first be laid upon the fact that the behavior of self-sterile plants among themselves and the relation between self-fertile and self-sterile plants are distinct problems. Compton (1913) found the relation between self-fertile and self-sterile plants of *Reseda odorata* to be that of a simple Mendelian monohybrid with self-fertility dominant. The same relation appears to hold in crosses between the self-fertile species *Nicotiana langsdorffii* and the two self-sterile species with which our work has been done, *Nicotiana forgetiana* and *Nicotiana alata*. There is some single differential between self-fertility and self-sterility. Given the proper composition a plant breeds true for self-sterility. The behavior of self-sterile plants among themselves therefore must be considered separately.

Our work, as stated before, has been done with the two self-sterile species, *Nicotiana forgetiana* and *Nicotiana alata*, and largely with crosses between these species. Both of these species are affected in their manifestation of self-sterility by certain environmental changes, *Nicotiana alata* much more than *Nicotiana forgetiana*. Self-sterility is determined by the inheritance received, but it can develop fully only under environmental conditions which promote a normal healthy growth, and during the period of intense flowering. Toward the end of the flowering period, especially under conditions adverse to vegetative growth, self-sterility sometimes shows a marked and rather sudden decline. A few seeds, or even a well-developed seed capsule may then be obtained. This is not a common occurrence; indeed, it is rare, but it is a possibility. Three cases of seed production out of over three hundred plants tested have been observed in *Nicotiana forgetiana*. A considerably higher percentage of fertility has been marked in *Nicotiana alata*. Self-sterility can be restored in such plants, however, if they are allowed to go through a period of rest and are then, by proper treatment, brought into vigorous flower again.

This is not the whole evidence that this occasional end-season fertility is a pseudo-fertility brought about by external conditions—a fluctuation. Three generations of *Nicotiana alata* plants have been grown from selfed seed produced by end-season fertility without the occurrence of a single plant which behaved in every way like a truly self-fertile individual. This phenomenon, therefore, while teaching us to test self-sterility only during the main part of the flowering season, has shown that there is no reason why fusion between gametes produced by a self-sterile plant may not occur provided the male generative nucleus enters the embryo sac. Such unions may take place without affecting the self-sterility of the progeny.

What is then the difference in behavior that makes a cross-pollination effect fertilization while a self-pollination produces nothing? What occurs is this: After a self-pollination the pollen grains germinate and the tubes pass down the style at such a slow even rate that they reach only about half way to the ovary before the flower wilts and falls off; while the pollen tubes after a cross-pollination, though starting at the same rate as the others, grow faster and faster until fertilization is effected in four days or less. The curve of distance traversed plotted against time is in the case of the self-pollination nearly a straight line, while in the case of the cross-pollination it simulates that of an autocatalytic reaction.

From these facts it seems reasonable to suppose that the secretions in the style offer a stimulus to pollen tubes from other plants rather than an impediment to the development of tubes from pollen of the same plant. And we believe that this stimulus is in some way caused by certain effective differences in the factorial composition characterizing two compatible plants and that if two plants do not have these effective differences in factorial composition they are by the same token cross-sterile with each other. It is clear that this assumption presumes that the pollen grains matured by a given plant behave as if they are sporophytic as regards that part of their constitution that affects self-sterility and cross-sterility. The pollen grains of any plant may carry many different hereditary factors, they may even carry several different factors which function in controlling the success or failure of particular cross-matings in the next generation, but in their own action on the stigmas of other plants they behave as if each carried the composition of the mother plant from which it came. In other words, as far as its action in fertilization is concerned, a pollen grain partakes of the character of its mother plant and is like its sisters; as far as the hereditary characters carried on to the next generation are concerned, sister pollen grains may differ both from their mother and from each other.

A part of our evidence on these points we shall present. For further details the reader is referred to a forthcoming paper in Genetics.[3]

The first experiment to which attention is called is an inbreeding experiment performed on a cross between *Nicotiana forgetiana* and *Nicotiana alata.* If sister plants are mated in successive generations after an original mating Aa × Aa, by Mendelian recombination there results a gradual approach to 1/2 AA, 1/2 aa and 0 Aa. Expectation of homozygosis in successive matings is 1/2, 5/8, 11/16, 24/32 ··· 1 (Jennings, 1916). If, therefore, plants of like constitution as far as effective factors are concerned are cross-sterile with each other, cross-sterility should become more and more apparent in generations succeeding F_2. To test this possibility, a comparatively small number of cross-matings was made on the F_2, F_3, F_4 and F_5 generations. In the F_2 generation, out of 131 intercrosses on 20 plants only 4 were unsuccessful. The percentage of unsuccessful matings increased from this time on, until in the F_5 generation about 21 percent of the cross-matings tried on 20 plants were impossible to make.

In this experiment as well as in all others, results showed that reciprocal crosses were alike in their compatibility. If two plants were fertile together, they were fertile reciprocally; if two plants were incompatible, they were incompatible reciprocally. This is proof of the sporophytic behavior of the factors affecting the behavior of self-sterile plants.

The two crosses to be described next are reciprocals made with the same two individuals. Made with *Nicotiana alata* and *Nicotiana forgetiana* as parents, they are in a sense repetitions of the cross just described, but it is hardly probable that they duplicate it. Both of these species must consist of plants which differ among themselves in the factors which affect self-sterility, hence any crosses in which different individuals are used may show different results.

All of the individuals resulting from this cross were grown in a greenhouse as potted plants. The F_1 generation came into blossom during the latter part of the winter. Conditions were extraordinarily favorable for growth and the pollinations were all made while the plants were vigorous, hence scarcely any trouble arose over classification of the results through end-season pseudo-fertility.

---

[3] This paper has since appeared. See "Studies on Self-sterility I. The Behavior of Self-sterile Plants." Genetics 2: 505–609. 1917.

Our study was made on a population of 53 plants. Pedigree numbers from 0 to 39 inclusive represent the cross *N. alata* × *N. forgetiana;* pedigree numbers 40 to 52 inclusive represent cross *N. forgetiana* × *N. alata.*

Each plant was selfed one or more times, and all proved absolutely self-sterile. Further *each plant* was *back-crossed* with pollen from a single plant of each of the parent species *with complete success in every case.* The plants used in this case were not the individuals that entered into the cross, however, for unfortunately these were not available.

TABLE I

RESULT OF MATINGS ON F_1 PLANTS 0 TO 39

N. alata × *N. forgetiana* and on Plants 41 to 52 *N. forgetiana* × *N. alata*

Ped. No.	Fertile with Ped. No.	Sterile with Ped. No.
0	44, 46	22, 34, 38, 49
1	2, 3, 4, 6, 41	8
2	4, 18, 41, 44, 52	9, 22, 23
3	2, 9, 14, 23, 29	4, 6, 18, 41, 46
4	2, 9, 10, 44	18
5	2, 3, 6, 9, 10, 18, 46	8, 44
6	5, 10, 43, 44	3, 4, 18, 40
7	2, 13, 22, 44	18, 46
8	6, 9, 10, 39, 40, 46	5, 44
9	3, 18, 44, 52	2, 10, 23, 37, 48
10	4, 6, 18, 40, 44	2, 23, 24, 27, 34, 48
11	2, 8, 12, 15, 34, 44, 46	
12	9, 16, 22, 43	6, 18, 46, 52
13	3, 8, 18, 44, 46	2, 9, 15, 21, 34
14	18, 20, 43	10, 34
15	1, 3, 16, 17, 18, 20	9, 13, 14, 23, 44
16	13, 14, 18, 25, 43, 46	17, 29
17	14, 18, 19, 20, 22, 30	16, 26, 44
18	2, 9, 21, 23, 28, 34, 36, 44	3, 46
19	17, 22, 28, 34, 44	18
20	2, 8, 9, 16, 18, 21, 22, 26, 36, 40, 44	43
21	4, 12, 16, 18, 46	2, 9, 22, 25, 27, 37
22	12, 42, 44	14, 23, 24, 36, 48
23	41	9, 10, 37, 48
24	3, 6, 20, 26, 28, 44	10, 22, 23, 30, 37
25	8, 33, 44, 46	2, 9, 23, 27
26	9, 18, 22, 23, 25, 40, 48	28, 29, 44
27	3, 18, 32, 44, 46	2, 9, 30, 34, 48
28	2, 3, 23, 27, 39, 46	8, 26, 29, 44
29	2, 14, 18, 22, 23, 24, 25, 30, 34, 37, 41, 46	5, 26, 28, 31, 44
30	8, 29, 33, 44, 45, 46	9, 21, 22, 27
31	22, 32, 52	8, 29, 36, 44
32	9, 21, 23, 29, 30, 34, 43, 44	18, 33, 46
33	8, 16, 23, 31, 46	18, 32
34	28, 41, 44, 46	10, 23, 24, 37
35	3, 9, 18, 21, 27, 30, 34, 37, 42	8
36	8, 33, 44, 46	10, 23
37	39, 42, 43, 44, 46	9, 10, 22, 23, 34, 38

38	28, 35, 39, 42, 43, 46	34, 37, 47
39	9, 44	18, 40, 42
40	22, 43, 44, 47, 49	6, 33, 46
41	10, 37, 44, 48	33, 40, 46
42	20, 44	39, 41, 45
43	5, 27, 33, 38, 39, 40, 42, 44, 46, 51	
44	10, 14, 23, 34, 45	
45	18, 44, 48	46, 52
46	10, 22, 37, 44, 51	52
47	20, 42, 44, 45, 46, 51, 52	38
48	40, 41, 43, 46	10, 23, 24, 27, 34
49	42, 44, 45	0, 9, 27, 34, 47
50	18, 39, 51, 52	9, 27, 37
51	9, 18, 23, 39, 45, 46, 50	8, 29
52	10, 23, 29, 37, 51	3, 4, 6, 18, 41, 45, 46

The numerous cross-matings made are shown in Table 1. There were 103 reciprocal matings. Of these 100 gave duplicate results, 39 pairs being fertile and 61 sterile. The three which did not check are:

2 × 3,	sterile, 1 pollination	classed as fertile,
3 × 2,	fertile, 1 pollination	
6 × 52,	fertile, 1 pollination	classed as sterile,
52 × 6,	sterile, 1 pollination	
37 × 21,	fertile, 1 pollination	classed as sterile.
21 × 37,	sterile, 1 pollination	

Since but one pollination was made in each of these cases we have made our decision as to fertility or sterility by a consideration of the circumstantial evidence. The behavior of these plants in other crosses shows conclusively that 3 should be fertile with 2, 6 sterile with 52, and 21 sterile with 37. They have been classed accordingly. That this grouping is correct is further shown by the fact that the mating 3 × 2 (classed fertile) was made at the height of the flowering season, while the matings 6 × 52 and 37 × 21 (classed sterile) were respectively the last and next to the last matings made on those plants.

In spite of the fact that plants 0–39 are from cross *N. alata* × *N. forgetiana*, and plants 40–52 are from cross *N. forgetiana* × *N. alata*, they behave as one family in intercrosses. The entire population can be grouped into 6 classes in which there is interclass fertility and intraclass sterility. The following explanation may be necessary to make it clear just how Table II was obtained from Table I. Table I shows all of the matings, but in the form given it is not easy to see at a glance every combination in which a particular plant was used, both as male and as female. It was necessary, therefore, to make a new table, in which the pedigree numbers in the column at the left were tabled as males, and the pedigree numbers in the columns headed "Fertile matings" and "Sterile matings" were tabled as females.

Thus plant 2, used as a female, was fertile with pollen from plants 4, 18, 41, 44 and 52, and sterile with plants 9, 22 and 23; but pollen from plant 2 was fertile on plants 1, 3, 4, 5, 7, 11, 18, 20, 28 and 29, and sterile on plants 9, 10, 13, 25 and 27. It is clear, therefore, that instead of the 8 matings on plant 2 that Table I appears to show, there are really 21, the 3 reciprocals of course being counted but once.

These tables were combined for analysis. In the interest of economy of space only one is shown, however, since the second can easily be made from the first.

The four exceptions in this huge set of matings are in reality negligible. Matings 15 × 44 and 31 × 36 were sterile, though they do not belong to the same class. Plant 15 was sterile to 4 plants of Class *A* and fertile to 2 plants of Class *B*, 3 plants of Class *C*, and to the isolated individuals forming classes *D* and *F*. It is unquestionably a member of Class *A*. Plant 44 was sterile to 7 individuals in Class *C* and fertile to 17 plants of Class *A*, 12 plants of Class *B* and to the singletons forming classes *D*, *E* and *F*. This evidence places it unmistakably as a member of Class *C*. Plant 31 is also a member of Class *C* as evidenced by 3 sterile matings within that class and by fertile matings with 1 plant of Class *A* and 3 plants of Class *B*. Plant 36 is like plant 15 thrown into Class *A* by its sterility with 3 others of that class, and by its fertility with 3 individuals of Class *B*, with 2 of Class *C*, and with the lone plant of Class *D*. In view of this evidence and the fact that in these two matings but one pollination was made in each case, they are much more likely to be errors of record or of technique than true exceptions to our classification.

The other two exceptions, matings 45 × 18 and 33 × 46, were fertile where from the evidence of numerous other matings they should have been sterile. Here again but one pollination was made in each case; and, coincidence though it may be, *each pollination was the last mating made on that particular plant.* What is more probable than that this is a pseudo-fertility appearing during the wane of the flowering season of the two mother plants, No. 45 and No. 33?

Six groups appear in Table II, but there is proof of the existence of only five. Groups *A*, *B*, *C*, *D* and *E* are definitely established. Plant 11, on the other hand, is an isolated individual rather than a class. It does not belong to groups *A*, *B* or *C*; but unfortunately it was not crossed either with Class *D* (plant 20) or with Class *E* (plant 43), hence one cannot say that it does not fall into one or the other of these two classes.

In the three large groups the distribution of individuals is 22, 16 and 12. About all that can be said about the type of this distribution is that the classes are not of equal size. On the other hand, it is interesting to note that the plants of both cross No. 2 and cross No. 3 fell into the three groups as if they were samples of the same population. There were 40 plants of Cross No. 1, and 13 plants of the

TABLE II

Plants of F_1 Generation of Reciprocal Cross between *N. forgetiana* and *N. alata*, Grouped in Accordance with their Behavior in Intercrosses

Plants 0–39 are products of the cross; plants 40–52 are products of its reciprocal

Group	Ped. No.	Cases Fertile in Group						Cases Sterile in Group					
		A	*B*	*C*	*D*	*E*	*F*	*A*	*B*	*C*	*D*	*E*	*F*
A.......	0	0	1	1	–	–	–	4	0	0	–	–	–
	2	0	6	5	1	–	1	8	0	0	0	–	0
	9	0	7	6	1	–	–	13	0	0	0	–	–
	10	0	7	3	–	–	–	10	0	0	–	–	–
	13	0	4	3	–	–	–	5	0	0	–	–	–
	14	0	2	4	1	1	–	4	0	0	0	0	–
	15	0	2	3	1	–	1	4	0	1	0	–	0
	21	0	5	2	1	–	–	8	0	0	0	–	–
	22	0	6	5	1	–	–	9	0	0	0	–	–
	23	0	6	5	–	–	–	11	0	0	–	–	–
	24	0	2	4	1	–	–	7	0	0	0	–	–
	25	0	2	5	–	–	–	5	0	0	–	–	–
	27	0	4	3	–	1	–	10	0	0	–	0	–
	30	0	4	5	–	–	–	5	0	0	–	–	–
	34	0	5	4	–	–	1	11	0	0	–	–	0
	36	0	3	2	1	–	–	3	0	1	0	–	–
	37	0	5	3	–	1	–	9	0	0	–	0	–
	38	0	3	2	–	1	–	4	0	0	–	0	–
	47	0	5	2	1	–	–	2	0	0	0	–	–
	48	0	4	1	–	1	–	7	0	0	–	0	–
	49	0	3	1	–	–	–	5	0	0	–	–	–
	50	0	3	1	–	–	–	3	0	0	–	–	–
B.......	3	8	0	5	–	–	–	0	6	0	–	–	–
	4	4	0	2	–	–	–	0	4	0	–	–	–
	6	2	0	4	–	1	–	0	6	0	–	0	–
	7	3	0	1	–	–	–	0	2	0	–	–	–
	12	3	0	1	–	1	1	0	4	0	–	0	0
	18	12	1	9	–	–	–	0	11	0	0	–	–
	19	2	0	3	–	–	–	0	1	0	–	–	–
	32	6	0	3	–	1	–	0	3	0	–	0	–
	33	4	1	3	0	1	–	0	4	0	–	0	–
	39	4	0	4	–	1	–	0	3	0	–	0	–
	40	5	0	3	1	1	–	0	5	0	0	0	–
	41	6	0	3	–	–	–	0	6	0	–	–	–
	42	5	0	2	1	1	–	0	3	0	0	0	–
	45	4	1	2	–	–	–	0	3	0	–	–	–
	46	14	1	7	–	1	1	0	9	0	–	0	0
	52	7	0	3	–	–	–	0	8	0	–	–	–
C.......	1	2	4	0	–	–	–	0	0	1	–	–	–
	5	3	4	0	–	1	–	0	0	3	–	0	–
	8	6	5	0	1	–	1	0	0	7	0	–	0

TABLE II—*Continued*

Group	Ped. No.	Cases Fertile in Group						Cases Sterile in Group					
		A	*B*	*C*	*D*	*E*	*F*	*A*	*B*	*C*	*D*	*E*	*F*
C.......	16	5	4	0	1	1	–	0	0	2	0	0	–
	17	4	2	0	1	–	–	0	0	3	0	–	–
	26	6	2	0	1	–	–	0	0	4	0	–	–
	28	6	5	0	–	–	–	0	0	4	–	–	–
	29	9	6	0	–	–	–	0	0	7	–	–	–
	31	1	3	0	–	–	–	1	0	3	–	–	–
	35	7	3	0	–	–	–	0	0	1	–	–	–
	44	17	12	0	1	1	1	1	0	7	0	0	0
	51	4	5	0	–	1	–	0	0	2	–	0	–
D.......	20	9	3	5	0	1	–	0	0	0	0	0	–
E.......	43	5	8	4	1	0	–	0	0	0	0	0	–
F.......	11	3	2	2	–	–	0	0	0	0	–	–	0

reciprocal, Cross No. 2. In the classes *A*, *B* and *C* the proportions were 18, 10, 10 and 4, 6, 2 respectively. This similar behavior of the progeny of reciprocals seems to us strong corroboratory evidence in favor of the conclusion that reciprocal crosses always behave in like manner as regards self-sterility.

The study on this family is but one of several that have been made but we believe that the data on it alone show unmistakably that the behavior of self-sterile plants in intercrosses is governed by a relatively small number of factors which act through pollen as if the pollen grain possessed the characters of the sporophyte from which it came, and that the gametes of plants having like constitutions as regards effective factors are incompatible in the sense that they do not make a normal pollen-tube growth and hence do not reach the ovary in time for fusion to occur. This interpretation shows both why plants are self-sterile and cross-sterile. It accords completely with the fact that a population of plants may be divided into groups on the basis of their mating proclivities and that each member of any group is cross-sterile with every other individual of that group although it is fertile with every individual of every other group.

These assumptions being true, it ought to be possible by continuous self-fertilization, utilizing end-season pseudo-fertility, to obtain ultimately a population in which every individual possesses the same effective self-sterility factors. In such a population all of the plants will not only be self-sterile, but will be cross-sterile. Such a population has been obtained.

REFERENCES CITED

Compton, R. H. Phenomena and Problems of Self-sterility. New Phytologist **12**: 197–206. 1913.

Correns, C. Selbststerilität und Individualstoffe. Festschr. d. mat.-nat. Gesell. zur 84. Versamml. deutsch. Naturforscher u. Ärzte Münster i.W. pp. 1–32. 1912.

Darwin, Chas. Effects of Cross- and Self-fertilisation in the Vegetable Kingdom. Ed. 2, 1878. N. Y. D. Appleton. 1876.

Hildebrand, F. Bastardierungs Versuche an Orchideen. Bot. Ztg. **23**: 245–249. 1865.

—— Ueber die Nothwendigkeit der Insektenhilfe bei der Befruchtung von *Corydalis cava.* Jahrb. wiss. Bot. **5**: 359–363. 1866.

—— Ueber die Bestäubungsvorrichtungen bei den Fumariaceen. Jahrb. wiss. Bot. **7**: 423. 1869.

Jennings, H. S. The Numerical Results of Diverse Systems of Breeding. Genetics **1**: 53–89. 1916.

Kölreuter, J. G. Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, nebst Fortsetzungen 1, 2 u. 3. Pp. 1–266. Ostwald's Klassiker, Nr. 41. Leipzig: Engelmann. 1761–6.

Morgan, T. H. Some Further Experiments on Self-fertilization in Ciona. Biol. Bull. 8. 313–330. 1904.

Müller, Fritz. Notizen über die Geschlechtsverhältnisse brasilianischer Pflanzen. Bot. Ztg. **26**: 113–116. 1868.

—— Bestäubungsversuche an Abutilon-Arten. Jen. Ztschr. f. Naturwiss. **7**: 22–45, 441–450. 1873.

Munro, Robertson. On the Reproduction and Cross-fertilization of Passifloras. Bot. Soc. Edin. **9**: 399–402. 1868.

Stout, A. B. Self- and Cross-pollinations in *Cichorium intybus* with Reference to Sterility. Mem. N. Y. Bot. Gard. **6**: 333–454. 1916.

CONNECTICUT

AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 207 SEPTEMBER, 1918

THE EFFECTS OF INBREEDING AND CROSSBREEDING UPON DEVELOPMENT

BY

D. F. JONES

The Bulletins of this Station are mailed free to citizens of Connecticut who apply for them, and to others as far as the editions permit.

CONNECTICUT
AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 207 SEPTEMBER, 1918

THE EFFECTS OF INBREEDING AND CROSSBREEDING UPON DEVELOPMENT

BY

D. F. JONES

The Bulletins of this Station are mailed free to citizens of Connecticut who apply for them, and to others as far as the editions permit.

CONNECTICUT AGRICULTURAL EXPERIMENT STATION

OFFICERS AND STAFF

BOARD OF CONTROL.

His Excellency, Marcus H. Holcomb, *ex-officio, President.*

James H. Webb, *Vice President*	Hamden
George A. Hopson, *Secretary*	Wallingford
E. H. Jenkins, *Director and Treasurer*	New Haven
Joseph W. Alsop	Avon
Wilson H. Lee	Orange
Elijah Rogers	Southington
William H. Hall	South Willington

Administration.	E. H. Jenkins, Ph.D., *Director and Treasurer.*	
	Miss V. E. Cole, *Librarian and Stenographer.*	
	Miss L. M. Brautlecht, *Bookkeeper and Stenographer.*	
	William Veitch, *In charge of Buildings and Grounds.*	
Chemistry, Analytical Laboratory,	*John Phillips Street, M.S.	
	E. Monroe Bailey, Ph.D., *Chemist in charge.*	
	*C. B. Morison, B.S., C. E. Shepard,	*Assistants.*
	M. d'Esopo, Ph.B.	
	H. D. Edmond, B.S.	
	Miss A. H. Moss, *Clerk.*	
	V. L. Churchill, *Sampling Agent.*	
Protein Research.	T. B. Osborne, Ph.D., D.Sc., *Chemist in Charge.*	
	Miss E. L. Ferry, M.S., *Assistant.*	
Botany.	G. P. Clinton, Sc.D., *Botanist.*	
	E. M. Stoddard, B.S., *Assistant Botanist.*	
	Florence A. McCormick, Ph.D., *Scientific Assistant.*	
	G. E. Graham, *General Assistant.*	
Entomology.	W. E. Britton, Ph.D., *Entomologist; State Entomologist.*	
	B. H. Walden, B.Agr., *First Assistant.*	
	*I. W. Davis, B.Sc., M. P. Zappe, B.S., *Assistants.*	
	Miss Martha de Bussy, B.A., *Stenographer.*	
Forestry.	Walter O. Filley, *Forester; also State Forester and State Forest Fire Warden.*	
	A. E. Moss, M.F., *Assistant State and Station Forester.*	
	Miss E. L. Avery, *Stenographer.*	
Plant Breeding.	Donald F. Jones, S.D., *Plant Breeder.*	
	C. D. Hubbell, *Assistant.*	
Vegetable Growing.	W. C. Pelton, B.S.	

---

* Absent on leave. In service of the United States.

CONTENTS

The Effects of Inbreeding and Crossbreeding Upon Development.*

INTRODUCTION.

Among the higher seed plants certain groups are characterized by almost universal and continuous self-fertilization. On the other hand certain other groups are completely, or to a large extent, cross-fertilized in every generation. Between these two extremes every gradation in the degree of self- and cross-fertilization can be illustrated. The structure and function of the floral organs have become more or less clearly adapted to the customary mode of sexual reproduction characteristic of each species. In the thallophytes, bryophytes and pteridophytes much the same situation exists whereby the gametes which enter into a sexual fusion may arise either from the same or from different organisms.

In the lower animals the same variation in the mode of sexual reproduction exists as in plants. Among the higher animals, however, hermaphroditism is replaced entirely by bisexuality; and sexual reproduction, except when parthenogenesis takes place, results only from the union of gametes originating in different organisms.

This array of facts has naturally led to searching inquiries as to the purpose of sexual reproduction as compared to other methods of propagation as well as to the effects of artificial inbreeding in bisexual animals and in naturally cross-fertilized plants. Bound up with this latter problem is that which is concerned with the effects of cross-fertilization in all types of animals and plants of different degrees of relationship.

The development of the Mendelian theory of heredity, carrying with it the conception of definable, hereditary units which are sufficiently stable in their transmission from generation to generation to be recognized and their somatic expression to be described,

---

* Submitted to the Faculty of the Bussey Institution of Harvard University in partial fulfillment of the requirements for the degree of Doctor of Science, December, 1917.

has made possible an attack upon these problems which has opened a way towards their solution.

From the knowledge of alternate inheritance it is possible to ascribe, very definitely and surely, certain of the results of inbreeding to the segregation and isolation of hereditary factors which results were formerly thought to be due solely to inbreeding as a cause in itself. Certain pathological, abnormal or otherwise undesirable conditions occurring more frequently in animals and plants produced by matings between nearly related individuals were formerly attributed to inbreeding as the cause, and it was thought that inbreeding must always show such undesirable results. It is now known that many of these pathological and abnormal conditions resulting from inbreeding do not owe their origin to that process, but are due solely to the segregation, into a pure state of the hereditary factors causing the anomalies which factors were present in the organisms previous to their being inbred. Inbreeding, then, has nothing to do with the origin of the undesirable characters under consideration but merely brings them into visible expression, and whether or not they appear depends upon their presence originally in the stock before inbreeding takes place. There still remains a conviction, however, that all the manifestations attending inbreeding and the converse effects of cross breeding cannot be accounted for solely on the basis of the operation of definable, hereditary factors, but that there is a stimulating effect resulting from crossing, which is lost by inbreeding, and that this stimulation differs somewhat from the expression of hereditary factors which can be transferred and fixed in different organisms. This stimulation is supposed to be of a physiological nature appearing when dissimilar germ-plasms are united, and disappearing as the germinal heterogeneity disappears in subsequent recombinations.

Since this physiological stimulation has always been purely hypothetical, having never been definitely proven, and since it has been used to account for certain facts heretofore inexplicable in any other way, the existence of such a stimulation may fairly be questioned, in so far as the facts can be logically accounted for in other ways. Recent advances in the knowledge of the methods of inheritance have made it possible to meet certain objections previously held against the view that the effects of inbreeding and crossbreeding can be attributed solely to the operation of hereditary factors without assuming an additional hypothetical stimulation.

Some of the previous work bearing upon the effects of inbreeding and crossbreeding is reviewed here and with this are given original data obtained from the naturally cross-fertilized corn plant, *Zea mays* L. The facts at hand co-ordinate with the existing knowledge of heredity in such a way that it seems to the writer unnecessary any longer to make the fundamental distinction between the effects of inbreeding and crossbreeding and of heredity in development.

No attempt is made to canvas the extensive literature on hybridization (a bibliography of which alone would fill a volume) in order to list all the cases in which crossing does or does not result in increased development and inbreeding in a reduction. It does not take one long in reading over the many published results of crossing in animals and plants to become convinced that an increase in development following a cross is a frequent occurrence. It is hoped that sufficient references are given to show something as to the universality and nature of the phenomenon and a review of the more important contributions is made in order to sketch briefly the development of the ideas concerning the cause of the stimulation and the part it has played in evolution and in breeding practice.

The experiments on inbreeding, which have resulted in the material from which the data given here have been gathered, were started by Professor E. M. East at the Connecticut Agricultural Experiment Station and carried on by him and subsequently by Professor H. K. Hayes and later by the writer. From time to time reports on these experiments have been made and conclusions drawn from the facts as observed. These include various publications under the titles "Inbreeding in Corn," "The Distinction between Development and Heredity in Inbreeding" published by Professor East in the Report of the Connecticut Experiment Station and in the American Naturalist and "Heterozygosis in Evolution and in Plant Breeding" by Professors East and Hayes in a Bureau of Plant Industry bulletin. Under the title of "Dominance of Linked Factors as a Means of Accounting for Heterosis" the writer had proposed a different view as to the cause of hybrid vigor. This was published in Genetics and its application is discussed here in more detail.

Further publications are planned which will discuss more adequately much of the data which are scantily treated here.

The significance which these investigations may have for the practical improvement of plants and animals has only been briefly alluded to here. This phase of the subject has been reserved for another time when the methods which have suggested themselves as the result of these investigations have been more thoroughly tested. Finally this collection of facts and theories should be viewed as a report of progress rather than a well rounded presentation of the subject of inbreeding and crossbreeding.

The writer is especially indebted to his predecessors whose work has made these experiments possible. Grateful acknowledgement is due Dr. E. M. East for his careful supervision of the work and for his kindly advice and helpful criticism as to the presentation of the results obtained. The writer alone, however, must assume the responsibility for the opinions expressed. Much credit is due Mr. C. D. Hubbell, Dr. Charles Drechsler and Mr. G. A. Adsit for their careful assistance in the collection and preparation of the data.

Definitions.

The knowledge of a stimulating effect resulting from a cross between different animals and between different plants which gives progeny which may excel their parents in general vigor, size or other visible characteristics has naturally led to the use of terms to describe this effect. This stimulation is variously spoken of as "vigor due to crossing" or "hybrid vigor." Since hybrid vigor occurs only in crosses of which the parents are dissimilar in hereditary constitution more exact and comprehensive terms were needed. The zygote resulting from a union of unlike gametes is spoken of as a heterozygote (following the usage of Bateson), hence the term heterozygosis (used by Spillman, '09) refers to that germinal heterogeneity which results from the union of unlike gametes, and the stimulation to development which accompanies such a condition is spoken of as a "stimulus of heterozygosis," or "heterozygotic stimulation," meaning the stimulating effects of hybridity or the stimulation due to differences in uniting gametes. The converse fact of a reduction in vigor accompanying a return to a homozygous condition is therefore said to be due to, or result from, homozygosis. Shull ('14) has proposed the term "heterosis" to designate this increase in development which may result from a heterozygous condition; hence, heterosis, as used here, will be considered synonymous with "hybrid vigor" or "stimulus accompanying heterozygosis," in whatever form this may be manifested or whatever cause or causes it may be due to. Shull proposed this term, as he says, ". . . . to avoid the implication that all the genotypic differences which stimulate cell-division, growth, and other physiological activities of an organism, are Mendelian in their inheritance and also to gain in brevity of expression. . . ." Hence the term heterosis is not meant as a mere contraction of heterozygosis and is not synonymous with it. The adjective "heterotic" has also been proposed and such an expression as "heterotic stimulation" is synonymous with heterosis.

Early Investigations with Plants.

Certain evidence remains from the carvings of the ancient Egyptians to show that they had some conception of a sexuality in plants. However, it was not until the last of the 17th century, when Camerarius first demonstrated such condition, that interest in the production of artificial hybrids began. It is significant that the first artificial hybrids to be systematically studied, those of Kölreuter (1776), furnished some of the best examples of heterosis. Kölreuter made many interspecific crosses in *Nicotiana, Dianthus, Verbascum, Mirabilis, Datura and others,* many of which astonished their producer by their greater size, increased number of flowers and general vegetative vigor, as compared to the parental species entering into the cross. Concerning one of the tobacco crosses he says: (pp. 57–58) "Hybrids obtained from the cross of *Nicotiana maj.* ♀ and *glut.* ♂ produced a far greater number of flowers and grew to an uncommonly greater height and a much greater circumference than the pure species under the same conditions; the height of the plants which were kept in the hot bed or were set out in the field after they had obtained full growth, amounted to eight feet and 1 to 10 inches; the whole circumference of the branches to 24 feet; the largest diameter of the stalks from 2 inches to 2 inches and 3 lines; and the largest leaves were 2 feet, 2 inches and 9 lines long and 1 foot and 4 inches wide. Never has anyone seen more magnificent tobacco plants than these were."

Thomas Andrew Knight (1799) was one among several at that time who experimented with hybrids with the view of producing more desirable varieties of vegetables, flowers and fruits. Knight observed many instances of high vigor resulting from crossing; among these we note the following remarks about a cross between two varieties of peas.

> (P. 200) "By introducing the farina of the largest and most luxuriant kinds into the blossoms of the most diminutive and by reversing this process, I found that the powers of the male and female in their effects on the offspring, are exactly equal. The vigor of the growth, the size of the seeds produced, and the season of maturity, were the same, though the one was a very early, and the other a very late variety. I had, in this experiment, a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet; whilst the height of the large and luxuriant kind was very little diminished."

It is evident that, in these crosses, Knight was dealing with dwarf and standard peas and the dominance of standardness is expected. A sufficient number of cases, however, were observed in which the crosses were more vigorous than an average of the parents to convince him that "nature intended that a sexual intercourse should take place between neighboring plants of the same species." It was this principle which Darwin elaborated 50 years later.

Sageret ('26) reports vigorous hybrids in *Nicotiana* and also between different types of the Cucurbitaceae. Among other things he notes that in human crosses between one individual which shows a hereditary pathological condition and a normal individual, that the disease disappeared in the first generation but reappeared in the second and following generations. Wiegmann ('28) gives instances of hybrids in the Cruciferae which showed distinct evidences of heterosis.

Probably the most extensive series of experiments on hybridization were those of Gärtner ('49) and of Focke ('81). According to Lindley ('52) Gärtner made 10,000 crosses between 700 different species and produced 250 different hybrids. Many of these hybrids showed distinct evidences of heterosis, and this phenomenon was manifested in many different ways. Gärtner speaks especially of their general vegetative luxuriance, increase in root development, in height, in number of flowers and their hardiness and early and prolonged blooming. Focke made equally extensive observations and catalogues his own experiments with many of those made previously. His valuable book shows clearly that the phenomenon of heterosis is widespread and may be expected in the gymnosperms and pteridophytes as well as in the angiosperms. Both the works of Gärtner and of Focke have been so thoroughly reviewed in recent times (East and Hayes '12) in connection with the problem in hand that it would be a needless repetition to say more about their results here. Special points in their observations, as they supplement the experiments recorded here, will be referred to later.

While the work of Gärtner and Focke must always rank high as contributions to our knowledge of genetics one cannot refrain from remarking that they both missed by their extensive studies of many species the point which Mendel discovered by his intensive and careful study in one species.

Naudin ('65) next to Mendel will always be remembered, no doubt, as the first to conceive of a method in the uniformity of the first generation and the variability of the second. His conception of the segregation of parental qualities as a whole leads up naturally to Mendel's law whereby the characters of the parents segregate as units and when finally appreciated the chaotic observations of Gärtner, Focke and their contemporaries began to be understood as orderly facts. In Naudin's classical experiments there are many excellent examples of heterosis. Out of 36 interspecific crosses which he made in *Papaver, Mirabilis, Primula, Datura, Nicotiana, Petunia, Digitalis, Linaria, Luffa, Coccinea* and *Cucumis*, 24 show positive evidence of heterosis. Among the most notable crosses in this respect was that of *Datura Stramonium* with *D. Tatula* in which both reciprocal hybrids were twice as tall as either parent. Concerning the Datura crosses Naudin says:

> "A shape very much taller than the two parental types, and the premature falling off of the flowers in the first dichotomies, which leads to tardy fructification are the principal characteristics of this hybrid of which all the plants in the collection present the greatest uniformity. We shall see that these different characteristics appear in all the hybrids of this section of the genus Datura."

Mendel ('65) also records instances of heterosis in his pea hybrids as is shown in the following passage:

"The longer of the two parental stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different lengths are crossed. Thus, for instance, in repeated experiments, stems of 1 foot and 6 feet in length yileded without exception hybrids which varied in length between 6 feet and 7½ feet."

THE OBSERVATIONS OF DARWIN UPON PLANTS.

Of all the contributors to our knowledge of the effects of inbreeding and crossbreeding no one has collected as many facts as Darwin ('75, '77). Although undoubtedly much confusion and misunderstanding have resulted from Darwin's conclusions on this problem, one cannot but admire his painstaking efforts to accumulate facts from the behavior of many species of plants through many generations of crossing and selfing before advancing his conclusions. No one was more frank to acknowledge the discrepancies between the facts as he found them and the conclusions he drew from them. Those parts of his results which were not clear to Darwin are clearer to us through our knowledge of Mendelism of which he was not permitted to know. Since his method of experimentation, and the results obtained are familiar to all interested in the problem at hand no extensive review of his work is necessary. Only a brief summary of the results obtained and the conclusions which he drew from them will be given here, reserving a more detailed review of special parts for a later part of this paper.

Among animal breeders in Darwin's time it was a common belief that whatever evil effects resulted from more or less close inbreeding were due to the accumulation of abnormal, diseased, or morbid tendencies in the offspring of parents which possessed such tendencies. Darwin refused to ascribe any large part of the effects of inbreeding to this cause because he knew so many cases were weakened and reduced types of both plants and animals which gave vigorous progeny when crossed among themselves. Instead of an accumulation of the undesirable traits of both parents the very reverse seemed to be true. Had Darwin known of the way by which recessive characters may exist for many generations without making their appearance, doubtless his views on this point would have differed materially.

Darwin clearly thought that the evil effects of inbreeding kept on accumulating until eventually a plant or animal propagated in that manner was doomed to extinction. His own results came far short of proving such an assumption. The two wild plants with which inbreeding was practiced the longest—*Ipomea* and *Mimulus*—showed very little further loss of vigor after the first generation. What these experiments did show, most clearly, was that there was segregation of the inbred stock into diverse types which differed in minor, visible, heriditary characters and which also differed in their ability to grow. In both species plants appeared which were superior to other plants derived from the same source and some were even equal or superior in vigor to the original cross-pollinated stock. They differed from this race, however, most noticeably in the uniformity of all visible characteristics.

After several generations of inbreeding Darwin found that it made no difference in the resulting vigor, whether the plants in an inbred lot were selfed or were crossed among themselves. This he correctly attributed to the fact that the members of such an inbred strain had become germinally alike. From his views on the effect of the environment on organisms, it is easy to see why he attributed this approach to similarity in inherited qualities to the fact that the plants were grown for several generations under the same conditions. This view he thought was supported by the fact that crosses of his selfed lines with the intercrossed lines (also inbred, but to a less degree) did not give as great increase in vigor as the crosses of either lines with a fresh stock from distant regions. The crosses between two inbred lines did give a noticeable increase in vigor, in many cases, equaling the original variety. This is illustrated in the *Dianthus* crosses in which the selfed line was crossed with the intercrossed line and with a fresh stock. The ratio of both crosses to the selfed plants in height, number of capsules and weight of seed produced is as follows:

	Selfed X Inter-crossed	Selfed X Fresh stock
Height, compared to selfed	100:95	100:81
No. Capsules, compared to selfed	100:67	100:39
Weight of seed, compared to selfed	100:73	100:33

Like Darwin we now attribute the greater increase of vigor in a cross with distinct stocks to a greater germinal diversity although we may differ in our ideas as to the way in which that diversity was brought about. Whatever may be the explanation of that, credit is due Darwin for being the first to see that it was not the mere act of crossing which induced vigor but the union of different germinal complexes. This he states clearly in the following sentences (Cross and Self Fert., p. 270):

> " These several cases taken together show us in the clearest manner that it is not the mere crossing of any two individuals which is beneficial to the offspring. The benefit thus derived depends on the plants which are united differing in some manner, and there can hardly be a doubt that it is in the constitution or nature of the sexual elements. Anyhow, it is certain that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during the several generations to different conditions."

Recent Investigations with Plants.

Although Darwin was the first to attack the problem from the standpoint of determining the effects of inbreeding, it is doubtful if he clearly recognized that the same phenomenon was concerned in both inbreeding and crossbreeding. It remained for Shull ('08, '09, '10, '11 and '14), East ('08, '09) and East and Hayes ('12) to bring out clearly the fundamental similarity of both processes and to put the matter in such a light that a far clearer understanding of the nature of the effects of inbreeding has resulted.

Their conclusions in regard to the causes of the effects of inbreeding and crossing were for the most part entirely new and dependent for their support upon the Mendelian principle of the segregation and recombination of inherited qualities as independent units and upon Johannsen's genotype conception of heredity. Stated briefly their main tenets, based upon their own careful experiments and a survey of previous results bearing upon the problem, are as follows:

1. Inbreeding automatically sorts out into homozygous, pure breeding lines, the diverse and variating complex of hereditary characters found in a naturally cross-pollinated species.

2. Although complete homozygosity is difficult to attain in practice, after several generations of selfing, members of the resulting inbred lines are uniform among themselves but the respective lines may differ greatly among each other in visible

hereditary characters. The strains may also differ in their power of development, some being larger, stronger and more productive than others at normal maturity. Some individuals are often isolated which are so lacking in necessary characters that they perish because of inability to reproduce themselves.

3. Those inbred strains which are able to survive finally become constant; no further reduction in vigor or change in visible characters is to be expected by continued inbreeding. These constant types are thus quite comparable to naturally self-fertilized species and may exist indefinitely.

4. When these pure breeding types are crossed there is commonly an immediate and striking increase in general size and vigor to be expected in the resulting first hybrid generation.

To account for this increase in development, following a cross, a physiological stimulation was postulated which accompanied heterozygosity of hereditary factors and disappeared as the organisms approached homozygosity. As an illustration the union of factor "A" with it allelomorph "a" was considered to evolve developmental energy which was lacking when either "A" or "a" were united with themselves. This stimulus to development was considered to be due to the union of unlike factors alone and to have an effect quite different from whatever part each factor had by itself in the development of the organism. Stated in their own words the main conclusions of East and Hayes ('12) are as follows (p. 8):

> "1. Mendel's law—that is, the segregation of character factors in the germ cells of hybrids and their chance recombinations in sexual fusions—is a general law.
>
> 2. Stimulus to development is greater when certain, or possibly all, characters are in the heterozygous condition than when they are in a homozygous condition.
>
> 3. This stimulus to development is cumulative up to a limiting point and varies directly with the number of heterozygous factors in the organism although it is recognized that some of the factors may have a more powerful action than others."

It was clearly apparent to recent investigators that many of the unfavorable characters which appear on inbreeding a naturally cross-pollinated species are recessive characters which are segregated out of the original complex. In a naturally crossed species, these are hidden from sight on account of being continually crossed with dominant characters. That dominance of factors could in any way be an essential factor in the vigor and excellence of hybrids, an idea first proposed by Keeble and Pellew ('10) and also by Bruce ('10), has not been accepted by most writers on this subject. They considered dominance to be totally inadequate to account for the widespread and almost universal occurrence of heterosis in plants and animals and the fact that nearly all naturally cross-fertilized domesticated species are reduced by inbreeding.

Collins ('10) has shown clearly that many crosses between varieties of Indian corn already widely crossed among themselves and grown in the same regions may not give any increase in productiveness, but when these same varieties are crossed with varieties from distinct geographical regions great increases in productiveness are obtained. Further evidence as to the occurrence of heterosis is seen in the many publications which have appeared from time to time urging the commercial utilization of this hybrid vigor as a method of increasing production in many plants. Among these are Beal ('76–'82), McCleur ('92), Morrow and Gardner ('93–'94), Swingle and Webber ('97), Hayes and East ('11), Hartley ('12), Wellington ('12), Hayes ('13), Hayes and Jones ('16).

In view of the innumerable cases in which an increase in development, in some character, results from crossing and the converse fact of reduction following subsequent inbreeding, of which the preceding paragraphs refer to only a small fraction, it is surprising to note such radically diverse opinions as are held by Burck ('08) and championed by Stout ('16).

Stout attributes the following statements to Burck: (p. 418)

> "That (1) plants that are regularly self-fertilized show no benefits from crossing and that (2) nowhere in wild species is there evidence of an injurious effect from self-fertilization, and that there is abundant evidence of continued vigor and high fertility resulting from long continued self-fertilization."

If by the first statement is meant that crossing between members of the same variety or between individuals of a uniform species does not give an increase in development such a result would be expected because of the germinal similarity brought about by long continued selfing and elimination by selection, either natural or artificial, of all but one type. On the other hand, there is abundant evidence to show that crossing between different varieties or between different wild species of self-pollinated plants often results in striking increases in size and vigor. It is only necessary to refer to the work of Kölreuter, Knight, Gärtner, Naudin and Mendel where many crosses between different species or between distinct types of *Nicotiana*, *Pisum*, and *Lathyrus*—plants which are naturally self-fertilized—give unmistakable evidence of heterosis.

Turning to the effects of inbreeding, almost no long-continued experiments have been carried out with strictly wild cross-pollinated species of plants. Collins ('18) in a brief note states that teosinte, a semi-wild relative of maize, is not affected by inbreeding to the extent that maize is. That there is "abundant evidence of continued vigor and high fertility resulting from long continued self-fertilization" no one longer doubts. There is, however, hardly enough evidence from plants, so far on record, to justify the sweeping statement, which the quotation implies, that cross-fertilized wild species are never reduced by inbreeding.

What evidence there is indicates that naturally crossed wild species are not reduced by inbreeding to anything like the extent that domesticated races are. More will be said about this difference between wild and domesticated races later. There is some evidence, however, to show that strictly wild species are affected by inbreeding. Darwin compared the progeny of artificially self-fertilized plants with the progeny of artificially intercrossed plants of many wild species. Many of these species were such as were for one cause or another almost completely cross-fertilized in their natural state at all times. Although the difference may be slightly exaggerated there can be no question but that the difference in the first generation which Darwin obtained between the selfed plants and the intercrossed plants represents in many cases the effect which inbreeding has upon these plants. As examples of widely crossed wild species in which a reduction in the first generation of inbreeding was obtained by Darwin, one can, therefore, cite: *Digitalis purpurea, Linaria vulgaris, Sarothamnus scoparius* and *Reseda lutea.*

Moreover, no matter how much domestication may change plants from the wild, one cannot cast aside, as of no consequence, the results obtained from cultivated plants.

Investigations with Animals.

According to Darwin, the mule, that classic example of hybrid vigor, was known in the time of Moses, when its hardihood and general good qualities doubtless endeared this animal to the Jews no less than to the Southern cotton planters of to-day. A similar cross of the ass with the wild zebra according to Riley ('10) gives a first generation hybrid animal of considerable merit.

In the early history of the establishment and fixation of breeds of livestock we note in Darwin's "Animals and Plants under Domestication" that certain crosses between different breeds often resulted in progeny excelling individuals of either parent breed; just as to-day it is not an uncommon practice for livestock raisers to cross certain well-established breeds to produce crossed animals to feed for market.

In looking over the reports of experiments designed to test the effects of crossing in both wild and domesticated animals there is little disagreement as to the results usually obtained. All are practically in accord that crossing diverse breeds or races of animals, if not too distantly related, may frequently result in vigorous, large and fertile offspring, excelling either parent in one or more respects. For example, Castle et al ('06) find that crossing diverse stocks of Drosophila results in an increase in fertility and that matings between different inbred lines give progeny with increased fertility up to or beyond that of the more fertile parental race. In Meriones Bonhote ('15) states that fertility and size are increased by crossing. Castle ('16) has crossed domesticated races of guinea-pigs with the wild species from Peru with the result that there is a noticeable increase in body weight over either pure parent. Gerschler ('14) crossed different genera of fishes and obtained large increases in size in the first hybrid generation. *Xiphophorus strigatus*, of which the males were 43.0 cm. long and the females 52.0 cm., when crossed with *Platypoecilius maculatus*, of which the males were 26.0 and the females 31.0 cm. in length, gave hybrid males 54.0 cm. and females 57.5 cm. He speaks of their "gigantic size."

Fischer ('13) in his study of the Rehoboth hybrids, a race in South Africa resulting from a mixture of Hottentots and Boers, states that their average height is somewhat greater than either the Hottentots or the Hollanders and South Germans of whom statistics are available. All the members of this new race are not first generation crosses by any means, but they are not many generations removed and crossing with the pure Hottentots, the shorter parental race, is frequent.

When, however, the literature on the effects of inbreeding in animals is examined one finds the greatest diversity of facts and opinions. We find the extreme views of Kraemer ('13) who states that "continued inbreeding always must result in weakened constitution, through its own influence" together with the equally extreme and biased opinion of Huth ('75) that in mankind there is no injurious effect resulting from consanguineous marriages which cannot be accounted for on other grounds.

Crampe ('83), Ritzema-Bos ('94), Guaita ('98), Fabre-Domengue ('98) and Weismann ('04) by inbreeding mammals and birds found that the process was accompanied by decreased fertility, attended more or less commonly by lack of vigor, diminution in size, and pathological malformations. Castle, Carpenter et al ('06) inbreeding extensively the fruit fly, Drosophila, maintained fertility by selection, so that at the end of 59 generations of brother and sister matings in one line the fecundity was no less at the end of the experiment than it was at the start. There was some indication of reduction in size of inbred flies when compared to normally crossed stock flies reared under the same conditions. Furthermore, fertility was increased by crosses between certain inbred lines and between the inbred lines and stock flies. From this fact and from the fact that their experiments show that the number of flies in a brood fluctuates greatly, due to temperature and food conditions, it is not positive that inbreeding was wholly without injurious effects. It is evident that their experiments do show clearly:

1. That inbreeding results in strains of unequal fertility.

2. That the occurrence of absolute sterility was pronounced in the first part of the experiment with the "A" line but almost entirely disappeared in the later part of the experiment. The figures as I have calculated them from their table I, p. 736, are as follows:

		Percent of matings totally sterile
Generations	6 to 24	17.80
"	25 to 42	18.47
"	43 to 59	3.37

This result is to be expected on the view that inbreeding isolates homozygous individuals and these whenever sterile are, of course, eliminated.

Moenkhaus ('11) and Hyde ('14) by similar inbreeding experiments with Drosophila have also found that sterility is increased in the first stages of inbreeding but tends to be eliminated after this process is long continued. Hyde found definite evidence that inbreeding caused reduction in size, vigor, rate of growth, longevity and fecundity and that there was a return to the normal condition on crossing. As in the other experiments Hyde found that selection was an effective agent in controlling sterility.

Both Whitney (12a) and A. F. Shull (12a) have shown that inbreeding and crossbreeding have considerable effect upon the rotifer, *Hydatina Senta,* in the size of family, number of eggs laid per day, rate of growth and in the difficulty of rearing the animals.

King ('16) has obtained results with albino rats which are quite in agreement with those of Castle. By growing about one thousand rats in each inbred generation, and selecting the best individuals for mating, animals have been carried through 22 generations of brother and sister matings without loss of size, fertility, longevity, resistance to disease and with constitutional vigor unimpaired. This writer states:

> "The results so far obtained with these rats indicate that close inbreeding does not necessarily lead to a loss of size or constitutional vigor or of fertility, if the animals so mated came from sound stock in the beginning and sufficient care is taken to breed only from the best individuals."

Here, as in Drosophila, inbreeding isolates diverse types of different degrees of excellence. In this case individuals are obtained which surpass the original stock before inbreeding. Thus we have "Goliaths" among inbred rats as Darwin found "Heroes" in morning-glories.

> Castle ('16) has found that in inbred rats "races of fair vigor and fecundity can be maintained under these conditions, but that when two of these inbred races are crossed with each other, even though they have their origin in a small common stock many generations earlier, an immediate and striking increase of fecundity occurs."

The evidence from relationship marriages in human stocks is even more conflicting and conclusions still more difficult to draw. Huth ('75) has certainly done a service in showing that consanguineous marriages seldom result in the disastrous effects usually attributed to them. He has shown that incest was not a rare custom and that races which have undergone such practices are many of them far from weak. Certainly, races have practiced close intermarriage for many generations with no marked deterioration. The Persians, Spartans, the ruling classes among the Egyptians and Polynesians are cited by Huth in support of this assertion. The data from human matings, however, are of little value since the close unions are seldom continued many generations in succession, and the results from isolated communities mean little, since often the original stock is exceedingly diverse so as to make the resulting races extremely heterogeneous in hereditary constituents. This is particularly true of the Rehoboths and the Pitcairn Islanders which are cited as instances of close intermarrying without loss of racial vigor.

Looking over the experiments upon animals it seems as unwise to expect that inbreeding may not have some deleterious effects, which, in some cases at least, cannot be overcome by the most rigid selection, as it is to hold that inbreeding must always result injuriously. It is to be expected that all breeds of domestic animals and wild species will not be equally affected by inbreeding. Domesticated animals in many cases are more widely crossed and diversified than wild species, and those characters affected by inbreeding are more accentuated. Certain wild species, which, by their mode of life, are forced to endure long periods of isolation, and consequently more or less close inbreeding, would be expected to show less change under artificial inbreeding. Finally, as I shall attempt to show that there is no longer a question as to whether or not inbreeding, *in itself*, is injurious, the effect which inbreeding will have on any organism depends solely on the hereditary constitution of that organism at the time the inbreeding process is commenced.

UNIVERSALITY OF HETEROSIS.

From the literature on the subject of crossbreeding it is to be observed, therefore, that the occurrence of an incentive to increased development accompanying germinal heterogeneity is widespread, as it has been noted in plants in the angiosperms, gymnosperms and pteridophytes, and according to Britton ('98) there is even some slight evidence that heterosis occurs in the sporophyte of the bryophytes.

In animals the mammals, birds, fishes, insects and rotifers show the phenomenon of heterosis although in some of the unicellular animals, as we shall see later, the evidence is not so clear.

I shall now take up, in some detail, experiments on inbreeding and crossbreeding in cultivated plants, principally in maize.

A THEORETICAL CONSIDERATION OF INBREEDING.

Up to the present time it has been maintained that the effects of inbreeding were of two kinds, an isolation of homozygous biotypes together with a loss of a physiological stimulation which was considered to be roughly proportional to the number of heterozygous allelomorphs present in the organism at any time. The reduction of the number of heterozygous allelomorphs in an inbred population is automatic and varies with the closeness of inbreeding.

Pearl ('15) on the basis of the number of ancestors which make up the pedigree of any individual has worked out a coefficient of inbreeding which is an indication of the degree to which that individual has been inbred. The fewer the number of ancestors the greater the degree of inbreeding which may vary from no inbreeding, in which no one ancestor appears more than once in the pedigree of an individual, to the closest kind of inbreeding in which no more than one ancestor is concerned in any one generation in the production of an individual (self-fertilization). The latter degree is only approached by hermaphroditic plants and animals, which are capable of self-fertilization and in functionally bisexual animals and plants by brother and sister matings. This statement of inbreeding must, of course, leave out of consideration any germinal change which might take place by means other than hybridization and as Castle ('16) has pointed out is modified by the differences in heterozygosity of the ancestors making up the pedigree.

The automatic reduction in the number of heterozygous allelomorphic pairs in an inbred population, by self-fertilization, follows the well known Mendelian formula by which any heterozygous pair forms in the next generation 50 percent homozygotes and 50 percent heterozygotes in respect to that pair. Since the homozygotes must always remain homozygous and the heterozygotes are halved each time and one half added to the homozygotes the reduction in the number of heterozygous elements proceeds as a variable approaching a limit by one half the difference in each generation. The curve illustrating this condition is shown as No. 1 in Fig. I. Various formulæ dealing with inbreeding have been discussed by East and Hayes ('12), Jennings ('12, '16), Pearl ('15) and Bruce ('17).

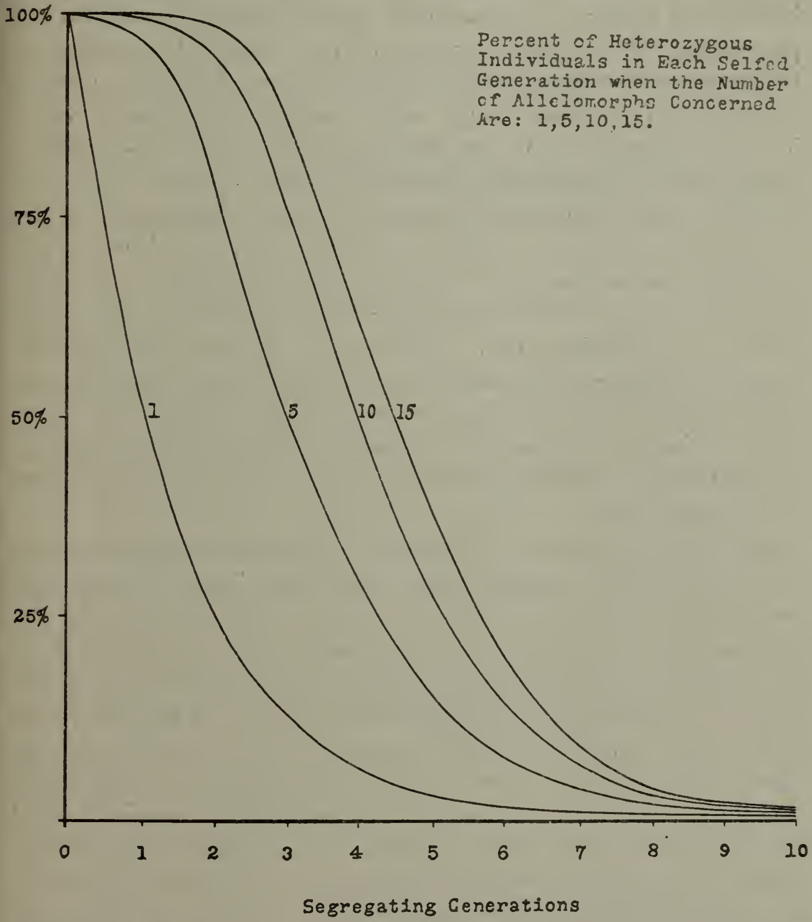


Figure I. The percent of heterozygous individuals and the percent of heterozygous allelomorphic pairs in the whole population in each generation of self-fertilization.

It should be remembered that this reduction applies only to the whole population in which every member is inbred and all the progeny grown in every generation. In practice, in an inbreeding experiment, only one individual in self-fertilization or two individuals in brother and sister matings are used to produce the next generation. Thus the rate at which complete homozygosis is approached depends on the heterozygosity of the individuals chosen. Theoretically in any inbred generation the progenitors of the next generation may either be completely homozygous or completely heterozygous or any degrees in between depending upon chance. The only condition which must follow in self-fertilization is that no individual can ever be more heterozygous than its parent but may be the same or less. Thus it is seen that inbreeding, as it is practiced, may theoretically never cause any reduction in heterozygosity, or it may bring about complete homozygosity in the first inbred generation. In other words the rate at which homozygosity is approached may vary greatly in different lines. However, as the number of heterozygous factors at the commencement of inbreeding increases the more nearly will the reduction to homozygosity follow the curve shown because the chance of choosing a completely homozygous or completely heterozygous individual in the first generations will become less.

In Table 1 is shown the theoretical classification of the progeny of a self-fertilized organism which was heterozygous with respect to 15 independent mendelizing units. It will be seen that the bulk of the individuals lie between classes 6 and 11 where none of the members are heterozygous for more than 10 factors nor less than 5. In other words any individual selected for the progenitor of the next generation would probably come from the middle classes and therefore it would be heterozygous for about half the factors that its parent was. The chance that this individual would not come from the mid-classes between 6 and 11 would be about 1 out of 10. The chance that it would be completely homozygous or completely heterozygous would be 1 out of 32,768. If 20 instead of 15 factors were concerned the chances would be 1 out of 1,048,576.

This condition by which the progenitor of each generation tends to be half as heterozygous as its parent holds true for any number of factors and in every generation. Also in Table 1 it can be seen that the progeny as a whole has an equal number of heterozygous factor pairs as homozygous factor pairs in respect to those

TABLE 1. THE THEORETICAL NUMBER AND RATIO OF INDIVIDUALS IN THE CLASSES OF DIFFERENT DEGREES OF HETEROZYGOSITY, AFTER RECOMBINATION, WHEN FIFTEEN MENDELIZING UNITS ARE INVOLVED.

Class No.	The total number of individuals in all the possible mendelian recombinations in F_2 when 15 factors are involved.	Ratio of individuals in the classes with different number of heterozygous and homozygous factors–coefficients $(a+a)^{15}$	The number of factors in respect to which the different classes are:		The total number of heterozygous and homozygous factor pairs in all the individuals in each class:	
			Heterozygous	Homozygous	Heterozygous factor pairs	Homozygous factor pairs
1	32,768	1	15	0	15	0
2	491,520	15	14	1	210	15
3	3,440,640	105	13	2	1,365	210
4	14,909,440	455	12	3	5,460	1,365
5	44,728,320	1,365	11	4	15,015	5,460
6	98,402,304	3,003	10	5	30,030	15,015
7	164,003,840	5,005	9	6	45,045	30,030
8	210,862,080	6,435	8	7	51,480	45,045
9	210,862,080	6,435	7	8	45,045	51,480
10	164,003,840	5,005	6	9	30,030	45,045
11	98,402,304	3,003	5	10	15,015	30,030
12	44,728,320	1,365	4	11	5,460	15,015
13	14,909,440	455	3	12	1,365	5,460
14	3,440,640	105	2	13	210	1,365
15	491,520	15	1	14	15	210
16	32,768	1	0	15	0	15
16 (n+1)	1,073,741,824 $(2^n)^2$	32,768 2^n	15 n	15 n	245,760 $\frac{1}{2}(n.2^n)$	245,760 $\frac{1}{2}(n.2^n)$

characters in which the parent was heterozygous. So it is that in practice the reduction in growth accompanying inbreeding (on the assumption that heterosis is correlated with heterozygosity) is greatest at first, rapidly becomes less and finally ceases for all practical purposes.

If there were no deviating factors the curve of reduction should, in the majority of cases, approximate curve 1 in Fig. I. However, it has never been assumed that the amount of heterosis was perfectly correlated with the number of heterozygous factors. Moreover, since the heterozygous individuals are more vigorous than the homozygous, selection, either unconscious or purposeful, would favor the more heterozygous so that the tendency might be that the actual approach to homozygosity would not proceed at as fast a rate as the theoretical curve would indicate.

Self-fertilization is the quickest and surest means of obtaining complete homozygosis for the reason that whenever any pair of allelomorphs becomes homozygous it must always remain so long as self-fertilization takes place, whereas in brother and sister mating a homozygote may be mated to a heterozygote. Thus we see from Jennings' ('16) tables that 6 generations of self-fertilization are more effective than 17 generations of brother and sister matings in bringing about homozygosis. The reduction in heterozygous allelomorphs in a population as a whole follows curve 1 in Fig I irrespective of the number of factors concerned, provided, as stated before, that a random sample of all the different classes of individuals are selfed and used as progenitors for the next generation and that there is equal productiveness and equal viability. If the heterozygotes are more productive, as in many cases they are, the reduction to complete homozygosity will be delayed.

The number of completely homozygous individuals in any generation, inbred by self-fertilization, differs according to the number of heterozygous factors concerned at the time that the inbreeding process is commenced. The curves showing the reduction in the number of individuals heterozygous in any factors, where, 1, 5, 10 and 15 factors are concerned at the start are given in Fig. I calculated from the formula given by East and Hayes ('12). The curve for the reduction in heterozygous individuals, where one factor only is concerned, is identical with the curve showing the reduction in heterozygous factors in an inbred population where any number of factors are concerned. In any case almost complete homozygosity is reached in about the tenth generation on the average, although theoretically it may be reached in the first generation, or may never be reached when a single individual is used in each generation to perpetuate the line.

Assuming, then, that the loss of the stimulation, accompanying heterozygosity, is correlated with the reduction in the number of heterozygous allelomorphs we should expect to find the decrease of heterosis greatest in the first generations, rapidly becoming less until no further loss is noticeable in any number of subsequent generations of inbreeding, and that, on the average, the loss will become negligible at about the eighth generation and from then on no further marked change will take place. Some cases are to be expected in which stability is reached before this generation and some cases in which it is not reached until later or may even theoretically never be reached. With these assumptions in mind let us see what are the actual results of long continued inbreeding in maize.

The Results of Inbreeding the Naturally Cross-pollinated Maize Plant.

The behavior of maize during six generations of inbreeding by self-fertilization has already been reported by East and Hayes ('12). The same inbred strains have been continued and in some cases the results up to the eleventh generation are given here.

In the previous publication it was stated that a loss of vegetative vigor has followed every case of inbreeding in maize. Some plants had been obtained which were unable to reproduce themselves. Those strains which were maintained became uniform but differed considerably from each other. It was considered at the end of the period of inbreeding that some strains were appreciably better than others in their ability to yield. Six additional years of inbreeding with this material has confirmed, in the main, these conclusions. A further appreciable reduction in productiveness, however, has taken place in all lines together with certain changes in various parts of the plants.

The original experiment began with four individual plants obtained from seed of a commercial variety of Leaming dent corn grown in Illinois. This variety was given the number 1 and the four plants which were self-pollinated and selected for continuation of the inbreeding experiment were numbered 1-6, 1-7, 1-9 and 1-12. These four strains were continued each year by self-pollination. In the second inbred generation two self-pollinated plants in the 1-7 line were saved for seed and from them two inbred lines were split off which therefore came originally from one line inbred two generations. These are numbered 1-7-1-1 etc. and 1-7-1-2 etc. In a similar way these, and the other inbred lines, were further split up in subsequent generations. After the experiment was started with the dent corn inbreeding was commenced with other material. Two inbred strains of floury corn, Nos. 10-3 and 10-4, originally from the same variety, have been maintained and also two strains of flint, Nos. 5 and 29, and two strains of popcorn Nos. 64 and 65. Chief attention has been paid to the inbred strains of Leaming corn (the longest inbred) and most of the data presented here have resulted from this material. Many other varieties besides these have been inbred for many generations in connection with other investigations and while they are not specifically mentioned the observations as a whole include these.

In Tables 2 and 3 the yield and height of some of these inbred strains are given. In 1916 seed of the original Leaming variety was obtained which had been grown in the meantime in the same locality whence it was originally secured and was grown for comparison with the inbred strains. This variety in Illinois in 1905 yielded at the rate of 88 bushels per acre, and in Connecticut in 1916 at the rate of 74.7 bushels. While there is no proof that any change has not taken place in the original variety there is no reason to suppose that it has changed to any great extent. Grown under the same conditions in 1916 the four inbred Leaming strains yielded from one-third to one-half as much as the original non-inbred variety.

With regard to rate of reduction in yield or the constancy of the varieties during the later generations it is difficult to draw conclusions from these figures owing to the fluctuation in yield from year to year due to seasonal conditions and to the difficulty of accurate testing in field plot work, which is recognized by all who have made such tests. As was stated in the first report the yields for 1909 were too low and in 1911 much too low on account of poor seasons. No yields were taken on any of the strains in

TABLE 2. THE EFFECT OF INBREEDING ON THE YIELD AND HEIGHT OF MAIZE.

Year grown	No. of generations selfed	Four inbred strains derived from a variety of Leaming dent corn.							
		1-6-1-3-etc.		1-7-1-1-etc.		1-7-1-2-etc.		1-9-1-2-etc.	
		Yield bu. per acre	Height inches	Yield bu. per acre	Height inches	Yield bu. per acre	Height inches	Yield bu. per acre	Height inches
1916	0	74.7	117.3	74.7	111.3	74.7	117.3	74.7	117.3
1905	0	88.0	....	88.0	....	88.0	....	88.0	....
1906	1	59.1	....	60.9	....	60.9	....	42.3	....
1908	2	95.2	....	^{1907}59.3	....	^{1907}59.3	....	51.7	....
1909	3	57.9	....	^{1908}46.0	....	^{1908}59.7	....	35.4	....
1910	4	80.0	....	63.2	....	68.1	....	47.7	....
1911	5	27.7	86.7	25.4	81.1	41.3	90.5	26.0	76.5
1912	6	....	....	....	....	....	....	^{1913}38.9	....
1913	7	41.8	....	39.4	....	....	....	^{1914}45.4	85.0
1914	8	78.8	96.0	47.2	83.5	58.5	88.0	^{1915}21.6	....
1915	9	25.5	....	24.8	....	....	....	^{1916}30.6	78.7
1916	10	32.8	97.7	32.7	84.9	19.2	86.9	^{1917}31.8	82.4
1917	11	46.2	103.7	42.3	78.6	37.6	83.8	....	....

TABLE 3. THE EFFECT OF INBREEDING ON THE YIELD OF MAIZE.

Year grown	No. of generations selfed	Two inbred strains of floury corn		One inbred strain of flint corn
		10-3-7-etc. Yield bu. per acre	10-4-8-etc. Yield bu. per acre	5-8-6-etc. Yield bu. per acre
1908	0	70.5	70.5	75.7
1909	1	56.0	43.0	47.5
1910	2	67.0	48.7	36.1
1911	3	39.1	29.3	11.5
1912	4	....	....	....
1913	5	32.2	49.5	30.4
1914	6	....	52.6	38.1
1915	7	....	....	....
1916	8	13.9	16.6	18.3
1917	9	26.6	24.0	......

1912. The yields in 1914 are too high and in 1915 too low for the same reasons. Also in 1915 the yields are unreliable because only a few plants were available to calculate yields from as most of them were used for hand pollination. During the last three years of the test samples of corn have been dried to a uniform moisture basis and the yields calculated to bushels of shelled corn per acre with 12 per cent. moisture. This has probably had a tendency to reduce the yields somewhat as these inbred strains are very late in maturing and consequently contain large amounts of water.

With these points in mind an examination of the table shows that from the beginning of the experiment to the ninth generation there has been a tremendous drop in productiveness, so that in that generation the strains are approximately only one-third as productive as the variety before inbreeding. From the ninth to the eleventh generation there has been at least no reduction in productiveness, and practically no change in visible plant or ear characters.

In the previous publication it was stated (U. S. Dept. of Agric., B. P. I. Bull. 243, pp. 23-24) that

> . . . . "strain No. 6, is a remarkably good variety of corn even after five generations of inbreeding. It yielded eighty bushels per acre in 1910. The yield was low in 1911, but since all yields were low that year it can hardly be doubted that this strain will continue to produce good normal yields of grain...... The poorest strain, No. 12, is partially sterile, never fills out at the tip of the ear and can hardly exist alone. In 1911 it yielded scarcely any corn but will no doubt continue its existence as a partly sterile variety."

These statements will have to be modified somewhat. Although No. 6 is, in the eleventh generation, still the most vigorous inbred strain, as a producer of grain, however, it can hardly be considered to give "good normal yields." The plants, nevertheless, are perfectly healthy and functionally normal in every way except for an extreme reduction in the amount of pollen which they produce. The strain No. 12 was lost. Since the difficulty of carrying along any inbred strain is very great owing to failure to pollinate at the right time, attacks of fungus on the ear enclosed in a paper bag, and poor germination in the cold, wet weather common in New England at corn planting time, the loss of this strain might be easily accounted for without supposing that it simply ran out. It may be that this strain could have been perpetuated if sufficient effort had been put forth to do so. In view of the further reduction in the other strains, however, the maintaining of this strain would have been extremely difficult.

Complete records on the height of plant are wanting for many of the generations, and, unfortunately, in the first part of the inbreeding period. What figures are available certainly show that very little change in height has taken place in all four strains during the last seven generations. Strain No. 6 has increased in height, if anything. Height is less affected by environmental factors than is yield and in that respect is a more reliable indicator. However, great changes in the structure, size and productiveness may take place without height of plant being greatly altered.

From the figures given in Table 2 there is some evidence that these strains have reached about the limit of reduction in productiveness and that there has been very little change in the last three years. This, however, is not proven. The continuation of inbreeding is necessary for conclusive evidence on this point. As the crosses between individual plants within these inbred strains have given very little increase over the selfed strains, as will be shown later, and from the fact that almost no visible change has taken place in these four strains during the past three years that I have had them under observation, it seems apparent to me that the reduction in vegetative vigor and productiveness is very nearly at an end.

In Tables 4, 5, 6 and 7 are given the frequency distributions of height, length of ear, number of nodes and the number of rows of grain on the cob of the original, non-inbred Leaming variety and several inbred strains derived from this variety after nine or ten generations of selfing. All the plants from which the data were taken were grown on the same field in the same year. Four different plots of the variety were grown in different parts of the field and the data on these plots are given separately and totaled in the tables. It can be seen from these that no great variations in range, mean, standard deviation or coefficient of variability were caused by environmental factors. The pedigree numbers show the relationship of the several inbred strains to each other.

From these tables it can be seen that both height of plant and length of ear have been reduced, but in different degrees in different lines. In some strains reduction in height amounts to 40 inches and in length of ear to 3.5 inches. The reduction in

TABLE 4. FREQUENCY DISTRIBUTION OF HEIGHT OF PLANT OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Height of plant in inches.																		N.	A.	S. D.	C. V.
	58.5	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	113.5	118.5	123.5	128.5	133.5	138.5	143.5				
1 (Original	..	..	..	..	..	..	..	1	4	5	7	11	9	6	3	2	..	..	48	114.0±.91	9.40±.64	8.24±.56
1 non-inbred	..	..	..	..	..	..	..	2	2	4	4	10	8	11	13	5	1	..	60	119.2±.91	10.50±.64	8.81±.54
1 Leaming	..	..	..	..	..	..	..	1	1	4	15	8	9	6	7	3	0	1	55	116.3±.90	10.05±.65	8.64±.55
1 variety)	..	..	..	..	..	..	..	1	0	4	7	8	6	10	8	3	3	..	50	119.3±.98	10.30±.69	8.63±.58
Total....	..	..	..	..	..	..	..	5	7	17	33	37	32	33	31	13	4	1	213	117.3±.48	10.33±.34	8.81±.29
1-6-1-3-4-4-4-2-4-4-3	..	..	..	..	..	..	4	11	30	11	..	..	..	..	..	..	..	..	56	97.8±.36	4.05±.26	4.14±.26
1-6-1-3-4-4-4-2-4-1-2	..	..	..	..	..	..	5	22	24	10	..	..	..	..	..	..	..	..	61	96.7±.37	4.25±.26	4.40±.27
1-6-1-3-4-4-4-2-5-5-1	..	..	..	..	2	2	9	16	14	3	..	..	..	..	..	..	..	..	46	93.6±.57	5.75±.41	6.14±.43
1-6-1-3-4-4-4-2-5-3-1	..	..	..	..	..	..	..	7	11	26	8	4	..	..	..	..	..	..	56	102.7±.47	5.25±.33	5.11±.32
1-7-1-1-1-4-7-5-2-6-1	1	3	8	3	11	20	6	..	..	..	..	..	..	..	..	..	..	..	52	78.5±.71	7.65±.51	9.75±.64
1-7-1-1-1-4-7-5-2-1-1	2	3	1	6	9	12	19	6	..	..	..	..	..	..	..	..	..	..	58	82.2±.77	8.75±.55	10.64±.67
1-7-1-1-1-4-7-5-4-7-2	..	..	..	1	3	3	18	26	2	..	..	..	..	..	..	..	..	..	53	90.2±.46	4.95±.33	5.49±.36
1-7-1-1-1-4-7-5-4-5-2	..	..	1	1	1	7	16	7	5	..	..	..	..	..	..	..	..	..	38	88.7±.70	6.45±.50	7.27±.56
1-7-1-2-2-9-2-1-1-4-1	..	1	1	8	9	18	13	3	1	..	..	..	..	..	..	..	..	..	54	82.6±.61	6.65±.43	8.05±.52
1-7-1-2-2-9-2-1-1-1-3	..	..	1	1	2	8	8	18	11	2	..	..	..	..	..	..	..	..	51	91.2±.68	7.25±.48	7.95±.52
1-9-1-2-4-6-7-5-6-4	2	2	2	14	26	12	1	..	..	..	..	..	..	..	..	..	..	..	59	77.0±.52	5.95±.37	7.73±.48
1-9-1-2-4-6-7-5-3-3	..	..	..	10	22	25	3	..	..	..	..	..	..	..	..	..	..	..	60	80.3±.35	4.05±.25	5.04±.31

TABLE 5. FREQUENCY DISTRIBUTION OF LENGTH OF EAR OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Length of ear in inches											N.	A.	S. D.	C. V.
	2	3	4	5	6	7	8	9	10	11	12				
1 (Original	..	..	..	7	12	20	13	3	1	0	1	57	7.0±.12	1.33±.08	19.00±1.24
1 non-inbred	..	..	2	6	9	12	11	7	3	1	..	51	7.2±.15	1.61±.11	22.36±1.55
1 Leaming	..	..	2	1	7	19	19	9	3	1	..	61	7.6±.11	1.31±.08	17.24±1.08
1 variety)	..	..	1	1	4	14	18	18	3	..	..	59	7.9±.10	1.20±.08	15.19± .96
Total............	..	..	5	15	32	65	61	37	10	2	1	228	7.5±.06	1.43±.05	19.07± .63
1-6-1-3-4-4-4-2-4-4-3	..	1	5	8	16	29	..	..	..	..	..	59	6.1±.09	1.05±.07	17.17±1.18
1-6-1-3-4-4-4-2-4-1-2	..	..	2	7	29	19	1	..	..	..	..	58	6.2±.07	.81±.05	13.06± .82
1-6-1-3-4-4-4-2-5-5-1	..	2	7	11	7	8	10	1	..	..	..	46	6.0±.16	1.57±.11	26.17±1.95
1-6-1-3-4-4-4-2-5-3-1	..	..	3	5	6	25	16	1	..	..	..	56	6.9±.10	1.12±.07	16.23±1.05
1-7-1-1-1-4-7-5-2-6-1	..	7	27	28	..	..	..	..	..	..	..	62	4.3±.06	.67±.04	15.58± .96
1-7-1-1-1-4-7-5-2-1-1	3	5	25	22	1	..	..	..	..	..	..	56	4.2±.08	.84±.06	20.00±1.31
1-7-1-1-1-4-7-5-4-7-2	5	10	24	18	..	..	..	..	..	..	..	57	4.0±.08	.91±.06	22.75±1.51
1-7-1-1-1-4-7-5-4-5-2	..	9	12	14	1	..	..	..	..	..	..	36	4.2±.09	.83±.07	19.76±1.62
1-7-1-2-2-9-2-1-1-4-1	1	3	10	11	14	4	..	..	..	..	..	43	5.1±.12	1.19±.09	23.33±1.77
1-7-1-2-2-9-2-1-1-1-3	..	1	6	15	18	2	..	..	..	..	..	42	5.3±.09	.85±.07	16.04±1.20
1-9-1-2-4-6-7-5-6-4	..	..	3	8	25	19	..	..	..	..	..	55	6.1±.08	.84±.06	13.77± .90
1-9-1-2-4-6-7-5-3-3	..	..	1	9	44	5	..	..	..	..	..	59	5.9±.05	.55±.04	9.32± .58

TABLE 6. · FREQUENCY DISTRIBUTION OF THE NUMBER OF NODES OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Number of nodes											N.	A.	S. D.	C. V.
	8	9	10	11	12	13	14	15	16	17	18				
1 (Original	..	..	..	..	4	12	19	22	1	3	1	62	14.3±.10	1.21±.07	8.46±.51
1 non-inbred	..	..	..	2	9	15	15	11	5	0	1	58	13.8±.12	1.40±.09	10.14±.63
1 Leaming	..	..	..	1	0	9	26	15	3	4	1	59	14.4±.10	1.20±.08	8.33±.52
1 variety)	..	..	2	2	10	13	19	12	2	5	1	66	13.8±.14	1.66±.10	12.03±.71
Total............	..	..	2	5	23	49	79	60	11	12	4	245	14.1±.06	1.42±.04	10.07±.31
1-6-1-3-4-4-4-2-4-4-3	..	..	..	2	25	28	3	..	..	..	..	58	12.7±.06	.65±.04	5.12±.32
1-6-1-3-4-4-4-2-4-1-2	..	..	1	30	30	..	..	..	..	..	..	61	11.5±.05	.53±.04	4.61±.28
1-6-1-3-4-4-4-2-5-5-1	..	..	..	6	24	13	6	..	..	..	..	49	12.4±.08	.86±.06	6.94±.47
1-6-1-3-4-4-4-2-5-3-1	..	1	0	6	34	18	..	..	..	..	..	59	12.2±.06	.73±.05	5.98±.37
1-7-1-1-1-4-7-5-2-6-1	..	1	2	11	35	5	..	..	..	..	..	54	11.8±.07	.74±.05	6.27±.40
1-7-1-1-1-4-7-5-2-1-1	1	1	7	15	21	14	..	..	..	..	..	59	11.6±.10	1.12±.07	9.66±.60
1-7-1-1-1-4-7-5-4-7-2	..	..	1	5	34	14	3	..	..	..	..	57	12.2±.07	.76±.05	6.23±.39
1-7-1-1-1-4-7-5-4-5-2	..	..	1	2	13	18	5	1	..	..	..	40	12.7±.10	.95±.08	7.48±.56
1-7-1-2-2-9-2-1-1-4-1	..	1	1	14	18	21	1	..	..	..	..	56	12.1±.09	.96±.06	7.93±.50
1-7-1-2-2-9-2-1-1-1-3	..	..	1	1	12	23	15	..	..	..	..	52	13.0±.08	.88±.06	6.77±.45
1-9-1-2-4-6-7-5-6-4	..	..	..	3	15	27	13	1	..	..	..	59	12.9±.07	.86±.06	6.67±.41
1-9-1-2-4-6-7-5-3-3	..	..	..	2	6	39	13	..	..	..	..	60	13.1±.06	.67±.04	5.11±.31

TABLE 7. FREQUENCY DISTRIBUTION OF THE NUMBER OF ROWS OF GRAIN ON THE EAR OF A NON-INBRED VARIETY OF MAIZE AND INBRED STRAINS DERIVED FROM IT.

Pedigree number	Number of rows on the ear.								N.	A.	S. D.	C. V.
	12	14	16	18	20	22	24	26				
1 (Original	..	2	14	18	14	5	2	2	57	18.7±.23	2.64±.17	14.12±.91
1 non-inbred	..	1	15	21	8	3	3	..	51	18.2±.21	2.26±.15	12.42±.84
1 Leaming	2	6	7	19	17	7	2	..	60	18.4±.23	2.70±.17	14.67±.93
1 variety)	1	5	15	17	13	6	0	2	59	18.2±.24	2.76±.17	15.16±.96
Total.............	3	14	51	75	52	21	7	4	227	18.4±.12	2.62±.08	14.22±.46
1-6-1-3-4-4-4-2-4-4-3	..	7	24	22	6	..	..	..	59	16.9±.14	1.66±.10	9.83±.61
1-6-1-3-4-4-4-2-4-1-2	..	12	42	4	..	..	..	..	58	15.7±.09	1.02±.06	6.48±.40
1-6-1-3-4-4-4-2-5-5-1	5	34	7	..	..	..	..	..	46	14.1±.10	1.02±.07	7.23±.51
1-6-1-3-4-4-4-2-5-3-1	6	37	13	..	..	..	..	..	56	14.3±.10	1.14±.07	7.96±.50
1-7-1-1-1-4-7-5-2-6-1	..	..	..	5	13	30	12	2	62	21.8±.16	1.84±.11	8.43±.51
1-7-1-1-1-4-7-5-2-1-1	..	..	..	6	14	14	19	3	56	22.0±.20	2.22±.14	10.10±.64
1-7-1-1-1-4-7-5-4-7-2	..	..	..	1	16	23	11	1	52	21.8±.15	1.63±.11	7.48±.49
1-7-1-1-1-4-7-5-4-5-2	..	..	1	10	13	11	1	..	36	20.1±.20	1.80±.14	8.94±.71
1-7-1-2-2-9-2-1-1-4-1	..	12	22	8	1	..	..	..	43	15.9±.15	1.49±.11	9.40±.68
1-7-1-2-2-9-2-1-1-1-3	..	12	20	10	..	..	..	..	42	15.9±.15	1.45±.10	9.06±.66
1-9-1-2-4-6-7-5-6-4	..	20	30	3	2	..	..	..	55	15.5±.13	1.43±.09	9.21±.59
1-9-1-2-4-6-7-5-3-3	..	19	40	..	..	..	..	..	59	15.4±.08	.94±.06	6.08±.38

length of ear is even more than it seems from this table because the variety contained plants which produced two ears of which the second is usually smaller than the first; whereas the inbred strains almost never produce more than one ear to a plant.

The number of nodes per plant is reduced but as compared to height and length of ear this reduction is very much less. In the number of rows of grain on the cob there is a reduction in some lines and an increase in others. These tables show in the clearest manner that inbreeding has a greater effect on some characters than on others, and that segregation of characters has occurred. Perhaps the most noticeable effect of inbreeding as shown by these tables is the reduction in variability as brought out by the range and statistical constants. This reduction in variability is most apparent in the characters which are the least reduced by inbreeding—number of nodes and number of rows of grain on the ear—although the low variability is also apparent in height and length of ear. In variability, also, there is a difference between different lines.

The variability in height and length of ear of the inbred strains is higher than it should be, owing to the fact that it was difficult to obtain a perfect stand of plants, on account of poor germination of the seeds of the inbred strains. The aim was to have three plants in a hill. From four to eight seeds were planted as far as a limited supply of seed would permit, and later, thinned to three plants. In spite of this precaution it was extremely difficult to get anything like a perfect stand, so missing plants were replanted as soon as possible. These replants, owing to their late start, never entirely caught up with the other plants and are shorter in height and have smaller ears in consequence. It is unfortunate that this practice was followed because it is believed that much more reliable results would have been obtained otherwise. On the other hand missing plants introduce another source of error—that of unequal opportunity to grow. Because there was abundant seed of the variety, and it germinated well, practically complete stands of these plants were obtained.

The reduction in variability is more apparent in the details of the structure of the plants and ears which cannot be expressed statistically. The beautiful uniformity of these plants in all characteristics at the present time is one of their most striking features. This can be seen fairly well in the accompanying photographs. (Plates I to V).

In view of this fact of great uniformity and constancy as a result of inbreeding one is astonished at the statement made recently by Stout ('16) in a discussion of the results obtained from inbreeding in maize by East and Hayes. Stout says (pp. 420–421):

> "strains similar in homozygosity show widest variation indicative of spontaneous variation in natural vigor which is suggested that in such highly cultivated varieties such as corn extreme sporadic variations may be constantly occurring, a condition which is well shown by the numerous and well-known results of the ear to row test."

Several curious misconceptions are to be noted in this statement. In the first place, it has never been maintained by anyone to my knowledge that an equal number of generations of inbreeding produce an equal amount of homozgosity in different lines. Secondly, it has never been proposed that the degree of heterozygosity determined the form or structure of any organism, but that such a condition was accompanied by a stimulus to development which merely increased the expression of many hereditary factors. This stimulus is considered to be without any great effect *in itself* on variability. Granted that the inbred strains were equal in homozygosity at that time, that was no reason why they should be similar in vigor or in any other respect—in fact the expectation is exactly the reverse of this. With regard to "spontaneous" and "sporadic" variation these inbred strains show unmistakably that there is practically no sporadic or spontaneous variation, that the individuals making up an inbred strain are remarkably constant and uniform after some degree of homozygosity is obtained and that the diversity between different lines can be perfectly accounted for on the basis of segregation of characters. Also, in the following paragraphs in his paper Stout fails to see the distinction between crosses of diverse inbred lines and between crosses of non-inbred commercial varieties. Because Collins ('14) and Hayes ('14) failed to obtain increases in all crosses between commercial varieties of similar type Stout would question whether crossing in maize was ever beneficial. It is quite to be expected that there are many varieties already so widely crossed that further crossing does not result in greater heterozygosity, but may even reduce it. It is only in crosses between somewhat different varieties, like flint and dent (Jones and Hayes '17) or between varieties from different geographical regions (Collins '10) that any great amount of heterosis in naturally widely crossed varieties is to be expected.

Although there has been a striking reduction in size of plant, general vegetative vigor and productiveness in these inbred strains of maize, and in comparison with non-inbred varieties the inbred plants are more difficult to grow, emphasis must be put on the fact that the plants are normal and healthy. The monstrosities which are common in every field of maize, such as the occurrence of seeds in the tassels, anthers in the ears, dwarf plants, completely sterile plants, mosaic and albino plants and other similar anomalies never appear in these inbred strains. Furthermore, in the details of the size, shape, structure and position of the tassels, leaves, stalks and ears, these inbred strains show the most striking uniformity. These minor details which characterize each of these groups of plants are difficult to describe but are perhaps the most noticeable feature about them. The stalks, the tassels or the ears of all of these four Leaming strains if mixed together could be separated without the slightest difficulty by anyone familiar with them. Some of the differences which characterize the ears of these four strains are shown in Plate Ib. It is to be noticed in this photograph that Nos. 1–7–1–2 and 1–7–1–1, which were originally from the same line, both have flat cobs. In one of them, however, it is colored, in the other uncolored. Other differences are to be seen in shape and color of seeds.

The segregation of row number accompanied by a reduction in variability in these two strains is shown in Table 8 and Fig II. Data previous to the third generation are not available but since then a noticeable change in average row number has taken place without any selection one way or the other. The variability of each line has decreased at the same time. Whether the increase in variability, after the eighth generation, has any significance is not known. It is possibly due to the fact that both lines have become irregular in row number so that the correct determination of the row number has been rendered more difficult in the later generations. Also the number of plants grown in the generations from the 7th to the 10th are much too few to base accurate conclusions upon. The sharp increase in average row number and decrease in variability in the 8th generation are probably due to the unusually favorable growing conditions of that year.

TABLE 8. REDUCTION IN VARIABILITY AND SEGREGATION OF EAR ROW NUMBER IN INBRED STRAINS OF MAIZE.

Year grown.	Generations selfed.	Pedigree number.	Number of rows of grain on the ear.									N.	A.	C. V.
			12	14	16	18	20	22	24	26	28			
1908	3	1-7-1-1	3	3	4	6	27	7	4	1	2	57	19.7±.30	17.00±1.10
1908	3	1-7-1-2	..	..	..	..	..	..	..	..	..	..	....	....
1910	4	1-7-1-1-1	..	2	5	11	17	19	6	1	..	61	20.2±.22	12.67± .78
1910	4	1-7-1-2-2	..	..	2	8	14	9	5	1	..	39	20.5±.25	11.20± .86
1911	5	1-7-1-1-1-4	..	..	3	4	10	16	4	1	..	38	20.9±.25	10.92± .85
1911	5	1-7-1-2-2-9	..	..	14	29	21	1	..	..	..	65	18.3±.13	8.34± .49
1912	6	1-7-1-1-1-4-7	..	..	..	..	..	..	..	..	..	..	....	....
1912	6	1-7-1-2-2-9-2	..	..	..	..	..	..	..	..	..	..	....	....
1913	7	1-7-1-1-1-4-7-5	..	..	1	3	5	1	..	..	..	10	19.2±.34	8.33±1.26
1913	7	1-7-1-2-2-9-2-1	..	4	12	2	..	..	..	..	..	18	15.8±.18	7.16± .80
1914	8	1-7-1-1-1-4-7-5-4	..	..	..	1	9	16	6	..	..	32	21.7±.18	4.72± .40
1914	8	1-7-1-2-2-9-2-1-1	..	..	17	20	6	..	..	..	..	43	17.5±.14	7.83± .57
1915	9	1-7-1-1-1-4-7-5-4-5	..	..	..	1	14	4	2	..	..	21	20.7±.21	6.90± .72
1915	9	1-7-1-2-2-9-2-1-1-4	..	6	16	7	..	..	..	..	..	29	16.1±.17	8.33± .74
1916	10	1-7-1-1-1-4-7-5-4-5-2	..	..	1	10	13	11	1	..	..	36	20.1±.20	8.94± .71
1916	10	1-7-1-2-2-9-2-1-1-4-3	..	12	22	8	1	..	..	..	..	43	15.9±.15	9.40± .68
1917	11	1-7-1-1-1-4-7-5-4-5-2-1	..	..	3	20	43	22	7	..	..	95	20.2±.13	9.15± .45
1917	11	1-7-1-2-2-9-2-1-1-4-3-1	3	23	45	22	2	..	..	..	..	95	15.9±.11	10.39± .51

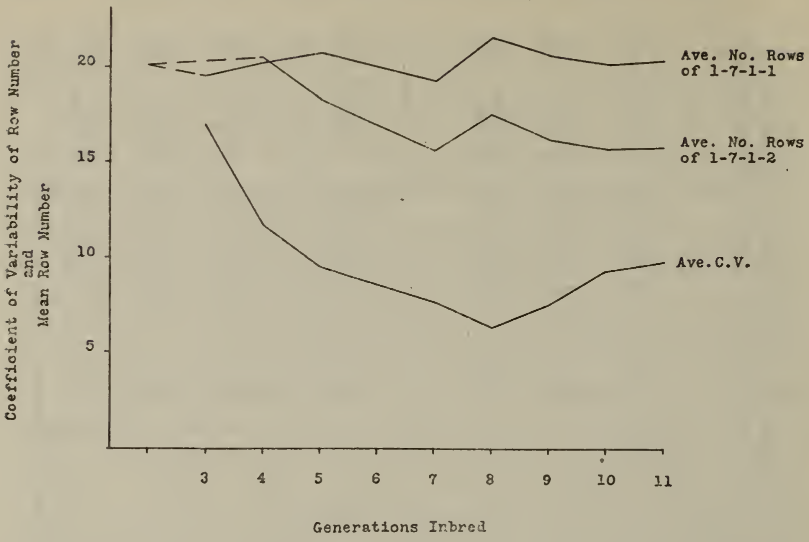


Figure II. The reduction in variability and segregation of number of rows of grain on the ear in selfed strains of maize.

East and Hayes ('12) have noted many characters which are isolated from maize by inbreeding. In addition to these, several other characters have been isolated in this and in other material. One of these characters is a constant difference in shade of color of the foliage—some are dark green, others are light, yellowish green. Some strains are lacking in root development and never stand upright throughout the season. Some have a single-stalked unbranched tassel, while others are profusely branched. Some strains have peculiarly wrinkled or wavy leaves, particularly noticeable in the first leaves. Some strains produce a small proportion of connate seeds similar to those observed by Kempon ('13) in nearly every ear, while their occurrence has never been observed on other inbred lines derived from the same source. There are also marked differences in susceptibility to disease as will be shown later.

These illustrations are sufficient to demonstrate beyond doubt that by far the greatest amount of the fluctuating variability found among ordinary cross-fertilized plants is due to the segregation and re-combination of definite and constant hereditary factors. Many of these characters are seldom seen in continually cross-pollinated plants, and never are so many combined together.

This is due to the fact that they are recessive in nature and complex in mode of inheritance. The most significant feature about the characters which make their appearance in inbred strains is that none of them can be directly attributed to a loss of a physiological stimulation, although undoubtedly many of them may be modified by the vigor of the plant upon which they are borne. There is no one specific character common to all inbred strains but simply a general loss of vigor, a general loss of size and of productiveness accompanied by the appearance of specific characters more or less unfavorable to the plants' best development but these unfavorable characters are never all found in one inbred strain, nor is any one character common to all inbred strains.

Probably the most common result of inbreeding in maize is a reduction in the amount of pollen produced. This becomes apparent in a smaller size of all parts of the tassel, in shrunken and abortive anthers which are often never released by the glumes, with a consequent reduction in the amount of pollen available for fertilization. A normal corn plant should produce, on the average, anywhere from 1cc. to 10cc. or, in some cases, very much more pollen. I have made no actual measurements of the amounts produced. Many of the inbred strains, however, now produce only a small fraction of a cubic centimeter of pollen, and the production of this small amount is much affected by weather conditions, so that many strains, otherwise well developed and productive, are maintained with the utmost difficulty.

It has been my experience that self-sterility in corn is due to ovule or pollen abortion. Whenever pollen is obtained it seems to be able to function. Failures to obtain seed after pollen is applied are common, but are usually attributed to external factors. At least I know of no clear case where pollen is produced in which it fails to fertilize the ovules of plants which were capable of being fertilized by other pollen. Many cases of complete abortion of the pistillate part of the plant must occur, as many plants are lost through failure to set seed when good pollen has been applied. Just where the trouble lies is not always possible to detect. Undoubtedly, many cases of complete abortion of either staminate or pistillate functions, or both, occur during inbreeding, and the plants are eliminated for that reason.

Reduction in the amount of pollen produced is less serious than a reduction in the number of ovules, as a very small amount of pollen suffices for fertilization when conditions are right. For that reason unconscious selection for good ovule production has been much more rigid than for pollen production. That is the reason, I believe, that more inbred strains now show a greater reduction in the staminate function than in the pistillate.

A significant feature of the effect of inbreeding upon sterility is that some inbred strains are perfectly normal in their production of pollen, and the amount of pollen produced is only a little less than non-inbred plants, owing to the reduced vigor and size of the plants which produce the tassels. Out of about twenty-five inbred strains carried through at least seven generations, three of them are perfectly normal in the structure and function of their staminate parts. One of the Leaming strains (No. 1–9) produces more pollen than many non-inbred varieties growing nearby. In every case, however, those plants which produce the best developed ears are the poorest producers of pollen, and those strains which produce abundant pollen have ears which are poorly developed. In other words, inbreeding is bringing about a tendency for maize to change from a functionally monoecious plant to a functionally dioecious plant although, morphologically, both staminate and pistillate parts are still present. This is illustrated in Plates VI, a and b, where tassels and ears of four of the inbred strains are shown.

Although no systematic selection has been practiced throughout the inbreeding experiment a great deal of selection upon many characters has been unavoidable as it is unavoidable in any inbreeding experiment. In maize, the difficulties of hand pollination result in the selection of plants whose staminate and pistillate parts are matured synchronously. Any great differences in this respect, particularly towards proterandry, would render self-fertilization difficult or impossible, as pollen, according to Andronescu ('15) has very short viability, which fact my own experience confirms. Of course, all plants which are weak, sterile, diseased or in any way abnormal tend to become eliminated wherever these causes reduce the chance of obtaining seed. This unconscious selection becomes more rigid as reduction in vigor and productiveness increases in the later generations of inbreeding. The small amount of seed produced by hand pollination, under the most favorable circumstances necessitates the using of the best ears obtained for planting in order to have enough plants upon which to make any fair observations.

In every case inbreeding in maize has so far resulted in a reduction in size, vigor and productiveness. Some thirty or forty inbred strains have been observed, many of which are additional to the ones reported previously.

From the preceding statements in regard to the effect of inbreeding it can be said that this process produces types which differ in their power of development as follows:

1. Plants which cannot be perpetuated.
2. Plants which fail to complete normal development and can be propagated only with the greatest difficulty.
3. Plants which are perfectly normal but varying in the amount of growth they attain at maturity.

These normal inbred plants, so far obtained in maize, are not as a rule as large, vigorous or productive as the original cross-fertilized plants. It is theoretically possible to obtain such plants, which cannot be reduced in vigor in a homozygous condition as will be explained later. There is some evidence from the experiments of Darwin, that such plants have been obtained by inbreeding in other material, for example, in Ipomea and Mimulus. Selection will help to obtain these vigorous, unreduceable individuals but may not be fully effective in doing so. More or less unconscious selection is unavoidable in any inbreeding experiment.

These homozygous, normal, inbred strains, after the reduction in growth has ceased, are quite comparable to plants of a naturally self-fertilized species. Darwin found that self-pollination caused no reduction in vigor in Nicotiana, Pisum, Lathyrus, Phaseolus and other genera which are naturally self-fertilized to a large extent. Hayes and Jones ('17) have found similar results with the tomato. The only effect that inbreeding may have on such plants is merely to isolate pure lines, which are quite uniform among themselves, but may be diverse from one another, as shown by soy beans (Jones and Hayes ('17), but which show no reduction in vigor on continued artificial inbreeding. These results are perfectly in accord with Johannsen's genotype conception.

THE APPROACH TO COMPLETE HOMOZYGOSITY.

It now remains to be seen whether or not these inbred strains are reaching the limit of reduction. There are two ways of determining this, one is by growing two successive inbred generations side by side in the same year, the other is by crossing different plants within the same inbred strain.

In Table 9 the results from two successive generations grown side by side in the same year are compared. On the whole, an additional year of inbreeding after the sixth produces very little change. In Table 10 are given the height, yield and length of ear of selfed and sib-crossed plants which were grown in 1917. In 1916, in each of the strains of which figures are given in the table, some plants were selfed and some were crossed by another plant within the same strain. Since all the plants grown that year in any one strain came from one individual of the preceding generation, that generation is the significant one. In other words if the plant in that generation was homozygous, no increase of the sib-crossed plants over the selfed plants would be expected. The figures show that there is, on the whole, a slight increase in all the characters studied. The increase, however, is no greater in the cases where the common ancestor was inbred for seven generations than in the cases where it was inbred nine generations.

Shull ('11) compared sib-crosses with selfed plants in which the significant generation, as I understand it, was the fourth, and found that the crossed plants slightly excelled the selfed plants in height, number of rows on the ear and yield of grain. Similarly the F_1 × Sibs exceeded F_1 × self in yield, showing that in the fourth generation complete homozygosis had not been attained.

Whether or not complete homozygosis has been attained by some or all of the strains shown in Table 10 cannot be stated positively from the data given. In most cases the increase of the sib-crosses over the selfs is slight and probably of no significance as there are about an equal number of cases in which the reverse condition is shown. A few of the sib-crosses are, however, considerably greater than the selfs in all three characters and it may very well be that these strains have not attained the degree of homozygosity that the other strains have. More data are needed to establish this point with certainty as environmental factors which favored a certain plot in one character would also favor the other character as well.

TABLE 9. THE YIELD, HEIGHT AND LENGTH OF EAR OF TWO SUCCESSIVE INBRED GENERATIONS OF MAIZE BOTH GROWN SIDE BY SIDE IN THE SAME YEAR.

Pedigree number in the Nth generation	Generations compared		Yield: bu. per acre		Difference of (N+1) above N	Height of plant in inches		Difference of (N+1) above N	Length of ear in inches		Difference of (N+1) above N
	N	(N+1)	N	(N+1)		N	(N+1)		N	(N+1)	
65-8-2-2-6-5-2...	6	7	20.9	28.4	+ 7.5	53.3±.47	54.3±.41	+1.0± .62	5.4±.12	5.6±.09	+.2±.15
1-9-1-2-4-6-7-5-3..	8	9	28.8	30.5	+ 1.7	78.0±.57	80.3±.35	+2.3± .67	6.1±.08	5.9±.05	—.2±.09
1-7-1-2-2-9-2-1-1-4	9	10	26.3	20.0	— 6.3	83.9±.45	82.6±.61	—1.3± .76	5.4±.09	5.1±.12	—.3±.15
1-7-1-1-1-4-7-5-2-1	9	10	44.5	30.4	—14.1	84.8±.64	82.2±.77	—2.6±1.00	4.7±.07	4.2±.08	—.5±.11
1-7-1-1-1-4-7-5-4-5	9	10	....	....	......	88.5±.47	88.7±.70	+ .2± .84	4.4±.08	4.2±.09	—.2±.12
1-6-1-3-4-4-4-2-4-4	9	10	46.3	34.9	—11.4	100.6±.44	97.8±.36	—2.8± .57	6.2±.08	6.1±.09	—.1±.12
1-6-1-3-4-4-4-2-5-3	9	10	29.7	31.5	+ 1.8	98.2±.44	102.7±.47	+4.5± .64	6.4±.12	6.9±.10	+5. ±.16
Average.......			32.8	29.3	— 3.5	83.9	84.1	+ .2	5.5	5.4	—.1

TABLE 10. A COMPARISON OF THE HEIGHT, YIELD OF GRAIN AND LENGTH OF EAR OF SELFED STRAINS OF MAIZE WITH CROSSES BETWEEN INDIVIDUAL PLANTS WITHIN THE STRAINS.

Pedigree number	Significant generation	Height of plant in inches			Yield of grain in lbs. per plant			Length of ear in inches		
		Selfed strains	Sib crosses	Difference of sib crosses above selfed	Selfed strains	Sib crosses	Difference of sib crosses above selfed	Selfed strains	Sib crosses	Difference of sib crosses above selfed
10-3-7-3-9-7-5-1-1......	7	91.3 ± .58	93.4 ± .50	+2.1 ± .77	.25	.20	−.05	5.8 ± .02	6.4 ± .08	+.6 ± .08
10-3-7-3-9-7-5-4-2......	7	93.1 ± .53	94.2 ± .52	+1.1 ± .74	.26	.31	+.05	6.4 ± .06	6.1 ± .06	−.3 ± .08
10-4-8-3-5-3-4-8-2......	7	89.6 ± .53	87.1 ± .73	−2.5 ± .90	.31	.40	+.09	5.3 ± .07	5.0 ± .06	−.3 ± .09
10-4-8-3-5-3-4-5-2......	7	94.4 ± .56	95.9 ± .46	+1.5 ± .73	.38	.34	−.04	5.6 ± .06	5.9 ± .07	+.3 ± .09
1-9-1-2-4-6-7-5-6-2....	8	82.7 ± .29	81.6 ± .29	−1.1 ± .41	.24	.19	−.05	5.7 ± .06	4.9 ± .06	−.8 ± .08
1-9-1-2-4-6-7-5-3-2....	8	82.0 ± .33	84.2 ± .37	+2.2 ± .50	.20	.19	−.01	5.3 ± .05	5.7 ± .04	+.4 ± .06
1-6-1-3-4-4-4-2-4-4-2...	9	103.0 ± .42	109.4 ± .36	+6.4 ± .55	.33	.47	+.14	6.1 ± .08	6.9 ± .06	+.8 ± .10
1-6-1-3-4-4-4-2-4-1-3...	9	113.5 ± .37	109.9 ± .58	−3.6 ± .69	.44	.36	−.08	7.5 ± .04	7.2 ± .04	−.3 ± .06
1-6-1-3-4-4-4-2-5-3-2...	9	102.6 ± .53	103.4 ± .36	+ .8 ± .64	.40	.44	+.04	7.2 ± .06	7.3 ± .06	+.1 ± .08
1-6-1-3-4-4-4-2-5-5-2...	9	95.6 ± .50	95.2 ± .63	− .4 ± .80	.37	.40	+.03	6.9 ± .08	6.6 ± .10	−.3 ± .13
1-7-1-2-2-9-2-1-1-4-3...	9	83.8 ± .63	85.9 ± .57	+2.1 ± .85	.20	.26	+.06	4.5 ± .08	4.9 ± .07	+.4 ± .11
1-7-1-1-1-4-7-5-4-5-2...	9	83.8 ± .53	81.5 ± .60	−2.3 ± .80	.23	.24	+.01	3.9 ± .07	3.8 ± .05	−.1 ± .09
1-7-1-1-1-4-7-5-4-7-1...	9	76.1 ± .72	81.2 ± .53	+5.1 ± .89	.15	.23	+.08	3.5 ± .06	3.7 ± .05	+.2 ± .08
1-7-1-1-1-4-7-5-2-1-1...	9	78.7 ± .60	80.2 ± .55	+1.5 ± .81	.29	.19	−.10	4.1 ± .07	3.8 ± .06	−.3 ± .09
1-7-1-1-1-4-7-5-2-6-1...	9	75.6 ± .49	78.3 ± .55	+2.7 ± .74	.26	.35	+.09	3.8 ± .05	3.9 ± .06	+.1 ± .08
Average...............		89.7	90.8	+1.1	.29	.30	+.01	5.4	5.5	+.1

The Effect of Heterozygosis on Vegetative Luxuriance.

The most noticeable manifestation of heterosis in plants is a general increase in vegetative luxuriance. In maize this is particularly noticeable in increased height of plant, diameter of stalk, root development, length of ear and productiveness of grain (see Plates III, V, VII, VIII, IX, X and XII). In crosses between inbred strains of maize the amount of heterosis shown is inversely proportional to the degree of relationship as shown in Table 11. Montgomery ('12) has obtained similar results.

Some characters are much more affected by heterozygosis than others. In comparing Tables 12, 13 and 14 with Tables 15 and 16 it will be noticed that the yield of the crosses is increased 180 per cent., height is increased 27 per cent. and length of ear 29 per cent. over the average of their parental lines. On the other hand, the number of nodes per plant and number of rows of grain on the ear is increased only 6 and 5 per cent. respectively. In other words, heterozygosis does not increase the number of parts to anything like the extent that it increases the size of those parts. Those parts of the plants which are more or less indeterminate in size, like internodes, ears and seeds are augmented by crossing as the result of an increase in the rapidity and rate of cell division. The increase in size of parts is probably brought about by an increase in size of cells as well as an enormous increase in number of cells. Tupper and Bartlett ('16) have shown that *gigas* mutants in *Oenothera* have larger cells than the non-mutant type, so that a change in cell size may accompany a germinal change.

From Table 11 it will also be seen that some first generation hybrids may even surpass the original variety in yield, height or length of ear, although the comparison is rather unfair as the Leaming variety was not acclimatized as were the inbred strains. The return of vigor realized in the first generation crosses is often enormous, and the same is true of crossing inbred strains derived from totally different types of maize as is shown in Table 17.

Although there is an immediate and striking return to the vigorous condition of the non-inbred stock there is not a return in variability as shown in Tables 18, 19, 20, 21 and 22. The first generation crosses are no more variable than the inbred strains by which they are produced, in many cases less variable, and show striking differences when compared to the original stock. The coefficient of variability is entirely inadequate in bringing out

TABLE 11. THE DEGREE OF RELATIONSHIP AND THE AMOUNT OF HETEROSIS SHOWN BY INBRED STRAINS WHEN CROSSED.

Pedigree number	Significant generation	Yield bu. per acre	Increase above ave. yield of parents	Height inches	Increase above ave. height of parents	Length of ear inches	Increase above ave. length of parents
1-6-1-3-4-4-4-2-4-4-3	..	34.9	......	97.8± .36	......	6.1±.09	......
1-7-1-1-1-4-7-5-4-7-2	..	30.3	......	90.2± .46	......	4.0±.08	......
1-7-1-2-2-9-2-1-1-4-1	..	20.0	......	82.6± .61	......	5.1±.12	......
1-9-1-2-4-6-7-5-3-3	..	30.5	......	80.3± .35	......	5.9±.05	......
(1-6-1-3-4-4-4-2-4-1) × (1-6-1-3-4-4-4-2-4-4)	7	19.2	−15.7	88.4±1.12	− 9.4	5.3±.09	− .8
(1-7-1-1-1-4-7-5-2-6) × (1-7-1-1-1-4-7-5-2-1)	7	31.1	+ .8	79.2± .64	−11.0	4.5±.10	+ .5
(1-7-1-2-2-9-2-1-1-1) × (1-7-1-2-2-9-2-1-1-4)	7	23.9	+ 3.9	86.0± .63	+ 3.4	5.5±.10	+ .4
(1-9-1-2-4-6-7-5-3) × (1-9-1-2-4-6-7-5-6)	6	....	......	66.8± .48	−13.5	4.1±.10	−1.8
(1-6-1-3-4-4-4-2-4-4) × (1-6-1-3-4-4-4-2-5-5)	6	43.9	+ 9.0	103.4± .47	+ 5.6	6.7±.09	+ .6
(1-6-1-3-4-4-4-2-5-5) × (1-6-1-3-4-4-4-2-4-4)	6	....	......	98.1±1.12	+ .3	5.7±.15	− .4
(1-7-1-1-1-4-7-5-4-7) × (1-7-1-1-1-4-7-5-2-1)	6	17.5	−12.8	88.1± .74	− 2.1	4.7±.09	+ .7
(1-7-1-1-1-4-7-5-4-7) × (1-7-1-2-2-9-2-1-1-4)	1	70.9	+45.7	102.4± .44	+16.0	6.4±.12	+1.8
(1-7-1-2-2-9-2-1-1-1) × (1-7-1-1-1-4-7-5-2-6)	1	55.9	+30.7	103.1± .44	+16.7	6.3±.09	+1.7
(1-7-1-2-2-9-2-1-1-1) × (1-7-1-1-1-4-7-5-4-5)	1	58.4	+33.2	103.0± .50	+16.6	6.5±.08	+1.9
(1-6-1-3-4-4-4-2-4-1) × (1-7-1-2-2-9-2-1-1-1)	0	101.0	+73.5	121.9± .46	+31.7	7.9±.10	+2.3
(1-7-1-2-2-9-2-1-1-4) × (1-9-1-2-4-6-7-5-3)	0	82.1	+56.8	109.5± .76	+28.0	7.6±.13	+2.1
(1-9-1-2-4-6-7-5-3) × (1-6-1-3-4-4-4-2-4-1)	0	71.5	+38.8	110.5± .58	+21.4	7.6±.09	+1.6
1 Non-inbred variety	..	80.8	......	116.3± .90	......	7.6±.11	......

TABLE 12. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE YIELD OF GRAIN.

Pedigree number of strain—A	Yield of bushels per acre				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	34.9	99.1	99.9	30.3	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	34.9	112.9	....	37.4	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	34.9	82.4	....	30.7	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	31.9	101.0	....	18.3	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	16.8	88.1	84.4	30.3	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	16.8	103.2	106.7	20.0	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	16.8	91.0	....	30.7	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	31.5	94.8	....	30.4	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	30.5	63.9	....	31.5	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	30.5	71.5	....	31.9	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	30.5	58.0	....	30.4	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	30.5	52.5	100.5	18.9	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	30.5	59.6	82.1	20.0	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	30.7	66.3	....	18.3	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	20.0	84.9	....	34.9	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	37.4	40.5	....	16.8	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	30.4	59.4	....	31.9	1-6-1-3-4-4-4-2-4-1
Average...........	28.8	78.4		27.2	
Increase...........		50.4			
Percent increase....		180.00			

TABLE 13. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE HEIGHT OF PLANT.

Pedigree number of strain—A	Height of plant in inches				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	97.8 ± .36	117.3 ± .61	117.2 ± .44	90.2 ± .46	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	97.8 ± .36	117.6 ± .38	....	78.5 ± .71	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	97.8 ± .36	115.4 ± .56	....	77.0 ± .52	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	96.7 ± .37	121.9 ± .46	....	91.2 ± .68	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	93.6 ± .57	112.9 ± 1.04	109.9 ± .77	90.2 ± .46	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	93.6 ± .57	116.1 ± .41	113.4 ± .51	82.6 ± .61	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	93.6 ± .57	113.8 ± .40	....	77.0 ± .52	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	102.7 ± .47	116.0 ± .42	....	82.2 ± .77	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	80.3 ± .35	111.1 ± .61	....	102.7 ± .47	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	80.3 ± .35	110.5 ± .58	....	96.7 ± .37	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	80.3 ± .35	109.2 ± .76	94.0 ± 1.36	82.2 ± .77	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	80.3 ± .35	110.9 ± .60	114.1 ± .55	88.7 ± .70	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	80.3 ± .35	108.1 ± .50	109.5 ± .76	82.6 ± .61	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	77.0 ± .52	111.1 ± .58	....	91.2 ± .68	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	82.6 ± .61	114.9 ± .68	....	97.8 ± .36	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	78.5 ± .71	98.7 ± .78	....	93.6 ± .57	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	82.2 ± .77	105.2 ± .71	....	96.7 ± .37	1-6-1-3-4-4-4-2-4-1
Average...........	88.0	112.4		88.3	
Increase...........		24.2			
Percent increase....		27.44			

TABLE 14. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE LENGTH OF EAR.

Pedigree number of strain—A	Length of ear in inches				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.1±.11	7.3±.10	4.0±.08	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.5±.11	....	4.3±.06	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	6.1±.09	7.8±.08	....	6.1±.08	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	6.2±.07	7.9±.10	....	5.3±.09	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.0±.16	7.5±.12	6.8±.15	4.0±.08	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.0±.16	8.2±.08	8.0±.09	5.1±.12	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.0±.16	7.8±.08	....	6.1±.08	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	6.9±.10	7.6±.09	....	4.2±.08	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.9±.05	7.7±.09	....	6.9±.10	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.9±.05	7.6±.09	....	6.2±.07	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.9±.05	6.5±.12	5.5±.11	4.2±.08	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.9±.05	6.5±.10	7.6±.09	4.2±.09	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.9±.05	7.1±.12	7.6±.13	5.1±.12	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	6.1±.08	7.1±.11	....	5.3±.09	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	5.1±.12	7.6±.14	....	6.1±.09	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	4.3±.06	5.5±.12	....	6.0±.16	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	4.2±.08	6.0±.10	....	6.2±.07	1-6-1-3-4-4-4-2-4-1
Average...........	5.8	7.2		5.3	
Increase...........		1.6			
Percent increase....		28.57			

TABLE 15. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE NUMBER OF NODES.

Pedigree number of strain—A	Number of nodes				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	12.7±.06	13.6±.07	13.2±.07	12.2±.07	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	12.7±.06	13.3±.04	....	11.8±.07	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	12.7±.06	14.0±.05	....	12.9±.07	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	11.5±.05	14.0±.05	....	13.0±.08	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	12.4±.08	12.9±.08	13.2±.05	12.2±.07	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	12.4±.08	13.5±.06	13.1±.06	12.1±.09	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	12.4±.08	13.4±.06	....	12.9±.07	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	12.2±.06	13.3±.06	....	11.6±.10	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	13.1±.06	12.8±.06	....	12.2±.06	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	13.1±.06	12.9±.06	....	11.5±.05	1-6-1-3-4-4-4-2-4-3
1-9-1-2-4-6-7-5-3	13.1±.06	13.2±.06	12.5±.13	11.6±.10	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	13.1±.06	13.3±.06	14.0±.06	12.7±.10	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	13.1±.06	13.3±.07	13.7±.07	12.1±.09	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	12.9±.07	13.7±.06	....	13.0±.08	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	12.1±.09	13.6±.06	....	12.7±.06	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	11.8±.07	11.3±.07	....	12.4±.08	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	11.6±.10	12.6±.07	....	11.5±.05	1-6-1-3-4-4-4-2-4-1
Average...........	12.5	13.2		12.3	
Increase...........		.8			
Percent increase....		6.45			

TABLE 16. THE EFFECT OF CROSSING INBRED STRAINS OF MAIZE AS SHOWN BY THE INCREASE IN THE NUMBER OF ROWS OF GRAIN ON THE EAR.

Pedigree number of strain—A	Number of rows of grain on the ear				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	16.9±.14	19.5±.15	20.8±.15	21.8±.15	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	16.9±.14	19.5±.13	....	21.8±.16	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	16.9±.14	17.2±.13	....	15.5±.13	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	15.7±.09	18.4±.13	....	15.9±.15	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	14.1±.10	17.4±.11	18.3±.14	21.8±.15	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	14.1±.10	16.9±.10	18.2±.13	15.9±.15	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	14.1±.10	17.0±.10	....	15.5±.13	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	14.3±.10	19.4±.15	....	22.0±.20	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	15.4±.08	15.7±.11	....	14.3±.10	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	15.4±.08	16.7±.12	....	15.7±.09	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	15.4±.08	19.9±.20	18.7±.25	22.0±.20	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	15.4±.08	17.8±.14	19.0±.17	20.1±.20	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	15.4±.08	16.8±.17	16.2±.09	15.9±.15	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	15.5±.13	16.2±.14	....	15.9±.15	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	15.9±.15	19.3±.17	....	16.9±.14	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	21.8±.16	17.6±.14	....	14.1±.10	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	22.0±.20	19.8±.16	....	15.7±.09	1-6-1-3-4-4-4-2-4-1
Average..........	16.2	17.9		17.7	
Increase..........		.9			
Percent increase....		5.29			

TABLE 17. THE EFFECT OF CROSSING INBRED STRAINS DERIVED FROM DIFFERENT TYPES OF MAIZE.

Type	Pedigree number	Yield bu. per acre	Increase above ave. of parents	Height inches	Increase above ave. of parents	Length of ear inches	Increase above ave. of parents
Dent..........	1-6-1-3-4-4-4-2-4-4-3	34.9	....	97.8	....	6.1	....
Floury........	10-3-7-3-9-7-5-4-3.....	10.4	....	75.5	....	6.1	....
Flint..........	29-5-2-3-8...........	9.2	....	88.7	....	5.9	....
Pop...........	65-8-2-2-6-5-2-4......	28.4	....	54.3	....	5.6	....
Dent × Floury..	(1-6-1-3) × (10-3-7-3)..	90.4	+67.7	122.8	+36.1	9.1	+3.0
Dent × Flint...	(1-6-1-3) × (29-5-2-3)..	94.6	+72.5	117.5	+24.2	8.9	+2.9
Floury × Dent..	(10-3-7-3) × (1-6-1-3)..	43.3	+20.6	108.2	+21.5	7.4	+1.3
Floury × Flint..	(10-3-7-3) × (29-11-4-4)	61.1	+51.3	104.5	+22.4	9.7	+3.7
Flint × Dent...	(29-5-2-3) × (1-6-1-3)..	80.7	+58.6	115.7	+22.4	9.6	+3.6
Flint × Floury..	(29-5-2-3) × (10-3-7-3).	73.0	+63.2	112.9	+30.8	10.0	+4.0
Pop × Dent....	(65-8-2-2) × (1-6-1-3)..	73.1	+41.4	88.9	+12.8	7.2	+1.3
Pop × Flint....	(65-8-2-2) × (5-8-6-3)..	51.3	......	79.5	......	7.1	.....

TABLE 18. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE HEIGHT OF PLANT.

Pedigree number of strain—A	Coefficient of variability of height				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	4.14±.26	6.10±.37	4.01±.26	5.49±.36	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	4.14±.26	3.74±.23	....	9.75±.64	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	4.14±.26	5.55±.34	....	7.73±.48	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	4.40±.27	4.22±.27	....	7.95±.52	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.14±.43	9.92±.66	7.32±.50	5.49±.36	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.14±.43	4.09±.25	5.20±.32	8.05±.52	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.14±.43	4.00±.25	....	7.73±.48	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	5.11±.32	4.05±.26	....	10.64±.67	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.04±.31	6.66±.39	....	5.11±.32	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.04±.31	6.15±.38	....	4.40±.27	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.04±.31	7.78±.49	12.61±1.04	10.64±.67	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.04±.31	6.18±.38	5.48±.34	7.27±.56	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.04±.31	5.27±.33	7.94±.49	8.05±.52	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	7.73±.48	6.26±.38	....	7.95±.52	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	8.05±.52	6.27±.41	....	4.14±.26	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	9.75±.64	8.81±.56	....	6.14±.43	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	10.64±.67	7.41±.47	....	4.40±.27	1-6-1-3-4-4-4-2-4-1
Average...........	5.98	6.03		7.11	

TABLE 19. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE LENGTH OF EAR.

Pedigree number of strain—A	Coefficient of variability of length of ear				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	17.17±1.18	19.86±1.18	16.99±1.05	22.75±1.51	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	17.17±1.18	17.33±1.02	....	15.58± .96	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	17.17±1.18	11.92± .74	....	13.77± .90	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	13.06± .82	14.94± .93	....	16.04±1.20	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	26.17±1.95	17.73±1.11	25.88±1.65	22.75±1.51	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	26.17±1.95	11.71± .72	12.37± .77	23.33±1.77	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	26.17±1.95	12.44± .76	....	13.77± .90	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	16.23±1.05	13.55± .85	....	20.00±1.31	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	9.32± .58	14.16± .87	....	16.23±1.05	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	9.32± .58	13.82± .84	....	13.06± .82	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	9.32± .58	20.46±1.36	15.45±1.47	20.00±1.31	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	9.32± .58	17.69±1.15	13.55± .83	19.76±1.62	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	9.32± .58	18.87±1.23	20.26±1.26	23.33±1.77	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	13.77± .90	18.73±1.16	....	16.04±1.20	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	23.33±1.77	19.87±1.30	....	17.17±1.18	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	15.58± .96	24.91±1.66	....	26.17±1.95	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	20.00±1.31	18.83±1.21	....	13.06± .82	1-6-1-3-4-4-4-2-4-1
Average...........	16.39	16.87		18.40	

TABLE 20. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE NUMBER OF NODES.

Pedigree number of strain—A	Coefficient of variability of number of nodes				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	5.12±.32	5.88±.36	5.91±.37	6.23±.39	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	5.12±.32	3.68±.22	....	6.27±.40	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	5.12±.32	4.50±.27	....	6.67±.41	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	4.61±.28	4.00±.25	....	6.77±.45	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	6.94±.47	6.82±.43	4.09±.27	6.23±.39	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	6.94±.47	5.48±.32	5.34±.33	7.93±.50	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	6.94±.47	5.67±.35	....	6.67±.41	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	5.98±.37	5.19±.32	....	9.66±.60	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.47±.33	....	5.98±.37	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	5.11±.31	5.66±.35	....	4.61±.28	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.53±.34	8.72±.73	9.66±.60	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	5.11±.31	5.41±.34	4.93±.30	7.48±.56	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	5.11±.31	5.86±.36	6.20±.38	7.93±.50	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	6.67±.41	5.62±.34	....	6.77±.45	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	7.93±.50	5.15±.33	....	5.12±.32	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	6.27±.40	7.61±.47	....	6.94±.47	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	9.66±.60	6.67±.42	....	4.61±.28	1-6-1-3-4-4-4-2-4-1
Average..........	6.05	5.54		6.80	

TABLE 21. THE EFFECT OF CROSSING UPON VARIABILITY AS SHOWN BY THE NUMBER OF ROWS OF GRAIN ON THE EAR.

Pedigree number of strain—A	Coefficient of variability of number of rows				Pedigree number of strain—B
	A	A×B	B×A	B	
1-6-1-3-4-4-4-2-4-4	9.83±.61	9.73±.55	8.68±.52	7.48±.49	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-4-4	9.83±.61	8.50±.48	....	8.43±.51	1-7-1-1-1-4-7-5-2-6
1-6-1-3-4-4-4-2-4-4	9.83±.61	8.79±.54	....	9.21±.59	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-4-1	6.48±.40	7.96±.49	....	9.06±.66	1-7-1-2-2-9-2-1-1-1
1-6-1-3-4-4-4-2-5-5	7.23±.51	7.31±.45	9.24±.55	7.48±.49	1-7-1-1-1-4-7-5-4-7
1-6-1-3-4-4-4-2-5-5	7.23±.51	6.62±.40	8.11±.49	9.40±.68	1-7-1-2-2-9-2-1-1-4
1-6-1-3-4-4-4-2-5-5	7.23±.51	6.60±.40	....	9.21±.59	1-9-1-2-4-6-7-5-6
1-6-1-3-4-4-4-2-5-3	7.96±.50	8.92±.55	....	10.10±.64	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	6.08±.38	8.00±.48	....	7.96±.50	1-6-1-3-4-4-4-2-5-3
1-9-1-2-4-6-7-5-3	6.08±.38	8.36±.50	....	6.48±.40	1-6-1-3-4-4-4-2-4-1
1-9-1-2-4-6-7-5-3	6.08±.38	11.11±.72	10.32±.98	10.10±.64	1-7-1-1-1-4-7-5-2-1
1-9-1-2-4-6-7-5-3	6.08±.38	8.92±.56	10.62±.65	8.94±.71	1-7-1-1-1-4-7-5-4-5
1-9-1-2-4-6-7-5-3	6.08±.38	11.35±.72	7.02±.42	9.40±.68	1-7-1-2-2-9-2-1-1-4
1-9-1-2-4-6-7-5-6	9.21±.59	10.42±.63	....	9.06±.66	1-7-1-2-2-9-2-1-1-1
1-7-1-2-2-9-2-1-1-4	9.40±.68	9.68±.63	....	9.83±.61	1-6-1-3-4-4-4-2-4-4
1-7-1-1-1-4-7-5-2-6	8.43±.51	8.75±.56	....	7.23±.51	1-6-1-3-4-4-4-2-5-5
1-7-1-1-1-4-7-5-2-1	10.10±.64	8.84±.56	....	6.48±.40	1-6-1-3-4-4-4-2-4-1
Average..........	7.83	8.82		8.58	

TABLE 22. FREQUENCY DISTRIBUTION OF HEIGHT OF PLANT OF A NON-INBRED VARIETY OF MAIZE, OF SEVERAL INBRED STRAINS DERIVED FROM THIS VARIETY AND FIRST GENERATION CROSSES BETWEEN THESE INBRED STRAINS.

Pedigree number	Height of plant in inches																	N.	A.	C. V.
	63.5	68.5	73.5	78.5	83.5	88.5	93.5	98.5	103.5	108.5	113.5	118.5	123.5	128.5	133.5	138.5	143.5			
1	..	..	..	..	..	..	1	1	4	15	8	9	6	7	3	0	1	55	116.3 ± .90	8.64 ± .55
1-6-1-3-4-4-4-2-4-4-3	..	..	..	..	..	4	11	30	11	..	..	..	..	..	..	..	..	56	97.8 ± .36	4.14 ± .26
1-7-1-1-1-4-7-5-4-7-2	..	..	1	3	3	18	26	2	..	..	..	..	..	..	..	..	..	53	90.2 ± .46	5.49 ± .36
1-7-1-2-2-9-2-1-1-4-1	1	1	8	9	18	13	3	1	..	..	..	..	..	..	..	..	..	54	82.6 ± .61	8.05 ± .52
1-9-1-2-4-6-7-5-3-3	..	..	10	22	25	3	..	..	..	..	..	..	..	..	..	..	..	60	80.3 ± .35	5.04 ± .31
(1-6-1-3-4-4-4-2-4-4) × (1-7-1-1-1-4-7-5-4-7)	..	..	..	..	..	..	2	2	1	2	9	27	17	1	..	..	..	61	117.3 ± .61	6.10 ± .37
(1-6-1-3-4-4-4-2-4-1) × (1-7-1-2-2-9-2-1-1-1)	..	..	..	..	..	..	1	0	0	1	2	10	39	4	..	..	..	57	121.9 ± .46	4.22 ± .27
(1-6-1-3-4-4-4-2-4-4) × (1-9-1-2-4-6-7-5-6)	..	..	..	..	1	0	0	1	2	3	20	26	6	..	..	..	..	59	115.4 ± .56	5.55 ± .34
(1-7-1-1-1-4-7-5-2-6) × (1-6-1-3-4-4-4-2-5-5)	..	1	0	2	3	3	5	14	20	8	..	..	..	..	..	..	..	56	98.7 ± .78	8.81 ± .56
(1-7-1-1-1-4-7-5-4-5) × (1-9-1-2-4-6-7-5-3)	..	..	..	..	..	..	..	2	6	6	19	19	6	..	..	..	..	58	114.1 ± .55	5.48 ± .34
(1-7-1-2-2-9-2-1-1-4) × (1-6-1-3-4-4-4-2-4-4)	..	..	..	..	..	..	2	0	2	9	13	18	4	3	..	..	..	51	114.9 ± .68	6.27 ± .41
(1-7-1-2-2-9-2-1-1-4) × (1-9-1-2-4-6-7-5-3)	..	..	1	0	1	0	1	3	10	14	23	6	..	..	..	..	..	59	109.5 ± .76	7.94 ± .49
(1-9-1-2-4-6-7-5-3) × (1-6-1-3-4-4-4-2-5-3)	..	..	..	..	..	3	2	0	5	16	23	17	..	..	..	..	..	66	111.1 ± .61	6.66 ± .39
(1-9-1-2-4-6-7-5-3) × (1-7-1-1-1-4-7-5-2-1)	..	..	..	..	..	2	2	9	5	8	18	12	1	..	..	..	..	57	109.2 ± .76	7.78 ± .49
(1-9-1-2-4-6-7-5-3) × (1-7-1-2-2-9-2-1-1-4)	..	..	..	..	..	2	1	4	7	25	19	1	..	..	..	..	..	59	108.1 ± .50	5.27 ± .33

the beautiful uniformity of these crosses between inbred strains. In every respect each plant is a replica of the other. A collection of such vigorous and uniform maize plants in the field is a novel sight (see Plates IIIb and Vb).

Shull ('14) has pointed out that vigorous plants may be less susceptible to the effect of the environment than weaker types and that first generation hybrids, between uniform strains, may even show a reduction in variability.

The results obtained show this quite noticeably. Particularly was this true of several F_1's grown between their parental strains in a demonstration plot on rich low ground. During both seasons (1916–'17) when they were grown on this piece of ground, the weather was especially unfavorable when the plants were just starting, the ground being saturated with water most of the time. The germination in the selfed lines was extremely poor and many plants which did grow were stunted, and remained so throughout the season and never attained full height nor did they produce either tassels or ears. The variability of height, in these plants, was far greater than in many non-inbred varieties. Several plants, when killed by frost in the fall, were not over 30 inches tall while the average height of this strain is from 80 to 85 inches. The hybrids also had a poorer start than non-inbred varieties grown on the same ground on account of the small seed, but were able to overcome their handicap and in a few weeks were quite uniform. At the end of the season the difference in variability between the F_1 on the one hand and the inbred strains and the varieties on the other was striking. These plants were not used in the statistical work given here. The crosses and parents which were used and which were apparently quite uniform show a slight reduction in variability, in the number of nodes and in height in the F_1's as compared with their parents as can be seen in Tables 18 and 20. As Shull also pointed out, the variability of some characters may be increased by heterosis. This is shown in number of rows on the ear. The inbred strains rarely or never produce a second ear. The vigorous hybrids almost always do, and as the data have been obtained by counting all the ears gathered from a plot, the variability of the crosses, as shown in Tables 19 and 21, consequently seems greater than it really is as the second ear on nearly every plant is smaller and contains a fewer number of rows.

Although reciprocal crosses are on the whole nearly equal in respect to the degree in which heterosis is shown, there is some evidence, from Table 12, that this is not always so. Observations from the crosses in the field showed clearly that those in which strain Number 1-6 was used as the female, were usually more vigorous and productive than the others. In Table 23 the yields of all the crosses and reciprocal crosses (from 1 to 4 of each) having the same parental races are averaged. An average of all those crosses in which each strain was used as the male and in which each was used as the female parent shows some striking results. Those crosses on the whole in which strain Number 1–9 was used as the female gave the lowest yield. Those crosses in which strain Number 1–6 was used as the female are clearly the most productive. Strain Number 1–6 is the one which has the largest seeds and in which the pistillate inflorescence is the best developed of the four strains and at the expense of the staminate inflorescence.

TABLE 23. YIELD OF RECIPROCAL CROSSES AMONG INBRED STRAINS OF MAIZE.

(All crosses grown 1916. Yield given as bushels per acre.)

	1-9-1-2 ♀	1-7-1-2 ♀	1-7-1-1 ♀	1-6-1-3 ♀	Average ♂
1-9-1-2 ♂		82.1	100.5	86.7	89.8
1-7-1-2 ♂	63.0		70.9	103.6	79.2
1-7-1-1 ♂	55.3	57.2		98.7	70.4
1-6-1-3 ♂	67.7	95.8	92.2		85.2
Average ♀	62.0	78.4	87.9	96.3	
Yield selfed:					
(1917)	31.8	37.6	42.3	46.2	
(1916)	30.6	19.2	32.7	32.8	
Ave. weight of seed-cg.	16.6	27.9	19.9	34.1	

Strain Number 1–9 is just the reverse of this. It is the best developed of all the inbred strains in its staminate inflorescence, always producing abundant pollen, but has the smallest seeds, and is one of the poorest in the development of its pistillate inflorescence. Approximately a uniform stand of plants was obtained in all these crossed plots. They were all grown side by side in the same field in the same year.* There seems, therefore, to be a marked correlation in the development of the pistillate inflorescence between the mother and her hybrid progeny. The high yield of the crosses in which Number 1–9 was used as the male is due to the fact that its average yield was not pulled down by the low yielding crosses in which it was used as a female. The crosses in which 1–7–1–1 and 1–7–1–2 were used cannot be compared fairly with the other two because these two strains are more closely related. This correlation bears a close relationship with the size and development of the seed which produces first generation hybrid plant. The seeds of strain 1–9 are the poorest developed, those of Number 1–6 are the best. Hence, the plants of crosses (1–6) x (1–9) have a better start than the plants of the reciprocal cross. This assumption is borne out by the fact that the second generation starting from large fully developed seeds grown on vigorous F_1 plants are larger at the start than the F_1 plants grown from small, poorly developed seeds produced on inbred plants. This is shown in Fig. III and Plate IX. The second generation, however, is surpassed by the first before the end of the season, as shown in Fig. III and Plate X. Somewhat similar results have been obtained by Castle ('16) in guinea-pigs. F_2 animals, out of vigorous F_1 females, are larger at the start than either parent but do not surpass the F_1 individuals as in this case. It will be seen from this that in plants or animals which are reduced by inbreeding, the F_1 is handicapped in comparison with the F_2 and the immediately following generations.

It is not certain that the differences between reciprocal crosses can be accounted for on a purely nutritional basis. There is the possibility of unequal germinal reactions with different cytoplasms.

---

*The crossed strains were not grown between their inbred parental strains as was the case in the yields reported in U. S. Dept. of Agric., B. P. I. Bull. 243. This accounts in part for the extraordinarily large yields obtained at that time.

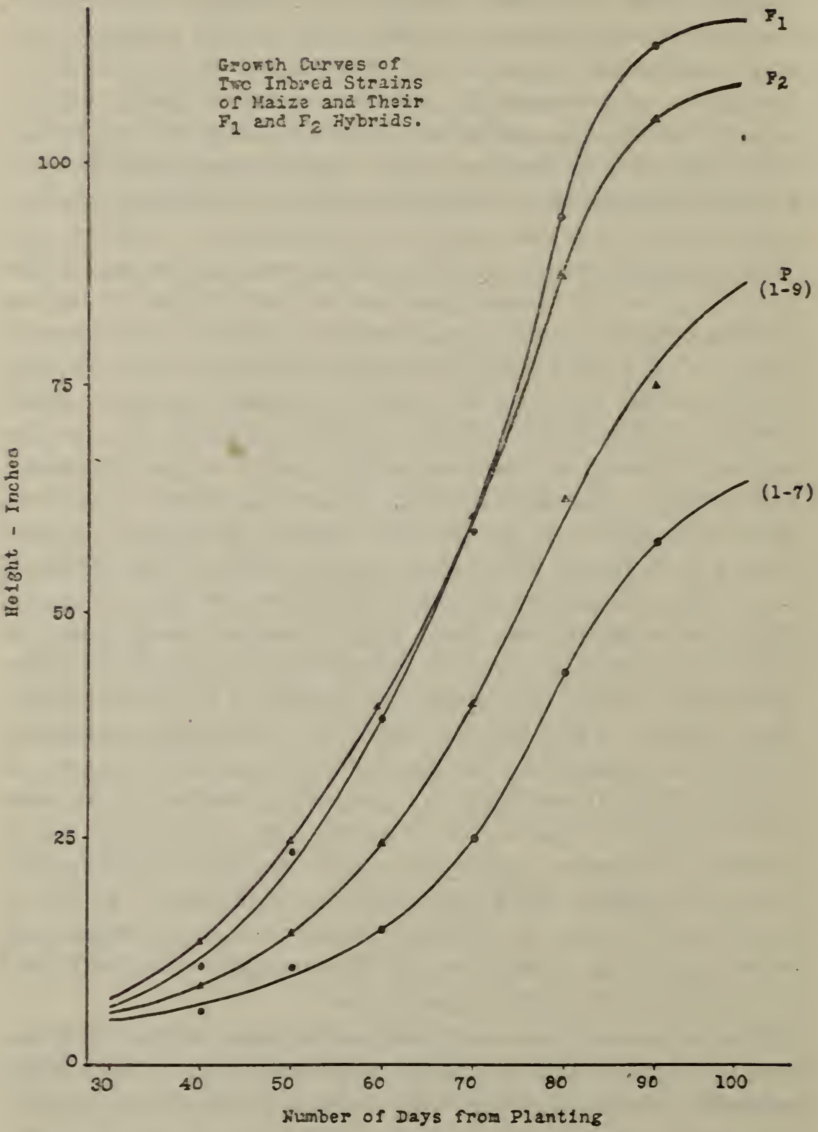


Figure III. Growth curves of two inbred strains of maize and their first and second generation hybrids.

The Value of Inbreeding in Plant and Animal Improvement.

These inbreeding and crossbreeding experiments on corn have considerable theoretical importance in the improvement of cultivated plants and domesticated animals. We have seen that inbreeding results in the elimination of abnormal, pathological and undesirable characters in general. This result has been obtained with a loss of size, vigor and productiveness. When these inbred strains are crossed, however, vigor and productiveness are returned in increased amount due to the uniform excellence of the individuals freed from undesirable characters. In this way a new variety or breed can be synthesized from the purified inbred strains of an old stock. A great sacrifice is thus made to attain a great good. Of course such a variety would have to be fixed by selection during a number of generations. The common practice of crossing in animals and plants already extremely heterozygous in order to obtain further improvement is like trying to solve a picture puzzle in the dark. It is only by resolving a naturally crossed species into homozygous types by inbreeding that it can be best analyzed and its desirable characters most surely selected for the recreation of an improved type.

The practical value of inbreeding has long been recognized by the breeders of domesticated animals. To gain uniformity and the highest expression of certain desirable characters they often practice inbreeding until the vigor of the breed is frequently impaired. From the results obtained with maize it seems that they stop just before the greatest good is to be accomplished. What if vigor is lost? It can always be regained immediately by crossing. There is no surer way of eliminating undesirable characters and discovering the best that there is in a stock than by a process of rigid inbreeding followed by subsequent testing in different crosses. This is not offered as a practical plan of procedure for the improvement of animals. It is merely intended to call attention to a principle which has probably not been used to its fullest extent. It may be that many domesticated breeds of animals cannot endure inbreeding to the extent that maize can. The cost of obtaining such pure types might very easily be prohibitive. The writer believes, however, that the splitting up of a breed of animals or a naturally crossed variety of plants by long continued inbreeding of the closest kind possible followed by the recombination of the most desirable inbred types, obtained in sufficient numbers to insure that nothing of value present in the stock at the start, is lost, is a valuable, practicable method of improvement in many animals and plants. According to this method a variety or breed would be recreated and then continued in a naturally crossed condition just as it was before. The value of this procedure as a method for plant improvement is now being tested. It is, of course, a long time proposition and one that must be carried on extensively to promise results.

With a few plants which are easily crossed it is possible to utilize hybrid vigor to the fullest extent by growing only first generation plants. Attention has been repeatedly called to this method of increasing the productiveness, particularly of maize and tomatoes. The greatest amount of hybrid vigor is shown in maize when the plants have been previously inbred. Unfortunately, when the inbreeding is carried on for several generations the reduction in the vigor of the resulting plants is so great that the small size and low vitality of the seeds borne on inbred plants seriously handicaps the hybrid plants grown from these seeds as just shown. So what is gained by an increased amount of heterosis may be partly lost by the poor start which the plants have. This handicap, in comparison with normally-crossed varieties, the F_1 may not be able to overcome entirely even though it is far more uniform and free from barren, mal-formed and otherwise undesirable plants—factors which count heavily in maximum production.

A way to overcome this handicap suggests itself which is to cross two vigorous first generation hybrids whose composition is such that the resulting cross will not be less heterozygous than either parent and, therefore, theoretically no less vigorous and productive. This is easily accomplished by taking four distinct inbred strains which are of such a composition that a cross between any two of them gives a vigorous product. Now by crossing two of these strains to make one first generation hybrid, and at the same time crossing the other two to make another, and then by combining the two first generation hybrids there should be no reduction in heterozygosity. These doubly crossed plants, however, starting from large seeds produced on large, vigorous hybrid plants would be freed from the handicap which their parents had and although somewhat less uniform should be more productive. While it may be out of place to say anything about this method until it has been thoroughly tested it is a method which is more promising than the plan originally advocated because by this method crossed seed for general field planting is produced much more abundantly than when non-vigorous inbred strains are crossed.

The Effect of Heterozygosis upon Endosperm Development and Selective Fertilization.

Together with the increase in size of other parts of the plant there is also an appreciable increase in the size and weight of seeds of maize immediately resulting from cross-pollination. This has been shown clearly by Collins and Kempton ('13) by pollinating several ears of maize with a mixture of the plant's own pollen and that of a different variety. Roberts ('12), Carrier ('13) and Wolfe ('15) have also shown that in maize the endosperm is increased by crossing. The writer ('18) has shown that this increase in endosperm development appears even more strikingly in reciprocal crosses between different inbred strains of maize. At that time reciprocal crosses had not been obtained between different individual plants. In Table 24 are given the distributions of the weights of the seeds shown in Plate XIa. Two plants were pollinated with a mixture of pollen obtained from these same two plants. One of the plants had white seeds and the other yellow and the selfed and crossed seeds on each ear could be easily distinguished. The same pollen mixture was also applied to a third plant of an inbred strain different from either of the other two but more nearly related to one than to the other. The average difference in weights between the selfed and crossed seeds on each ear are large. The two out-crossed lots of seeds on the third ear do not differ as greatly but the heavier seeds resulted from the wider cross.

Table 25 gives a number of averages of the weights of seeds from similar pairs of ears each having selfed and reciprocally crossed seeds. In every case there is a noticeable increase in weight as the result of crossing. In Table 26 the weights of the out-crossed seeds resulting from some of the same pollen mixtures are given. Here again the heavier seeds are those which have resulted from the wider cross. A and C are two inbred strains derived from one variety at the start while B is derived from a

TABLE 24. THE IMMEDIATE EFFECT OF POLLINATION ON THE WEIGHT OF SEEDS OF MAIZE AS SHOWN BY SELFED, RECIPROCALLY CROSSED AND OUT-CROSSED SEEDS OBTAINED FROM A MIXTURE OF POLLEN FROM TWO PLANTS OF TWO DIFFERENT INBRED STRAINS.

Type	Color of seeds	Weight of seeds in centigrams																N.	A.	Difference
		12.3	14.2	16.1	18.0	19.9	21.8	23.7	25.6	27.5	29.4	31.3	33.2	35.1	37.0	38.9	40.8			
A	White..................	..	1	0	0	0	6	7	35	66	60	10	..	..	..	..	..	185	27.6±.11	....
A×B	Light yellow............	..	..	..	..	..	1	2	4	6	15	35	87	25	3	..	..	178	32.3±.12	4.7±.16
B×A	Light yellow............	..	1	0	1	5	5	9	11	15	18	19	18	8	11	6	1	128	29.9±.31	6.1±.34
B	Dark yellow............	..	2	2	3	9	41	49	39	19	4	0	0	0	1	..	..	169	23.8±.15	....
C×A	White..................	1	2	10	17	27	16	14	8	3	..	..	..	..	..	..	..	98	20.5±.22	....
C×B	Light yellow............	..	..	..	1	13	57	56	26	5	1	..	..	..	..	..	..	159	23.1±.10	2.6±.24

TABLE 25. THE IMMEDIATE EFFECT OF POLLINATION UPON THE WEIGHT OF SEEDS OF MAIZE. (Selfed and reciprocally crossed seeds from the same ears.)

Pollen mixture number	Pedigree number of parent plant—A	A	A×B	B×A	B	Pedigree number of parent plant—B
		Selfed	Crossed	Crossed	Selfed	
		White	Light yellow		Yellow	
1	21-3-13-9-7-57-1	27.0	32.1	30.3	22.3	14-10-30-4-3-7-11-4
2	21-3-13-9-7-57-2	20.3	21.9	25.2	21.4	14-10-30-4-3-7-11-3
3	21-3-13-9-7-57-3	26.0	31.1	30.9	22.5	14-10-30-4-3-7-11-10
4	21-3-13-9-7-57-5	22.2	24.3	31.4	25.3	14-10-30-4-3-7-11-2
5	21-3-13-9-7-57-7	26.9	31.1	35.2	28.3	14-10-30-4-4-2-7-6
6	21-3-13-9-7-57-10	27.8	32.4	29.9	23.7	14-10-30-4-3-7-11-1
7	21-3-13-9-7-57-14	28.0	30.3	39.4	29.5	14-10-30-4-4-2-7-3
8	21-3-13-9-7-57-20	30.9	35.5	21.6	21.1	14-10-30-6-11-3-11-3
9	21-3-13-9-7-57-24	28.5	33.0	29.1	25.5	14-10-4-6-4-7-8-5
10	21-3-13-9-7-57-25	24.6	29.7	36.6	30.1	14-10-4-6-16-2-12-8
11	21-3-13-9-7-57-29	32.4	38.4	24.1	19.3	14-10-30-4-3-7-11-7
12	21-3-13-9-7-57-31	14.7	17.3	24.3	20.5	14-10-30-4-3-7-11-8
13	21-3-13-9-7-57-33	16.5	18.9	23.6	18.5	14-10-30-4-3-7-11-9
14	21-3-13-9-7-57-35	19.2	23.6	31.3	25.5	14-10-30-4-3-7-11-18
15	21-3-13-9-7-57-36	22.3	25.1	36.4	28.9	14-10-30-4-4-2-7-14
16	21-3-13-9-7-57-43	20.6	22.7	34.5	27.3	14-10-30-4-4-2-7-2
Average..............		24.2	28.0	30.2	24.4	
Increase of crossed above selfed........			3.8	5.8		
Percent increase.......			15.70	23.77		

TABLE 26. THE IMMEDIATE EFFECT OF POLLINATION UPON THE WEIGHT OF SEEDS OF MAIZE. (Out-crossed seeds resulting from some of the same pollen mixtures used in Table 25.)

Pedigree number of parent plant—C	Pollen mixture number	Average weight of seeds in centigrams			
		Cross C×A		Cross C×B	
20A-8-5-35-8.......	1		20.5		24.5
20A-8-5-35-3.......	2		19.7		23.7
20A-8-5-35-4.......	3		25.4		25.0
20A-8-5-35-11......	6		20.3		22.9
20A-8-5-35-24......	8		27.3		27.5
20A-8-5-35-26......	9		25.9		27.7
20A-8-5-35-6.......	13		20.2		20.1
20A-8-5-35-13......	16	20.1		25.8	
20A-8-5-35-15......		23.9		27.5	
20A-8-5-35-18......		21.6		20.9	
20A-8-5-35-21......		20.2		18.9	
20A-8-5-35-30......		21.7		21.2	
20A-8-5-35-37......		21.6		21.0	
		Ave. 21.5	21.5	22.6	22.6
Average.........................			22.7		24.3
Increase of (C×B) over (C×A)....					1.6
Percent increase.............					7.05

different variety. All the data taken together clearly show that an increase in endosperm development in maize is one of the common manifestations of heterosis.

Since the crossed seeds receive a noticeable impetus in development it seemed quite likely that the foreign pollen might be more efficient in fertilizing than the self pollen and hence a greater number of crossed seed than selfed would be produced. Such is not the case, however, as an examination of a large amount of data has shown.

In performing the mixed pollinations no attempt was made to have more than approximately equal quantities of pollen. It is impossible to get a mixture of equal quantities of functional pollen because it varies so in respect to viability. Since the same mixture of pollen was applied to both plants the ratio of the seeds resulting from "yellow" pollen to the seeds produced by the "white" pollen should be the same on both ears. Thus if there were no selective fertilization the percent of white seeds on one ear plus the percent of dark yellow seeds on the other, selfed seeds in both cases, should equal the sum of the percents of the crossed seeds on each ear. An excess of crossed seeds would then indicate a selective fertilization in favor of the crossed pollen. As a small excess of selfed seeds was obtained any selective fertilization in favor of the foreign pollen certainly did not take place.

The numbers of the crossed and selfed seeds, of which the weights are given in Tables 25 and 26, together with a large amount of similar data are not given here for fear of unduly burdening this publication with tables but they show, on the whole, a small excess of selfed seeds instead of crossed seeds. The results of an experiment designed to test this point in a somewhat different way are given in Table 27. Here instead of taking a mixture of pollen from two plants of two different strains a large amount of pollen was collected from an approximately equal number of plants of two long inbred and exceedingly uniform strains of maize. The two lots of pollen were sifted to obtain pure pollen and equal quantities of each were carefully measured out, thoroughly mixed together and applied to a number of ears of each of the two strains which furnished the pollen— A and B— and to a third strain— C—distinct from either. Although the tassels were bagged on the same day and the pollen collected two days later and equal quantities of each taken there

TABLE 27. THE NUMBER AND PROPORTION OF SELFED, RECIPROCALLY CROSSED AND OUT-CROSSED SEEDS OBTAINED BY MEANS OF A MIXTURE OF POLLEN FROM TWO DIFFERENT INBRED STRAINS OF MAIZE.

	Plant number	Selfed seeds from yellow pollen	Crossed seeds from white pollen	Plant number	Crossed seeds from yellow pollen	Selfed seeds from white pollen	Plant number	Out-crossed seeds from	
								yellow pollen	white pollen
		A	A×B		B×A	B		C×A	C×B
	A1	317	1	B1	319	5	C1	361	10
	A2	189	2	B2	224	9	C2	429	15
	A3	270	7	B3	369	10	C3	421	13
	A4	389	8	B4	348	26	C4	445	1
	A5	332	8	B5	330	6	..	...	..
	A6	260	1	..	...	..	..	...	..
Total number		1757	27		1590	56		1656	39
Actual proportion, percent		98.49	1.51		96.60	3.40		97.70	2.30
Closest perfect proportion, percent		97.545	2.455		97.545	2.455		97.545	2.455
Deviation		+.945	−.945		−.945	+.945		+.155	−.155
Probable error		±.195			±.301			±.246	
Ave. wt. per seed in centigrams		13.8	18.1		18.0	15.7		20.5	20.3
Increase		..	4.3		2.3	..		.2	..
Percent increase			30.4		14.6			1.0	

Note: The yellow seeded plants A = 1-9-1-2-4-6-7-5-6-2-1; the white seeded plants B = 10-4-8-3-5-3-4-8-2-1 and the yellow seeded plants C = 1-6-1-3-4-4-4-2-4-4-2-5. All seeds resulted from one mixture of pollen obtained from approximately equal numbers of plants of the two strains—A and B.

was not equal quantities of functional pollen as the number of seeds given in Table 27 show. The great inequality of functional pollen may have been due to the fact that the pollen of the B strain was more moist and tended to aggregate into a flocculent mass while the pollen of the other was perfectly dry and each grain remained separated from the others. For this reason it was difficult to measure the two lots of pollen equally and the dry pollen clustered about the fine lumps of moist pollen when the two kinds were mixed and was probably first to gain access to the stigmas. The difference between the two kinds of pollen was not due to any external differences, as far as could be seen, and indicate differences in the rate of maturing after shedding.

Whatever may be the cause of the great difference in fertilizing power this does not effect the point under investigation. However different the pollen may be, the seeds resulting from "yellow" pollen should be in the same ratio to the seeds resulting from the "white" pollen on one ear as the ratio of the same two kinds of seeds on the other ear within the limits of the error of random sampling if there is no selective fertilization one way or the other. And both these ratios should be the same as the third ratio obtained when this same mixture of pollen is used to produce seeds on a plant of a different variety of maize. Let us see what the figures given in Table 27 show. Of the reciprocal crosses and selfs the proportion, expressed as percent, is as follows:

Seed color carried by pollen	Yellow		White		Yellow		White
Type of Seeds	Selfed		Crossed		Crossed		Selfed
Actual proportion obtained	98.490	:	1.510	::	96.600	:	3.400
Closest perfect proportion	97.545	:	2.455	::	97.545	:	2.455
Deviation	+.945		–.945		–.945		+.945

The deviation from the closest perfect proportion is in favor of the selfed seeds. This theoretical ratio agrees very closely with the actual ratio obtained from the out-crossed seeds as shown in Table 27 although there is considerable difference in the results from the different ears. Letting S stand for selfed and C for crossed the probable error of the determination $\frac{S}{S + C}$ is $\pm \frac{.6745}{S + C} \sqrt{\frac{(S)(C)}{S + C}}$. The fraction $\frac{S}{S + C}$ gives the percent of selfed seeds and the probable error is stated as percent. Likewise the fraction $\frac{C}{S + C}$ gives the percent of crossed seeds and the probable error is the same as for the percent of selfed seeds.

This same experiment was repeated with about the same number of plants with the result of a similar excess of selfed seeds greater than would be expected from the probable error on the assumption that there is no selective fertilization. Does this mean that there is a selective fertilization in favor of a plant's own pollen and that the plant discriminates against foreign pollen even though the seeds resulting from that foreign pollen are greatly increased in size, weight, viability and the rate of growth of the ensuing plants? Unless there has been a constant error in classifying the seeds this seems to be the necessary conclusion to be drawn from the results so far given by maize. A sufficient number of plants will be grown from this seed to determine definately whether or not there has been any error in the separation of the seeds so that this question can be answered with a high degree of certainty.

In the meantime there is little doubt but that there is no great selective fertilization in favor of cross-pollination, if any, however much that cross-pollination may benefit the resulting seeds and the plants grown from them. If this is true crossing is without effect until the zygote is formed at the time of the union of the male and female nuclei.

In a consideration of selective fertilization it should be remembered that there are two different conditions which may be included in the term selective fertilization. One may be said to be the selection of different germ-plasms; the other the selection of different cytoplasms. For example a heterozygous plant produces pollen grains with different germinal compositions but all enclosed in the same cytoplasm. On the other hand pollen from different plants may differ in the nature of the cytoplasm as well as in hereditary factors carried in the nuclear material. East and Park ('18) have demonstrated that in tobacco there is no selective fertilization between gametes coming from one plant although the pollen grains differ in factors which determine fertility or sterility of the ensuing plants. The case is quite similar to that of the shape of pollen grains in peas which may be either all round or all cylindrical according to the germinal composition of the sporophyte which produced them and not according to the factors which they carry. Where pollen grains differ both in the factors which they carry and in the plants from which they come, as is the case with these experiments with maize, the conditions are quite different. It would not be surprising that there should be selective fertilization in one case and not in the other. East and Park have shown that a tobacco plant which was self-sterile, pollinated with a mixture of its own and pollen from another plant with which it was fertile, gave all crossed seeds—a maximum of selective fertilization.

Darwin (" Cross and Self Fertilization ") found that there was a selective fertilization in favor of foreign pollen in different plants. Many of Darwin's experiments, however, were made in such a way as to be open to doubt whether or not he really did obtain such an effect. His experiments, in applying foreign pollen sometime after self-pollination had taken place, in which he obtained in some cases many or all apparently crossed progeny, are open to other interpretations. The purity of the plants pollinated was not known. External conditions influencing fertilization were not guarded against. Taken as they stand, however, his experiments with *Mimulus*, *Iberis*, *Brassica*, *Raphinus*, *Allium* and *Primula* do indicate that in these plants there may be a selective fertilization in favor of foreign pollen. It is to be expected that plants which show partial self-incompatibility would show selective fertilization when a mixture of self and foreign pollen was applied. In maize, however, as mentioned before, the sterility shown is in the nature of pollen and ovule abortion, and whenever well formed pollen is produced it seems to be able to fertilize equally any plants if not too distinct in type. A distinction should be made, then, between self-fertile plants and self-sterile plants when dealing with selective fertilization.

Hyde ('14) has shown clearly that in Drosophila both males and females of inbred lines are more productive of offspring when mated to an individual of a different line than when mated to one of their own. Both males and females, therefore, produce more functional gametes than are utilized when individuals of the same inbred lines are paired. Hence a female, impregnated with a mixture of two kinds of spermatozoa from the same and from different lines would produce more hybrid progeny than inbred progeny even if equal quantities of both types of spermatozoa were available for fertilization. In other words there would be selective fertilization in favor of cross-fertilization.

Whether or not there may be a similar condition in other animals I do not know. Even in Drosophila, fertilization by the two types of sperm may take place equally, and a greater proportion of close-fertilized eggs, than cross-fertilized, fail to hatch, due to lesser vigor or lethal factors. In Hyde's experiments the type of fertilization had no marked effect on the number of eggs laid, only on the percentage which hatched.

In maize, and possibly all plants which show no self-incompatibility, the fact seems clear that crossing is wholly without effect until the fertilization process is completed.

Although there is apparently no effect of crossing in maize until the zygote is formed, such an effect is apparent immediately afterwards. In addition to the increase in endosperm development there is also an increase in the vigor of the embryo. Whether or not the size of the embryo in the seed is increased has not been actually determined, other than by inspection, but it undoubtedly is, along with the endosperm. When crossed and selfed seeds from the same ear, grown on a plant which has been inbred previously for several generations, are planted a striking difference is soon apparent. The crossed seedlings appear from one to two days before the selfed seedlings and may be two or three inches above ground before any of the selfed plants begin to appear. (See Plate XIb). From then on the superiority of the crossed over the selfed plants increases rapidly as shown by the curves in Figure III.

THE EFFECT OF HETEROZYGOSIS UPON LONGEVITY, HARDINESS AND VIABILITY.

An increased longevity, viability and endurance against unfavorable climatic conditions have been frequently noted in hybrids. Kölreuter and Wiegmann both mention this fact. Gärtner in his book "Bastarderzeugung im Pflanzenreich" devotes considerable attention to this feature. Under the heading "Ausdauer und Lebenstenacität der Bastardpflanzen" he makes the following statements.

> "There is certainly no essential difference between annual and biennial plants and between these and perennials in regard to their longevity; for it is not seldom that different individuals of the same species have a longer life at times as, for example, *Draba verna*, which has annual and

biennial forms; the longevity of a plant furnishes thereby no specific differences but signifies at most a variability as Prof. W. D. I. Koch has shown. However, in hybrids this difference deserves special consideration. In most hybrids an increased longevity and greater endurance can be observed as compared with their parental races even if they come into bloom a year earlier. The union of a annual, herbaceous female plant with a perennial, shrubby species through hybridization does not shorten the life cycle of the forthcoming hybrid as the union of *Hyoscyamus agrestis* with *niger*, *Nicotiana rustica* with *perennis*, *Calceolaria plantaginea* with *rugosa* shows, and so also in reciprocal crosses when the perennial species furnishes the seed and the annual species supplies the pollen, as *Nicotiana glauca* with *Langsdorfii*, *Dianthus caryophyllus* with *chinensis*, *Malva sylvestris* with *Mauritiana* or biennials with perennials and reciprocally as *Digitalis purpurea* with *Ochroleuca* or *lutea* and *lutea* with *purpurea* or *ochroleuca* with *purpurea*. From the union of two races of different longevity comes usually a hybrid into which the longer life of one or the other of its parent races is carried whether it comes from the male or female parent species."

Many more instances are given by Gärtner from his own observations and those of others to enable him to reach the following conclusion:

" These examples support the statement of Kölreuter's that the longer life of hybrid plants is to be counted among their usual properties."

With regard to the resistance of hybrids to unfavorable weather conditions he goes on to say:

" With their longevity stands, in the closest relation, the fairly common property of hybrids to withstand lower temperatures than their parental races without injury to their growth and vegetative life. Kölreuter first observed that *Lycium barbara-afrum* in south Germany withstood the winter in the open field; although *Lycium afrum* must be wintered over, at least, in a cold frame. The cross of *Nicotiana Tabaco-undulata*, according to Sageret in France had an increased life, although in a protected place, in open field. W. Herbert reports that *Rhododendron altaclarae*, which is a hybrid union of *R. pontica-cantawbiense* ♀ with the very sensitive *Nepalense arboreum coccineum* ♂, has been grown in the open in England; also Robert Sweet confirms the same result by a hybrid *crinum* and many other hybrids of bulbous plants grown in open field whose parental species must be grown in the hothouse.

" *Lobelia syphilitica-cardinalis* wintered over with a light covering in the winter of 1832-1833 with 5°F in open field. *Lychnicucubalus albus* and *ruber* lasted three years in open field although *cucubalus viscosus* in south Germany did not survive in open field. All hybrids of genus *coccineum* stood over the winter of 1842-1843 with 5°F. in the open, although the pure species seldom lives through our usual winters of 43° to 9.5° F. Prof. Wiegmann reports similar results.

> " Very frost sensitive species of Nicotiana and their hybrids did not withstand, under the same conditions, such low temperatures as the afore-mentioned plants; but we have flowered and carried over part of them wherever they were well covered with snow, for example, *N. quadri-valvis glutinosa, rustica-quadrivalvis,* these withstood 25° F. and yet have continued blooming although *N. glutinosa, quadrivalvis, paniculata, Tabacum* and *rustica* were already frozen by 32° F. Moreover other crosses of very sensitive and tender species of this genus as *paniculata-Langsdorfii, vincaeflora-Langsdorfii, vincae-flora-quadrivalvis* have been carried over in an active growing condition two to three years, and *glauca-Langsdorfii* three years in a cold house with 39° to 42°. The hybrid *N. paniculatarustica-paniculata* was kept over in a cold house in the cold winter of 1839-40 but its leaves were yellow. Among all the species of this genus the cross of *N. suaveolenti-macrophylla* showed itself to be the most hardy. On the 16th of October of its first year (1828) its top was frozen but it did not suffer from this, and 12 days later put out a new shoot from the root and its leaves lasted through the winter in a cold house in a fresh, green condition although the other species were yellow and this plant was the first to start into growth in the spring. The same endurance Sageret observed in *Nicotiana suaveolenti-virginica.* All these plants in the last year of their vegetative life seemed to die off more as the result of the unfavorableness of the weather than of old age."

Exceptions are noted by Gärtner in that some species which were not resistant to cold did not give resistant hybrids. In many cases the hybrids were weak because of the distant relationship of the parental races.

Sargent ('94) reports a remarkably vigorous and hardy hybrid tree supposed to be a cross of the tender English walnut, *Juglans regia* and the common butternut *Juglans cinerea.* He says: p. 434

> "My attention was first called to the fact by observing that a tree which I had supposed was the so-called English walnut—*Juglans regia,* in the grounds connected with the Episcopal School of Harvard College at Cambridge, was not injured by the cold of the severest winters, although *Juglans regia* generally suffers from cold here— and rarely grows to a large size. This individual is really a noble tree; the trunk forks ab u five feet above the surface of the ground into limbs and girths, at the point where its diameter is smallest, fifteen feet and two inches. The divisions of the trunk spread slightly and form a wide, round-topped head of pendulous branches and unusual symmetry and beauty, and probably sixty to seventy feet high."

Heterosis is also shown in a resistance to bacterial and fungus diseases. Some of the inbred strains of maize are very susceptible to the bacterial leaf-wilt and in some years at the end of the season all the plants of these strains appear as if they had been scorched by fire while other strains in adjoining rows are untouched. Other strains have quite a large percentage of plants attacked by smut. Crosses, however, of these susceptible strains with those which are not affected by these parasitic organisms are only slightly or not at all affected.

TABLE 28. SUSCEPTIBILITY TO SMUT (*Ustilago zeae*) OF A NON-INBRED VARIETY OF MAIZE, SEVERAL INBRED STRAINS DERIVED FROM THIS VARIETY AND THE FIRST AND SECOND GENERATION CROSSES BETWEEN THE MOST SUSCEPTIBLE AND THE LEAST SUSCEPTIBLE STRAINS.

Pedigree number	Percent of plants affected			Total number of plants grown	Total percent of plants affected
	Plot I	Plot II	Plot III		
1	....	....	1.75	114	1.75
1-9-1-2-4-6-7-5	0	.27	.56	596	.34
1-7-1-2-2-9-2-1	2.17	.35	0	408	.49
1-7-1-1-1-4-7-5	8.79	10.16	5.77	950	9.79
1-6-1-3-4-4-4-2	0	0	0	992	0
(1-6-1-3) × (1-7-1-1) F_1	....	2.48	0	439	2.28
(1-6-1-3) × (1-7-1-1) F_2	....	....	5.15	97	5.15

In Table 28 are given the per cent. of plants affected by smut (*Ustilago zea*, Beck. Ung.) of the original, non-inbred Leaming variety of maize previously spoken of and four inbred strains derived from this variety by ten or eleven generations of self-pollination. Seed of the four inbred strains was planted in three rather widely separated plots in the same field in 1917. Two of the strains showed only a small infection by this parasite; one showed about 10 per cent infection and one had not a single plant affected in all three plots in a total of nearly one thousand plants. Since the differences which these four strains show are fairly consistent in the different places grown it can hardly be doubted but that segregation of susceptibility to parasitism has occurred in the inbreeding process. The first generation hybrid between the most resistant and the most susceptible strain was free from smut in one plot and but slightly affected in another. The second generation hybrid grown side by side with first generation showed considerably more infection although the number of plants grown was small. This is fairly good evidence that resistance to smut in maize tends to dominate in crosses between plants which differ in this respect.

Tisdale, according to L. R. Jones ('18) also finds that in flax disease resistance tends to be dominant although the hybrids are more or less intermediate in this respect and the method of inheritance is rather complex. Biffen ('12), on the other hand, concluded that the resistance to rust in wheat was recessive. Likewise, Weston ('18) states that maize and teosinte-maize hybrids are extremely susceptible to a downy mildew (*Peronospora Maydis*, Rac.) in Java and other places, although teosinte (*Euchlaena mexicana*, Schrad.) is immune.

Data from another source have been obtained from the garden radish (*Raphanus sativus*, L.). A white-rooted variety of radish was allowed to go to seed alongside a red-rooted radish. Seed collected from the white-rooted plants was sown thickly in a flat and when they came up it was seen that a number of the seedlings were crossed from their red colored stems. The seedlings were quite badly attacked by the "damping-off" fungus and large numbers of them were killed, but a far less number of the crossed seedlings were affected as shown by the decay of the tissues at the base of the stem. The figures obtained are given in Table 29.

TABLE 29. COMPARATIVE SUSCEPTIBILITY TO "DAMPING-OFF" DISEASE OF SELFED AND CROSSED RADISH SEEDLINGS.

Variety of Radish	White Seedlings, Selfed			Red Seedlings, Crossed		
	Number grown	Number affected	Percent affected	Number grown	Number affected	Percent affected
Short, white...	349	142	40.7	30	4	13.3
Long, white...	76	28	36.8	7	0	0

Gernert ('17) reports a case of immunity to aphis attack of teosinte-maize hybrids in which the maize parent was badly infested whereas the teosinte parent and the hybrid entirely escaped injury.

Together with these manifestations of heterosis in its influence on hardiness there is an increase in the viability of crossed seeds as compared to selfed seeds from the same ears as shown in Table

TABLE 30. THE EFFECT OF HETEROZYGOSIS UPON GERMINATION—A COMPARISON OF CROSSED AND SELFED SEEDS FROM THE SAME EARS OF MAIZE

Pedigree number of female parent	Pedigree number of male parent	Percent increase in weight of crossed seeds over selfed	Number of seeds planted of each	Number of selfed seeds germinated	Number of crossed seeds germinated	Percent selfed seeds germinated.	Percent crossed seeds germinated.	Excess of percent crossed seeds germinated over selfed
21-3-13-9-7-57-13	14-10-30-6-2-13-5-13	8.2	121	24	46	19.8	38.0	18.2
21-3-13-9-7-57-17	14-10-30-6-11-3-11-17	18.8	39	26	37	66.7	94.9	28.2
21-3-13-9-7-57-21	14-10-30-6-11-3-11-4	7.1	32	28	29	87.5	90.6	3.1
21-3-13-9-7-57-38	14-10-30-4-4-2-7-38	68.0	22	14	22	63.6	100.0	36.4
21-3-13-9-7-57-39	14-10-30-4-4-2-7-7	18.3	33	16	26	48.5	78.8	30.3
21-3-13-9-7-57-54	14-10-30-4-4-2-7-7	3.9	97	19	27	19.6	27.8	8.2
21-3-13-9-7-57-58	14-10-4-6-4-7-8-15	8.8	100	43	68	43.0	68.0	25.0
21-3-13-9-7-57-59	14-10-4-6-4-7-8-10	10.0	12	9	12	75.0	100.0	25.0
21-3-13-9-7-57-63	14-10-4-6-4-7-8-29	17.5	31	26	30	83.9	96.8	12.9
21-3-13-9-7-57-64	14-10-4-6-4-7-8-29	13.3	14	9	14	64.3	100.0	35.7
21-3-13-9-7-57-65	*	13.5	47	41	45	87.2	95.7	8.5
14-10-30-4-4-2-7-12	21-3-13-9-7-57-38	8.3	87	84	86	96.6	98.9	2.3
	Total	16.3	635	339	442	53.4	69.6	16.2

* Seeds crossed but number of parent unknown.

30. Seeds which were secured from some of the mixed pollinations, reported previously, were sown in flats. Without exception the crossed seeds showed a higher percentage of germination than the selfed seeds from the same ears as can be seen in Plate XIb. These seeds were planted two months after ripening. Whether or not an increase in age would show greater differences in viability is not known but it is quite likely that the difference might become even greater with age up to a certain point. The low germination of both crossed and selfed seeds in some of the ears was due to the fact that they were moldy on account of late ripening and damp weather.

The increased vegetative vigor as manifested by an increased facility of vegetative propagation in hybrids has been repeatedly spoken of. Kölreuter, Wiegmann, Sageret and Focke make a special mention of this phenomenon.

Moreover there is no positive evidence that plants which are propagated vegetatively lose any of their hybrid vigor which they may have, no matter how many generations of asexual reproductions take place. Undoubtedly most varieties of cultivated fruits, flowers, ornamental plants and field crops which are commonly propagated vegetatively, owe their excellence in part to heterosis.

From time to time the supposed degeneration of plants in long-continued vegetative propagation has been much disputed. Knight ('99) and Van Mons ('36) contended that they did degenerate, but Lindley ('52) reviewing Knight's work thought that the evidence did not support such a view. Gärtner states that the characteristics of a hybrid do not change throughout the whole life cycle of the individual, even when it is propagated and disseminated by buds, cuttings or layers.

Darwin believed that a degeneration took place largely for the same reason that he thought long continued self-fertilization was injurious. Asa Gray ('76), in reviewing Darwin's opinions on this matter, says (p. 347):

> "The conclusion of the matter, from the scientific point of view is, that sexually propagated varieties of races, although liable to disappear through change, need not be expected to wear out and there is no proof that they do, but that non-sexually propagated varieties, though not especially liable to change, may theoretically be expected to wear out, but to be a very long time about it."

Gray, however, cites cases of horticultural varieties propagated since the time of the Romans with no apparent loss of vigor. Whitney ('12a, b, c) and A. F. Shull ('12b) believe that an actual degeneration takes place in parthenogenetic reproduction in the rotifiers. The work of Enriques ('07), Woodruff ('11) and Jennings ('12) on Paramecium proves almost beyond doubt that there is no degeneration in this organism although reproduction by fision in the infusoria may be considerably different from vegetative propagation in the higher plants. Hedrick ('13), from the evidences of long-continued varieties of fruits, and East ('08) working with potatoes and reviewing extensively the whole question believe that there is no evidence that a real degeneration takes place which cannot be accounted for on the basis of the accumulation of disease or other external effects. East ('10), however, suggested that such a degeneration, if ever proven, might be accounted for on the basis of a decreasing effect of the physiological stimulation assumed to be derived from heterozygosity. A. F. Shull (12a) holds a similar opinion. From the nature of the problem it can hardly be settled satisfactorily one way or the other by experimental means. As it stands at present there is no clear evidence that there is a degeneration in long continued asexually propagated plants. The burden of proof rests with the positive side.

THE EFFECT OF HETEROZYGOSIS UPON THE TIME OF FLOWERING AND MATURING.

Many investigations have indicated that there is a hastening of the time of maturity due to heterozygosis. That there is an acceleration in the rate of growth is, of course, evident from the great increase in size shown by hybrids grown in the same season with their parents. There is, moreover, considerable evidence from previous work and from the data to be given here to show that hybrids not only grow to a larger size but complete their growth in a shorter time than the parents take to complete a smaller amount of growth. In other words, heterozygosis tends to hasten the time of maturity as well as to increase size.

The investigations of Kölreuter, Gärtner, Focke and Darwin show a large number of specie- and variety-crosses wherein the hybrid flowers before either of the parents. Both Kölreuter and Gärtner give instances of perennials which commonly bloom in the second or third year whose hybrids bloom in the first year.

The most extensive observations bearing on this relation of heterosis to time of flowering are those given by Darwin in his "Cross and Self Fertilization in the Vegetable Kingdom." He gives the time of flowering of 28 crosses between different strains within many different species—which show positive evidence of hybrid vigor. Of these 28 crosses 81 per cent. flower before the parents. Four cases are given where the crosses are less vigorous than the parents and in each of these the parents flowered first.

Recent experiments in hybridization show, almost without exception, that crosses which result in an increase in vigor also result in a hastening of the time of flowering. One exception to this statement must be noted in the cross between a large dent and a small pop variety of corn reported by Emerson and East ('13). This cross showed distinct evidence of hybrid vigor in an increase in internode length over that of both parents. The parents differed in time of flowering by 25 days. The first generation of the cross grown the same year as the parents was "distinctly intermediate" in time of flowering. There was an increase in the rate of growth necessarily as the plants were larger than the average of the parents.

Data bearing upon the relation of heterozygosis to the time of maturing has been secured from two different plants, tomatoes and corn. A large part of the data on tomatoes was collected by Prof. H. K. Hayes, now at the Minnesota College and Station.

Four commercial varieties of tomatoes were successively self-pollinated for four years. Two first generation crosses between these varieties were grown in each of the four years and compared as to yield of fruit and time of production with the two selfed parents. In every case the same plants which were used to produce the selfed seed for the next generation were also used to make the crosses. For this reason and because tomatoes are naturally self-pollinated and are hence in a homozygous condition the first generation crosses can be compared strictly with their parents.

From thirty to fifty plants of each variety and cross were grown each year. The fruit was picked as it ripened at intervals of from 3 to 5 days and the average production per plant was determined. One of the crosses was between varieties which had approximately the same time of ripening. This first generation cross did not exceed, in total yield, the average of the two parents and did not differ from them in respect to time of production.

The other cross, however, yielded, each year, an average of 16 percent above the better parent. The two varieties used in making this cross differed in time of production by an average of five days. The first generation cross while yielding 16 percent more than the late parent was each year fully as early as the early parent. Although the difference in time of production between these varieties is small the consistent results obtained in four successive years are certainly significant.

Similar results were secured with sweet corn. A first generation cross between an early variety of sweet corn, Golden Bantam and a late variety, Evergreen, was grown in 1916 together with the two parental varieties and compared in time of flowering, number of ears per plant and in height. They were all planted at the same time but rather late in the season so that the early and late varieties bloomed at more nearly the same time than is usually the case. About half of the plants of the early variety were showing silks before the late variety commenced to silk out. The first generation cross was slightly earlier than the early parent in producing silks. The cross was noticeably affected by vigor of crossing in that it was fully as tall as the taller parent and averaged more ears per plant than either parent although the ears were not as large as those of the Evergreen variety.

Much more extensive and authoritative data have been secured from a comparison of inbred strains of corn with their first generation crosses. Forty-two strains of corn which had been continuously selfed for from 5 to 11 generations and 100 first generation crosses representing different combinations between these selfed strains were grown under the same conditions as to time of planting and culture. Both the inbred strains and their crosses were exceedingly uniform in time of flowering and maturing. All the plants in any selection flowered and matured within a few days. About 60 plants of each were grown. At intervals of one week during the flowering season the number of selections of the selfs and crosses which had flowered by that time were noted. Similarly at the end of the season the selections which were mature were noted at intervals. Although the time of maturity can not be so definitely determined as the time of flowering all the plants in a selection were uniform in this respect. For the flint varieties the glazing of the ears and for the dent varieties the denting of the kernels were taken as indications of maturity. The crosses yielded, on the average, 180 per cent more than their parents.

Together with this increase in the amount of growth there was a noticeable hastening of both the time of flowering and maturing. In time of flowering the crosses were four days and in maturing eight days earlier than the average of their parents. Since the crosses gave a large increase in the total amount of growth and produced this growth in a somewhat shorter time than their inbred parents it is all the more evident that heterozygosis increases the rapidity of growth. See Plates VII a and b.

THE RELATION OF THE EFFECTS OF HETEROZYGOSIS AND OF THE ENVIRONMENT.

East ('16) has stated that heterozygosis "affects a result comparable to favorable external conditions." In a cross between two varieties of *Nicotiana* he found that the first generation gave a noticeable increase in the amount of growth as shown by the height and general size of the plant as the result of heterozygosis. The corolla length of the flowers, which is very little affected by environmental factors, was not increased above the average of the two parents.

The similarity of the effects of heterozygosis to the environmental effects is also shown in the affect of crossing on the number of nodes and internode lengths of corn. As was noted from Tables 15 and 13 the number of nodes is increased only 6 percen while the height of plant is increased 27 percent. This is exactly the effect that nutritional factors have. The height of plant is reduced under poor conditions by a reduction in internode length without reducing appreciably the number of nodes.

In general it is evidently true that heterozygosis affects many characters in the same way as the environment, but it should be noted that in time of maturity these two factors have directly opposite effects. It is generally recognized, I believe, that favorable external conditions such as increased moisture or fertility, where these are limiting factors, which result in a greater total amount of growth tend to prolong both the time of flowering and the completion of growth. Conversely unfavorable external conditions which stunt the plants and limit their growth tend to hasten their period of flowering and maturity. There are, of course, certain exceptions to this statement.

Whether or not the effect of heterozygosis in hastening maturity can manifest itself independent of any increase in vegetative luxuriance or other manifestations of hybrid vigor is not known. The results given here would indicate that the vigor derived from crossing enables the plant to carry on its life processes more easily and more efficiently and thus to accomplish its task in a shorter time.

With regard to the effects of heterozygosis in animals much the same relation is shown with the external environmental effects as in plants although the rate of growth and size obtained at maturity may be more definitely fixed in animals than in plants. According to Castle ('16) there is an increase in the rate of growth as well as the attainment of a larger size at maturity in hybrid guinea-pigs. Hyde ('14) also finds an increase in rate of growth and hastening of sexual maturity on crossing in Drosophila. These effects in animals are probably greater than could be obtained by any amount of feeding or care just as it is the case in plants.

It may be stated briefly that the effects of heterozygosis in both animals and plants, not too distantly related, all together contribute towards an increased reproductive ability and this effect has probably been of fundamental importance in evolution in establishing sex.

In the foregoing account of some of the most noticeable effects of crossbreeding upon development we have been dealing only with crosses among closely related organisms. It is of course, well known that in crosses between distantly related forms the beneficial effects of crossing may disappear and the effects become increasingly more injurious as the degree of dissimilarity becomes greater. The most frequent, pronouncedly injurious effect is the reduction or complete loss of fertility. This may or may not be accompanied by a great acceleration of growth. This is shown in many plants, notably by Gravatt's Radish-Cabbage hybrid and by Wichura's Willow hybrids as well as by many good illustrations given by Gärtner and Focke. It is perhaps not surprising that the reproductive ability should be the first to suffer since reproduction is the most difficult task the organism has to perform. The failure of the reproductive mechanism might divert the energies into bodily growth and thus in part account for the large size and great vigor of some sterile hybrids but, as all are agreed, this can not entirely account for the great increases in size nor obviously does it apply to the more common cases where both size and productiveness are increased at the same time.

To sum up one can therefore say that, in plants, crossing may have a great range of effects, according to the degree of relationship of the parents, from a condition in which: the cross is not possible and no seed produced; seed may be produced but fail to germinate; plants may be produced which are either very weak, normal or very vigorous without being able to reproduce themselves; plants which are both more vigorous and more productive than their parents; to a condition in which they are so closely related that the crossed plants do not differ appreciably from selfed plants. A similar series can be arranged with animals.

SUMMARY OF THE EFFECTS OF INBREEDING AND CROSSBREEDING.

Before taking up a theoretical consideration of the cause of hybrid vigor and its importance in the establishment of sex it is well to summarize briefly some of the main conclusions, with regard to the effects of inbreeding and crossbreeding on development, to be arrived at from a study of the investigations discussed.

EFFECTS OF INBREEDING.

1. Continued inbreeding results in the segregation of a variable complex into a number of diverse types which are uniform within themselves.
2. The segregates which differ in visible, qualitative characters also differ in quantitative characters; types with abnormalities appear which cannot reproduce themselves; others appear which are perpetuated with difficulty; others are obtained which are perfectly normal in structure and function. These latter are usually less well developed, but may be as well or better developed than the original stock from which they are derived.
3. The change in size, structure, or function and reduction in variability is most noticeable in the earlier generations of inbreeding, rapidly becomes less and the surviving inbred strains are uniform and constant.
4. The rate of approach to uniformity and constancy differs in different lines.
5. These uniform and constant inbred strains are quite comparable to naturally self-fertilized species.
6. No single effect can be attributed to inbreeding other than the reduction in variability.
7. All these results are in conformity with Mendel's law and Johannsen's genotype conception.

THE EFFECTS OF CROSSBREEDING.

1. Heterosis accompanies heterogeneity in germinal constitution whether or not the organisms crossed are from the same or diverse stocks.
2. Heterosis is widespread in its occurrence throughout the plant and animal kingdoms.

3. Heterosis is shown as an increase in the size of parts rather than an increase in the number of parts.

4. Cross-fertilization is without effect until the zygote is formed; from that time on heterosis may be apparent throughout the life of the individual.

5. Heterozygosis has an undiminished effect on plants propagated vegetatively.

6. Heterozygosis may have a stimulating effect on some characters and a depressing effect on others in the same organism.

A Mendelian Interpretation of Heterosis.

It is due to the work of G. H. Shull ('08, '09, '10, '11) and of East ('08, '09) and East and Hayes ('12), supplemented and confirmed by the results given here, that we no longer believe that inbreeding is a process of continuous degeneration. Also these investigators first demonstrated clearly that the same principle was involved in the loss of vigor accompanying inbreeding and the increase in vigor resulting from crossing.

To account for this well nigh universal loss of vigor when domesticated races of plants and animals are inbred, they thought it necessary to assume a physiological stimulation which was present when unlike germplasms were united and which disappeared as homozygosis was brought about automatically by inbreeding. Part of the effects of inbreeding were due, according to their views, to the segregations into pure lines of different hereditary complexes and the appearance of previously hidden recessive characters, and part were due to the loss of this stimulation.

G. H. Shull's ('14) opinion as to the way germinal heterogeneity induces vigor is stated briefly as follows (p. 126):

> "The essential features of the hypothesis may be stated in more general terms as follows: The physiological vigor of an organism, as manifested in its rapidity of growth, its height and general robustness, is positively correlated with the degree of dissimilarity in the gametes by whose union the organism has been formed. In other words, the resultant heterogeneity and lack of balance produced by such differences in the reacting and interacting elements of the germ-cells act as a stimulus to increased cell-division, growth, etc. The more numerous the differences between the uniting gametes—at least within certain limits—the greater, on the

whole, is the amount of stimulation. These differences need not be Mendelian in their inheritance, although in most organisms they probably are Mendelian to a prevailing extent."

Both the view stated above and that of East and Hayes assume that the increase in development is due to a reaction between different elements in the nucleus and that this stimulus disappears when homozygosity is reached. A. F. Shull ('12a) has proposed a slightly different idea in that he assumes the stimulus to be due to the reaction of new elements in the nucleus, brought in by cross-fertilization, to the maternal cytoplasm. According to his view there might still be a stimulation even after complete homozygosity is attained. Also in asexual propagation he supposes that the cytoplasm might become gradually accustomed to a heterozygous nucleus, hence long continued asexual reproduction might lead to a gradual reduction in vigor which this writer finds does occur in the rotifer, *Hydatina senta.* ('12b).

It should be remembered, however, that both these hypotheses, as to the effect of germinal differences, postulate a stimulation to account for an increase in development as the facts demand. It would have been even more plausible to postulate a depressing effect had the facts been otherwise. The only basis for a stimulation of this kind is in the fact that fertilization initiates the development of the egg. Heterozygosis, however, is not concerned with the starting of the development of the egg, but only with the rate of development after growth is commenced. Is it not more plausible that "a lack of balance" occasioned by the union of unlike germplasms would retard development rather than stimulate it?

Keeble and Pellew ('10) first suggested that dominance of characters contributed by both parents might be a factor in the increased vigor of hybrids. They illustrated this conception by a cross between two varieties of peas which possessed features of both parents, and were taller than either.

Bruce ('10) has shown that the total number of dominant factors is greater in a hybrid population than in either parental population and that there is consequently a correlation between the number of dominant factors and hybrid vigor. As far as I know, Bruce has never followed up this suggestion. He did not show why it was that the presence of a greater number of dominant factors brought about an increase in growth, nor did he show why it was that all the dominant features could rarely or never be accumulated in certain individuals and races which would therefore show no reduction in vigor when inbred.

East and Hayes ('12) attempting to distinguish between dominance and the effects of heterozygosis make the following statement (p. 31):

> "The term vigor has hitherto been used with the general meaning which the biologist readily understands. We will now endeavor to show in what plant characters this vigor finds expression. It is not an easy task because of the possibility of confusing the phenomenon of Mendelian dominance with the physiological effect due to heterozygosis. The confusion is due to a superficial resemblance only. Dominance is the expressed potency of a character in a cross and affects the character as a whole. A morphological character, like the pods of individual maize seeds, or the product of some physiological reaction like the red color of the seed pericarp in maize, may be perfectly dominant, that is, it may be developed completely when obtained from only one parent. Size characters, on the other hand, usually lack dominance or at least show incomplete dominance. The vigor of the first hybrid generation theoretically has nothing to do with these facts. This is easily demonstrated if one remembers that the increased vigor manifested as height in the F_1 generation cannot be obtained as a pure homozygous Mendelian segregate, which would be possible if due to dominance. Furthermore, the universality with which vigor of heterozygosis is expressed as height shows the distinction between the two phenomena. If the greater height were the expression of the meeting of two factors (T_2, t_2, x t_1, T_2) both of which were necessary to produce the character, one could not account for the frequency of the occurrence. Nevertheless, in practice the confusion exists, and while we have considerable confidence in the conclusions drawn from our experiments, we have no intention of expressing them dogmatically."

G. H. Shull's statements of the way in which crossing brings about increased development, and the relation that this stimulation of growth has to dominance of Mendelian characters is fairly stated, I believe, in the following passage ('11, pp. 244–245):

> "In 1908 I suggested a hypothesis to explain the apparent deterioration attendant upon self-fertilization, by pointing out that in plants, such as maize, which show superiority as a result of cross-fertilization, this superiority is of the same nature as that so generally met with in F_1 hybrids. I assumed that the vigor in such cases is due to the presence of heterozygous elements in the hybrids, and that the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous. I do not believe that this correlation is perfect, of course, but approximate, as it is readily conceivable that even though the general principle should be correct, heterozygosis in some elements

> may be without effect upon vigor, or even depressing. The presence of unpaired genes, or the presence of unlike or unequal paired genes, was assumed to produce the greater functional activity upon which larger size and greater efficiency depend. This idea has been elaborated by Dr. East and shown to agree with his own extensive experiments in self-fertilizing and crossing maize. He suggests that this stimulation due to hybridity may be analogous to that of ionization.
>
> Mr. A. B. Bruce proposes a slightly different hypothesis in which the degree of vigor is assumed to depend upon the number of dominant elements present, rather than the number of heterozygous elements. While all of my data thus far are in perfect accord with my own hypothesis, and I know of no instance in which self-fertilization of a corn-plant of maximum vigor has not resulted in a less vigorous progeny, it is quite possible that I have still insufficient data from which to distinguish between the results expected under these two hypotheses. However, for the purpose of the present discussion, it is not necessary to decide which of these two hypotheses (if either) is correct. Both of them are based upon the view that the germ-cells produced by any plant whose vigor has been increased by crossing are not uniform, some possessing positive elements or genes not possessed by others."

A. F. Shull does not consider dominance as an adequate means of accounting for heterosis, agreeing with East and Hayes and G. H. Shull, as the following quotation shows: ('12a, p. 10)

> "The view that vigor depends upon heterozygosis of the individual seems to me inherently more probable than that it is due to the presence of certain dominant genes. The former view admits of a plausible foundation in cell physiology, and the essence of it may be extended to cases of decrease of vigor in which there is no change in genotypic constitution, and which are therefore without the pale of either theory."

Castle is also in accord with the general belief that heterosis is not due to dominance of factors and draws a distinction between the effects of inherited characters and the stimulus resulting from crossing. In speaking of the increase in size in crosses between diverse races of guinea-pigs he says: ('16, p. 212.)

> "So far as heredity is concerned, the inheritance is blending, but F_1 shows an increase in size due to hybridization. This increased size, however, does not persist into F_2. It seems to be due not to heredity at all."

(And again on pages 223 and 224.)

> "Cross breeding has, then, the same advantage over close breeding that fertilization has over parthenogenesis. It brings together differentiating gametes, which, reacting on each other, produce greater metabolic activity. Whether or not the uniting gametes differ by Mendelian unit-characters

is probably of no consequence. That they *differ chemically* is doubtless the essential thing in producing added vigor. Heterozygosis is mentioned merely as an evidence of such chemical difference."

These quotations suffice to show that a distinction is held by biologists at the present time between the effects of inbreeding and cross breeding and of heredity in development, and they believe that dominance of hereditary factors is inadequate to account for the widespread, if not universal phenomenon of heterosis. The reason why biologists in general have refused to believe that dominance was in any way responsible for the increased vigor of hybrids has been due to two objections which have seemed to make this hypothesis untenable. They thought that if hybrid vigor was due to the dominance of definitely inherited characters that all these favorable characters which bring about heterosis could be easily recombined into a homozygous individual which would show no reduction on subsequent inbreeding. Since no clear case was known in maize where a plant did not lose vigor on inbreeding this seemed to be a convincing argument. Another objection to dominance as a means of accounting for heterosis was raised by Emerson and East ('13) in that the distribution in F_2 should be unsymmetrical in respect to those characters in which heterosis was shown in F_1. Since the usual frequency distributions in cases of this kind are symmetrical, this objection appeared to be valid.

How both of these objections do not hold when linkage of heredity factors is taken into consideration, the writer has attempted to show in a recent publication ('17). Because of linkage, characters tend to pass from one generation to the next in groups and are not easily recombined. Furthermore, on account of linkage skewness is not expected in the second hybrid generation. All of the recently acquired knowledge of heredity makes it seem highly probable that heterosis may be largely, if not entirely, accountable on the basis of dominance of linked factors.

In considering these two hypotheses, both attempting to account for heterosis, the following facts about dominance should be kept in mind:

1. Partial dominance of characters is a widespread occurrence in plants and animals.

2. Dominance, of course, does not appear until after the zygote is formed.

3. In most cases dominance does not change throughout the life of the individual and remains the same through innumerable clonal generations.

While none of these features of dominance offers any definite means of proving the truth of the hypothesis advanced, is it only a coincidence that they fit in exactly with what the facts of heterosis demand? It remains to show that those characters which enable a plant or animal to obtain the best development are, for the most part at least, partially dominant over those characters which retard or prevent maximum growth.

The essential difference between the two hypotheses may be stated briefly. According to the previous view the hybrid combination of factors Aa carried the ability to stimulate development because of the union of unlike elements. This stimulation was absent in either of the homozygous combinations AA and aa, and this stimulation had no direct relation to the part that either A or a had in development as hereditary entities. According to the conception of dominance, first proposed by Keeble and Pellew and carried out more fully by the writer, the hybrid union of AAbb with aaBB, resulting in the heterozygous combination of Aa Bb, increases development because two dominant characters are present here together, whereas each parent has only one dominant character. A similar factorial arrangement has been proposed by Hyde ('14) to account for the increased fertility of his crosses among partially sterile strains of Drosophila.

In crosses between different types of domesticated animals and of cultivated plants it has frequently been noted that there is a tendency towards a return to the characters of the wild species from which they were derived. Sageret ('26) makes particular note of this point. It is well known that crosses between different breeds of pigeons is quite apt to bring back the wild-type of plumage. The hybrid between radish and cabbage described by Gravatt ('14) illustrates this point strikingly. The hybrid produced had neither a succulent "head" like its cultivated male parent nor a fleshy root like its female parent. In other respects, as well, it showed this return to wild-type characters. It was also exceedingly vigorous, but sterile, like so many hybrids between diverse stocks.

Drosophila furnishes the best illustration of the appearance of wild type characters in the first hybrid generation. Of the more than one hundred mutations found in Drosophila by far the largest number of these are recessive. Almost all of them are characters which are less favorable to development. It is stated that any attempt to collect a large number of the recessive characters into one race is rendered difficult by the weakened constitution of the flies possessing any great accumulation of recessive characters (Muller, '16). Whenever crosses are made between diverse types the first generation fly is in many of its characters more like the wild stock and hence more vigorous than its parents. All lethal factors, well illustrated in Drosophila, furnish additional support to the hypothesis of dominance as a means of accounting for heterosis. Muller ('17) has shown that a condition of "balanced lethals" may be brought about in which only the heterozygotes can live. As dominant lethal factors are always eliminated as soon as they occur, so, also, is there always a strong tendency for selection to eliminate any dominant character which is at all unfavorable to the organism's best development. Unfavorable recessive factors also tend to be eliminated, but much more slowly.

If the results obtained in Drosophila are applicable to other animals and to plants we must infer that recessive mutations occur the most commonly. Hence recessive mutations make up the characters, to a large degree, that man has selected in the production of domesticated animals and plants. Just as in Drosophila, crosses between diverse domesticated types tend to result in the reappearance of wild-type characters which are more useful to the plant or animal whose chief aim in life is, apparently, to reproduce itself.

This is well shown in an illustration from maize. As stated before, inbred strains have been obtained which are markedly deficient in root development. On these plants the large brace roots which commonly appear when the plants begin to need extra support, are almost completely lacking. Consequently, the plants are blown over when they become heavy at the time of ear formation. I have observed these strains three years and each time they have fallen down. This character is not determined by soil conditions or insect damage or any external conditions as far as can be seen. Other plants on either side are perfectly upright. When these strains are crossed with other strains, inbred for an equal or longer period, which have well developed brace roots, the first hybrid generation has remarkably well developed brace roots, and usually does not show the slightest tendency to go down, as shown in Plates XIIa and b. Emerson ('12) describes similar plants in which the root deficiency is also recessive. Another striking feature is shown in this illustration. The inbred strain which lacks brace roots is derived from a floury variety of corn and shows a decided tendency to branch at the base of the stalk. These branches form stalks with tassels and ears and many of them are fully as well developed as the main stalk. In this way two or three stalks may be developed from one seed. The other parent of the cross shown never branches in this way and never even develops small branches or "suckers." The first hybrid generation shows this tendency to branch even more strongly developed than the branching parent. The plants shown are from three hills grown side by side and each hill is the product of three seeds. Thus it will be seen that both parents have contributed characters to the hybrid. Both these characters are such as to enable the plants to attain a greater development in general vegetative luxuriance than would be possible if either were lacking. Emerson ('12) gives an even better illustration of two extremely unproductive types of maize which give a vigorous hybrid, one of the parents contributing tall stature, the other green chlorophyll.

Many more illustrations of a similar operation of hereditary factors favoring a hybrid in its development might be cited. I believe that enough have been given to clear the way towards the acceptance of the doctrine that hybrid vigor is due largely to the normal functioning of definable, hereditary factors.

It is recognized that the characters used as illustrations here are superficial in nature. The characters which are really concerned in heterosis are those deep-seated, fundamental, physiological processes which govern metabolism and cell-division. As to the mode of inheritance of these characters we, as yet, know little. There is no reason to believe, however, but that many or all of them are Mendelian in mode of inheritance and that many of them operate in the same way to enable hybrid progeny to attain a more complete development than their parents. If this hypothesis, as to the way in which heterosis is brought about, is in its essential features correct, it points the way towards a more fundamental application of Mendelism to the physiological processes of growth than is generally acceded.

There now remains to be discussed the part that crossing-over or breaks in the linkage of hereditary factors would play according to this hypothesis. If any large number of characters are concerned and the dominant and recessive genes are equally apportioned between the two parents, and distributed at random on the chromosomes, the chance of crossovers occurring in such a way as to bring all the dominant factors in one individual at one time would be almost inconceivably small, especially when the phenomenon of interference is taken into consideration. However, when crossing-over does occur in such a way as to bring about more fortunate combinations in certain individuals, those individuals would be the ones selected by man in domesticated races, or by nature in the wild. Partial linkage does not prevent recombination but merely adds to the complexity of the process. The chance of fortunate recombinations would be greater in the more widely crossed animals and plants but such combinations would be again broken up by further crossing. The tendency would be, however, for the best combination of characters to survive and gradually supplant the others in time. In naturally selfed plants, most of which are crossed at more or less infrequent intervals, a fortunate homozygous combination would be fixed and the plants possessing such combinations would in time supplant their less fortunate relations.

Thus there would always be the tendency for all the more favorable characters to be gathered together and the others eliminated. In time all the individuals of a locality would tend to become equal in their hereditary characters and crossing between individuals in a given locality would not accumulate any greater number of favorable characters than the parents possessed and hence would not show any evidences of heterosis.

That this is the condition which is brought about Darwin has shown. Individuals from the same locality derive little or no benefit from crossing while crosses between individuals from different geographical regions show a greater effect of crossing. The work of Collins ('10) and the results obtained at the Connecticut Station (Jones and Hayes '17) show this also—varieties of maize of similar characters and from the same region give less increase when crossed than do varieties of diverse type or from widely separated geographical regions.

If by crossing-over and subsequent recombination the characters which bring about the great development in F_1 can all be accumulated in a homozygous condition in an individual, that individual should show a greater development even than the F_1 as A. F. Shull ('12) has pointed out. This is on the assumption that most characters which play a part in heterosis are not fully dominant. That a factor in the diploid condition has a greater effect than when in the haploid condition is indicated by the work of Hayes and East ('15) on endosperm characters in maize. Their results show that in reciprocal crosses a double dose of one allelomorph in the maternal endosperm fusion nucleus overcomes a single dose in the paternal endosperm nucleus. In other words factors have an accumulative effect.

The evidence that such superior individuals have been obtained by inbreeding is not very convincing it must be admitted. Darwin, however, in Ipomea obtained plants—"Hero" and its descendants—which were certainly no less vigorous than any plants at the beginning of the inbreeding period and the same thing occurred in Mimulus. These are the two species which were the most extensively inbred. Miss King, as mentioned before, has obtained inbred rats which are larger and more vigorous than individuals present in the original stock. Nothing of this kind has occurred in maize and on account of the small chance of recombining many of the most desirable characters in one plant, it is not at all surprising that such individuals have not as yet been produced.

The production of individuals by inbreeding which excel any of the original crossbred stock offers some means of deciding between the two hypothesis attempting to account for heterosis. According to the hypothesis of a physiological stimulation it would be difficult to see how individuals more vigorous than the parents could be produced by inbreeding.

The hypothesis of dominance also, possibly, makes it easier to understand why naturally crossed wild species, which have not been outcrossed with fresh stocks for long periods of time, may not show any markedly injurious effects from artificial inbreeding. According to the former view different characters of equal value to the organism which might persist indefinitely in a species, would supply a stimulation when united in a heterozygous combination. This stimulation would be lost whenever individuals were reduced to homozygosity by artificial self-fertilization. According to the view of dominance if the allelomorphs were all equal in their contributions to development there might be differences in a species and still no loss of vigor would result from inbreeding. It is assumed that the less favorable characters have been eliminated by selection. On either hypothesis there would be no reduction from inbreeding if all the members of species were exactly alike whether they are naturally crossed or naturally self-fertilized.

The hypothesis of physiological stimulation also implies the assumption that naturally crossed species of cultivated plants are inherently more efficient as producers than naturally selfed plants. This is hardly justified when we recall such vigorous and productive plants as wheat, oats, barley, rice, peas, beans, tobacco, tomatoes and many others which are usually self pollinated. It is, however, difficult to make a fair comparison on this basis.

To sum up, it may then be stated briefly that dominance of characters as opposed to the former idea of an indefinable physiological stimulation makes more understandable the facts that:

1. Heterozygosis produces a stimulating, and not an indifferent or depressing effect in crosses between related stocks and that the reverse is true in widely diverse stocks.
2. Heterozygosis operates throughout the lifetime of the individual even through many generations of vegetative propagation.
3. Inbreeding may result in individuals more vigorous than the original cross-bred stock.
4. Inbreeding may not bring about a reduction in some naturally crossed wild species.

Whether or not dominance of factors is wholly adequate to account for all of the immediate effects of exogamy remains to be seen. The former view that dominance was not concerned at all has been maintained so insistently that I have taken the extremely opposite view in order to show that dominance at least can be held responsible for a large part of the increased development shown by hybrids. The treatment of the subject in this light has been dogmatic. That cross-fertilization may produce some effect which can never be attained in self-fertilization or asexual reproduction is still possible. The view of the problem which is presented here makes certain heretofore indefinite effects more intelligible. It is not meant to preclude entirely any beneficial physiological stimulation resulting from germinal diversity, if such an effect can be demonstrated.

The difference between the two hypotheses are not as great as might seem at first sight. The older hypothesis is general in its application and does not commit itself to the interpretation of specific effects. The view presented here is specific in its application and may be shown to be inadequate for the interpretation of all phases of the problem of increased development following cross-fertilization.

The greatest progress in our knowledge of inbreeding and cross-breeding was made when their effects were linked with Mendelian phenomena. This was the big step forward. The two ways of interpreting these effects discussed here, differ only in minor features and it is not putting the matter fairly to hold them up as two rival hypotheses, one to be chosen from the other. Placing the effects of inbreeding and cross-breeding entirely on a Mendelian basis is merely the logical outgrowth of the older view as knowledge of the methods of inheritance increased.

THE PART THAT HETEROSIS HAS PLAYED IN THE ESTABLISHMENT OF SEX.

Since heterosis is widespread in its manifestation it can hardly be doubted that it has played some part in the initiation and maintenance of sexual differentiation in organisms. Jennings ('13), however, has shown that conjugation in Paramecium does not result, immediately, to the advantage of the organism. The rate of reproduction is actually diminished and many of the organisms perish. The advantage which is derived from conjugation, he considers with Weismann, is due to the fact that biparental inheritance makes possible a greater variability and consequently a greater chance of recombinations, some of which are better able to persist. Hence, while many offspring from conjugating paramecia die, some may be able to survive. Conjugation therefore makes possible a greater elasticity in adaptiveness to new and varied surroundings.

If this immediately depressing effect found in Paramecium is general in the lower animals, heterosis would probably have played no part in the inauguration of sex. Both A. F. Shull ('12a) and Whitney ('12a) have shown, however, that heterosis occurs in the rotifer, *Hydatina senta.*

In the lower plants heterosis would have significance only in spore formation, as the main life of the plant is carried on in the haploid condition where heterozygosis could not, of course, operate. As organisms became more differentiated and specialized the accumulation of factors in the zygote from two somewhat different parents would have increasing significance. If, for example, an organism should vary in a character A by one new dominant mutation A′, the heterozygote AA′, according to the hypothesis of dominance, would be superior to the combination AA but not to the combination A′A′. According to the former view of a physiological stimulation the heterozygous combination AA′ might be superior to either homozygous combination. The matter is not so simple as this, however. The breeding facts show that recessive unfavorable variations are far more common than dominant favorable ones. The chances would be that those individuals which varied by dominant mutations would also vary from the parental stock, sooner or later, by recessive mutations as well, so that any hybrid union would tend to accumulate more favorable factors than either parental individual possessed and hence show heterosis. Heterosis would be an immedate factor for natural selection to work upon.

Moreover it seems possible that heterosis has had considerable to do with the rise of the sporophyte and the decline of the gametophyte in plants. Recombination of characters can take place as well when the dominant generation is the haploid as well as when it is diploid in respect to the chromosome arrangement. From the standpoint of adaptiveness through recombination of characters it might even be to the organism's advantage to retain the haploid generation as the one in which the principal life processes were carried on, since the different combinations would then be more surely tested and the best more easily selected in the simplex than in the duplex condition. Heterosis can only operate in the sporophyte. The union of different hereditary complexes gives to the sporophyte an advantage over the gametophyte in that all new favorable variations work together whereas segregation in the formation of the gametophyte reduces the efficiency of this generation. On the basis of the complimentary action of factors according to the dominance hypothesis of heterosis the gametophyte would practically always be at a disadvantage as compared to the sporophyte as long as variations were occurring so that heterosis must have played some part in these important changes.

Either on the basis of inducing variability or stimulating development, sex would be a creation of no value to organisms which are never cross-fertilized. It may be questioned if many such exist. In either case the sexual mechanism is so complex and deep-seated in the life of the organism that it is not to be discarded easily. Whenever the best possible combination of factors for a given environment is produced, it is to the advantage of the organism possessing that combination to give up cross-fertilization and resort to either self-fertilization or some form of asexual reproduction, for the reason that these are more efficient means of propagation. When the environment changes, those organisms which are not cross-fertilized may either be doomed to extinction or handicapped in becoming adapted to new conditions and the perpetuation of the sexual mechanism thereby accounted for.

Whatever may be the value or significance of heterosis, to account for this phenomenon it is, for the most part, unnecessary to assume that there is an indefinite stimulating effect of hybridization along with the expression of definable hereditary factors. Hence the distinction is no longer needed between the effects of self-fertilization and cross-fertilization and of heredity in development. The heretofore indefinite physiological stimulation resulting from heterozygosis and the related effects accompanying the loss of this stimulation following inbreeding can therefore be given a strictly Mendelian interpretation.

This being so there is no longer a question as to whether or not inbreeding *per se* is injurious. Whether good or bad results from inbreeding depends solely on the constitution of the organisms before inbreeding is commenced. Inbreeding is concerned only with the manifestation of conditions pre-existing. As a means of analyzing and of purifying a cross-bred stock by the elimination of undesirable qualities, inbreeding is therefore a method of first importance in plant and animal improvement.

LITERATURE CITED.

Andronescu, D. I., 1915. The physiology of the pollen of *Zea Mays* with special regard to vitality. Thesis, Univer. of Illinois.

Beal, W. J., 1876–1882. Reports, Michigan Board of Agriculture, 876, 1877, 1881 and 1882.

Biffen, R. H., 1912. Studies in the inheritance of disease resistance. Jour. Agr. Science **4**:421–429.

Bonhote, J. L., 1915. Vigour and heredity. pp. xii+263. London: West, Newman and Co.

Britton, E. G., 1898. A hybrid moss. Plant World **1**: 138.

Bruce, A. B., 1910. A Mendelian theory of heredity and the augmentation of vigor. Science, N. S. **32**: 627–628.

1917. In-breeding. Jour. Gen. **6**: 195–200.

Burck, W., 1908. Darwin's Kreuzungsgesetz und die Grundlagen der Blütenbiologie. Rec. Trav. Bot. Néerl. **4**: 17–118.

Carrier, L., 1913. The immediate effect on yield of crossing strains of corn. Virginia Agr. Exp. Sta. Bull. 202, pp. 11.

Castle, W. E., 1916. Genetics and eugenics. pp. vi+353. Cambridge: Harvard Univer. Press.

Castle, W. E., Carpenter, F. W., Clark, A. H., Mast, S. O., and Barrows, W. M., 1906. The effects of inbreeding, cross-breeding and selection upon the fertility and variability of Drosophila. Proc. Am. Acad. of Arts and Sciences **41**: 731–786.

Collins, G. N., 1910. The value of first generation hybrids in corn. U. S. Dept. of Agr., Bur. of P. I. Bull. 191.

1910. Increased yields of corn from hybrid seed. Yearbook, U. S. Dept. of Agr., 1910, pp. 319–328.

1914. A more accurate method of comparing first generation hybrids with their parents. Jour. Agric. Research **3**: 85–91.

1918. Maize: its origin and relationships. Notes of the 123d regular meeting of the Botanical Society of Washington by H. N. Vinall. Jour. Wash. Acad. of Sciences **8**: 42–43.

Collins, G. N., and Kempton, J. H., 1913. Effects of cross-pollination on the size of seed in maize. U. S. Dept. of Agr., Cir. 124.

Crampe, H., 1883. Zucht-Versuche mit zahmen Wanderratten. Landwirtsch. Jahrbücher **12**: 389–458.

Darwin, C., 1875. The variation of animals and plants under domestication. 2 vols. 1898, New York: Appleton and Co.

1877. The effects of cross- and self-fertilization in the vegetable kingdom. pp. viii+482. London: Appleton and Co.

East, E. M., 1908a. Inbreeding in corn. Connecticut Agr. Exp. Sta. Report for 1907. pp. 419–428.

1908b A study of the factors influencing the improvement of the potato. Illinois Agr. Exp. Sta. Bull. 127. pp. 375–456.

1909. The distinction between development and heredity in inbreeding. Am. Nat. **43**: 173–181.

1910a. A Mendelian interpretation of variation that is apparently continuous. Am. Nat. **44**: 65–82.

East, E. M., 1910b. Inheritance in potatoes. Am. Nat. **44**: 424–430.

1915. The chromosome view of heredity and its meaning to plant breeders. Am. Nat. **49**: 457–494.

1916. Studies on size inheritance in Nicotiana. Genetics **1**: 164–176.

East, E. M., and Hayes, H. K., 1912. Heterozygosis in evolution and in plant breeding. U. S. Dept. of Agr., Bur. of P. I. Bull. 243, pp 58.

East, E. M., and Park, J. B., 1917. Studies on self-sterility I. The behavior of self-sterile plants. Genetics **2**: 505–609.

Emerson, R. A., 1912. The inheritance of certain "abnormalities" in maize. Report Am. Breeders' Assoc. **8**: 385–399.

Emerson, R. A., and East, E. M., 1913. The inheritance of quantitative characters in maize. Nebraska Agr. Exp. Sta. Research Bull. 2, pp. 120.

Enriques, P., 1907. La coniugazione e il differenziamento negli Infusoria. Archiv. f. Protistenkünde **9**:195–296.

Fabre-Domengue, P., 1898. Unions consanguines chez les Colombins. L'Intermédiarie des Biologistes **1**: 203.

Fischer, E., 1913. Die Rehobother Bastards und das Bastardierungsproblem beim Menschen. Jena. Reviewed in Jour. Her., 1914, **5**: 465–468.

Focke, W. O., 1881. Die Pflanzen-Mischlinge. pp. iv+569. Berlin: Borntraeger.

Gärtner, C. F., 1849. Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich, pp. xvi+791. Stuttgart: Hering & Comp.

Gernert, W. B., 1917. Aphis immunity of teosinte-corn hybrids. Science, N. S. **46**: 390–392.

Gerschler, M. W., 1914. Über alternative Vererbung bei Kreuzung von Cyprinodontiden–Gattungen. Zeitschr. f. ind. Abst. u. Vererb **12**: 73–96.

Gravatt, F., 1914. A radish-cabbage hybrid. Jour. Her. **5**: 269–272.

Gray, A., 1876. Darwiniana: essays and reviews pertaining to Darwinism. xii+396. New York: Appleton and Co.

Guaita, G. von, 1898. Versuche mit Kreuzungen von verschiedenen Rassen der Hausmaus. Ber. naturf. Gesellsch. zu Freiburg **10**: 317–332.

Hartley, C. P., Brown, E. B., Kyle, C. H., and Zook, L. L., 1912. Crossbreeding corn. U. S. Dept. of Agr., Bur. of P. I. Bull. 218.

Hayes, H. K., 1914. Corn improvement in Connecticut. Connecticut Agr. Exp. Sta., Part vi of the Annual Report for 1913. pp. 353–384.

Hayes, H. K., and East, E. M., 1911. Improvement in corn. Connecticut Agr. Exp. Sta. Bull. 168, pp. 21.

1915. Further experiments on inheritance in maize. Connecticut Agr. Exp. Sta. Bull. 188, pp. 31.

Hayes, H. K., and Jones, D. F., 1917. The effects of cross- and self-fertilization in tomatoes. Connecticut Agr. Exp. Sta., Part v of the Annual Report for 1916, pp. 305–318.

Hedrick, U. P., and Howe, G. H., 1913. Apples: old and new. New York Agr. Exp. Sta. Bull. 361, pp. 79–135.

Huth, A. H., 1875, The marriage of near kin, pp. lxvii+359. London: Churchill.

Hyde, R. H., 1914. Fertility and sterility in *Drosophila ampelophila*. i–iv, Jour. Exper. Zool., Vol. 17.

Jennings, H. S., 1912a. Age, death and conjugation in the light of work on lower organisms. Pop. Science Monthly **80**: 563–577.

1912b. The production of pure homozygotic organisms from heterozygotes by self-fertilization. Am. Nat. **46**: 487–491.

1913. The effect of conjugation in Paramecium. Jour. Exper. Zool. **14**: 279–391.

1916. The numerical results of diverse systems of breeding. Genetics **1**: 53–89.

Jones, D. F., 1917. Dominance of linked factors as a means of accounting for heterosis. Proc. Nat. Acad. of Sciences **3**: 310–312 and also Genetics **2**: 466–479.

1918. Bearing of heterosis upon double fertilization. Bot. Gaz. **65**: 324–333.

Jones, D. F., and Hayes, H. K., 1917. Increasing the yield of corn by crossing. Connecticut Agr. Exp. Sta., Part v of the Annual Report for 1916, pp. 323–347.

1917. The purification of soy bean varieties. Same, pp. 348–353.

Jones, L. R., 1918. Disease resistance in cabbage. Proc. of the Nat. Acad. of Sciences **4**: 42–46.

Keeble, F., and Pellew, C., 1910. The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*). Jour. Gen. **1**: 47–56.

Kempton, J. H., 1913. Flower abnormalities in maize. U. S. Dept. of Agr., Bur. of P. I. Bull. 278, pp. 16.

King, H. D., 1916. (Experiments of Miss King on inbreeding rats for 22 generations discussed in Jour. Her. **7**: 70–76.)

Knight, T. A., 1799. An account of some experiments on the fecundation of vegetables. Philosophical Transactions of the Royal Society of London **89**: 195–204.

1841 A selection from the physiological and horticultural papers published in the Transactions of the Royal and Horticultural Societies.

Kraemer, H., 1913. Über die ungünstigen wirkungen naher Insucht. Mitteilung der Deutsches Landwirtschafts Gesellschaft, 6 and 13 Sept., 1913. Translated in Jour. Her. **5**: 226–234.

Kölreuter, J. G., 1766. Dritte Fortsetzung der Vorläufigen Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Gleditschen Handlung. Reprinted 1893 in Ostwald's Klassiker der Exakten Wissenschaften, No. 41. Leipzig: Engelmann.

Lindley, J., 1852. The theory of horticulture. pp. 20–364. 2d Amer. Edition by A. J. Downing, New York: Wiley.

Mendel, G., 1865. Experiments in plant-hybridisation. Translated in Castle's Genetics and Eugenics, 1916, pp. vi+353. Cambridge: Harvard Univ. Press.

McCluer, G. W., 1892 Corn crossing. Illinois Agr. Exp. Sta. Bull. 21, pp. 82–101.

Moenkhaus, W. J., 1911. The effects of inbreeding and selection on the fertility, vigor and sex-ratio of *Drosophila ampelophila*. Jour. Morph. **22**: 123–154.

Montgomery, E. G., 1912. Preliminary report on effect of close and broad breeding on productiveness in maize. Nebraska Agr. Exp. Sta., 25th Annual Report, pp. 181–192.

Morrow, G. E., and Gardener, F. D., 1893. Field experiments with corn. Illinois Agr. Exp. Sta. Bull. 25, pp. 173–203.

1894. Experiments with corn. Illinois Agr. Exp. Sta. Bull. 31, pp. 359–360.

Muller, H. J., 1916. The mechanism of crossing-over III. Am. Nat. **50**: 350–366.

1917. An Oenothera-like case in Drosophila. Proc. Am. Acad. of Sciences **3**: 619–626.

Naudin, C., 1865. Nouvelles recherches sur l'hybridité dans les végétaux. Nouvelles Archives du Museum d'Histoire Naturelle de Paris. **1**: 25–174.

Pearl, R., 1915. Modes of research in genetics. pp. vi+182. New York: Macmillan.

Roberts, H. F., 1912. First generation hybrids of American and Chinese corn. Report Am. Breeder's Assoc. **8**: 367–384.

Riley, E. H., 1910. A new zebra hybrid. Am. Breeder's Magazine **1**: 107–110.

Ritzema Bos, (J.), 1894. Unterschungen über die Folgen der Zucht in engster Blutsverwandtschaft. Die Biologisches Centrallblatt **14**: 75–81

Sageret, A., 1826. Considérations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacées en particulier. Annales des Sciences Naturelles **8**: 294–314.

(Sargent), C. S., 1894. A hybrid walnut tree. Garden and Forest **7**: 434–436.

Shull, G. H., 1908. The composition of a field of maize. Report Am. Breeder's Assoc. **4**: 296–301.

1909. A pure line method of corn breeding. Same **5**: 51–59.

1910. Hybridization methods in corn breeding. Am. Breeder's Magazine **1**:98–107.

1911. The genotypes of maize. Am. Nat. **45**: 234–252.

1914. Duplicate genes for capsule form in *Bursa bursa-pastoris*. Zeitschr. f. ind. Abst. u. Vererb. **12**:97–149.

Shull, A. F., 1912a. The influence of inbreeding on vigor in *Hydatina Senta*. Biol. Bull. **24**: 1–13.

1912b. Studies in the life cycle of *Hydatina Senta* III. Jour. Exp. Zool. **12**: 283–317.

Spillman, W. J., 1909. Application of some of the principles of heredity to plant breeding. U. S. Dept. of Agr., Bur. of P. I. Bull. 165, pp. 74.

Stout, A. B., 1916. Self- and cross-pollinations in *Chichorium intybus* with reference to sterility. Mem. N. Y. Bot. Gard. **6**: 333–454.

Swingle, W. T., and Webber, H. J., 1897. Hybrids and their utilization in plant breeding. Yearbook, U. S. Dept. of Agr. for 1897, pp. 383–420.

Tupper, W. W., and Bartlett, H. H., 1916. A comparison of the wood structure of *Oenothera stenemeres* and its tetraploid mutation *gigas*. Genetics **1**: 177-184.

Van Mons, J. B., 1836. Arbres fruitiers ou pomologie Belge Expérimentale et Raisonnée. Vol ii. Louvain.

Weismann, A., 1904. The evolution theory. 2 Vols. (Translated by J. A. Thomson and M. R. Thomson) London: Arnold.

Wellington, R., 1912. Influence of crossing in increasing the yield of the tomato. New York Agr. Exp. Sta. Bull. 346, pp. 57–76.

Weston, W. H., 1918. The downy mildews of maize, their origin and distribution. Notes of the 123d regular meeting of the Botanical Society of Washington by H. N. Vinall. Jour. Wash. Acad. of Sciences **8**: 43.

Whitney, D. D., 1912a. Reinvigoration produced by cross-fertilization in *Hydatina Senta*. Jour. Exp. Zool. **12**: 337–362.

1912b. "Strains" in *Hydatina*. Biol. Bull. **22**: 205-218.

1912c. Weak parthenogenetic races of *Hydatina Senta* subjected to a varied environment. Biol. Bull. **23**:321–330.

Wichura, M., 1865. Die Bastardbefruchtung im Pflanzenreich erläutert an den Bastarden der Weiden. pp. iv+95. Breslau: Morganstern.

Wiegmann, A. F., 1828. Ueber die Bastarderzeugung im Pflanzenreich. pp. 40. Braunschweig.

Woodruff, L. L., 1911. Two thousand generations of Paramoecia. Archiv. f. Protistenkunde **21**: 263–266.

Wolfe, T. K., 1915. Further evidence of the immediate effect of crossing varieties of corn on the size of seed produced. Jour. Am. Soc. of Agr. **7**: 265–272.

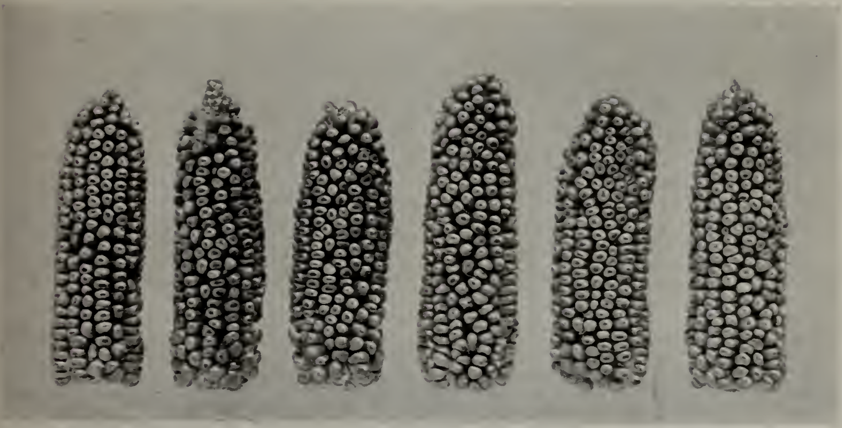
a. A non-inbred variety of Leaming dent corn.

b. Four inbred strains derived from the Leaming variety after nine generations of self-fertilization showing an ear, a cob and a cross-section of a cob of each.

PLATE II.

a. Representative ears of inbred strain No. 1-6-1-3, etc.

b. Representative ears of inbred strain No. 1-9-1-2, etc., above and No. 1-7-1-1, etc., below.



a Representative ears of inbred strain No. 1-7-1-2, etc.

b. The first generation cross of inbred strain No. 1-6-1-3 by 1-7-1-2.

(Plates I to III inclusive, with the exception of Ib, are on the same scale). The plants which produced these ears were all grown on the same field and the non-inbred variety and the first generation cross were grown in adjoining rows. The ears of these latter two represent the best ears produced by 60 plants of each.

PLATE IV.

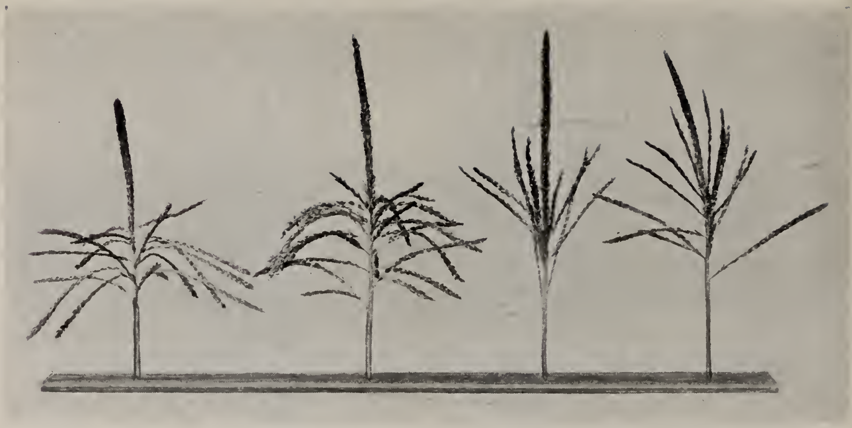
a. Representative plants of the original, non-inbred Leaming variety.

b. Representative plants of the inbred strain No. 1-6-1-3, etc.

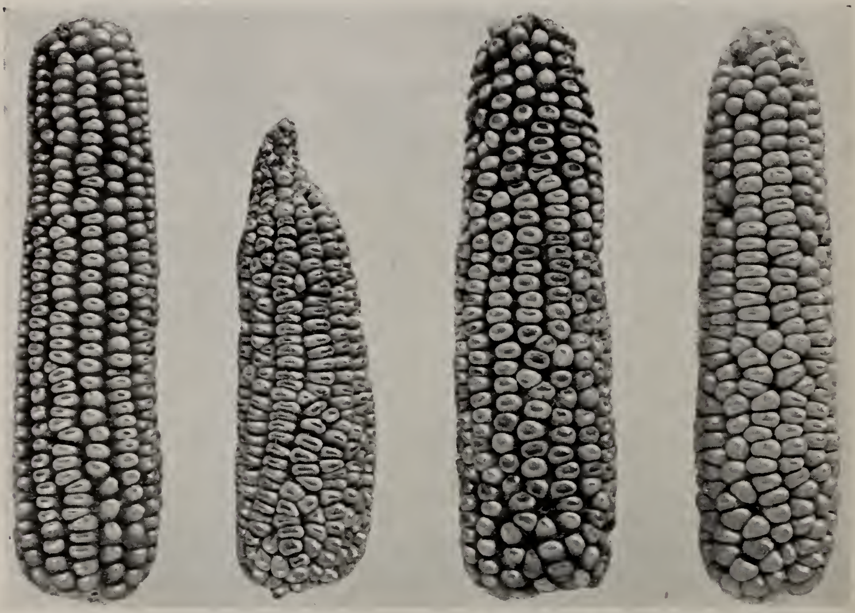
a. Representative plants of the inbred strain No. 1-7-1-2, etc.

b. Representative plants of the first generation cross of inbred strain No. 1-6-1-3 by 1-7-1-2.

(Plates IV and V are on the same scale.)

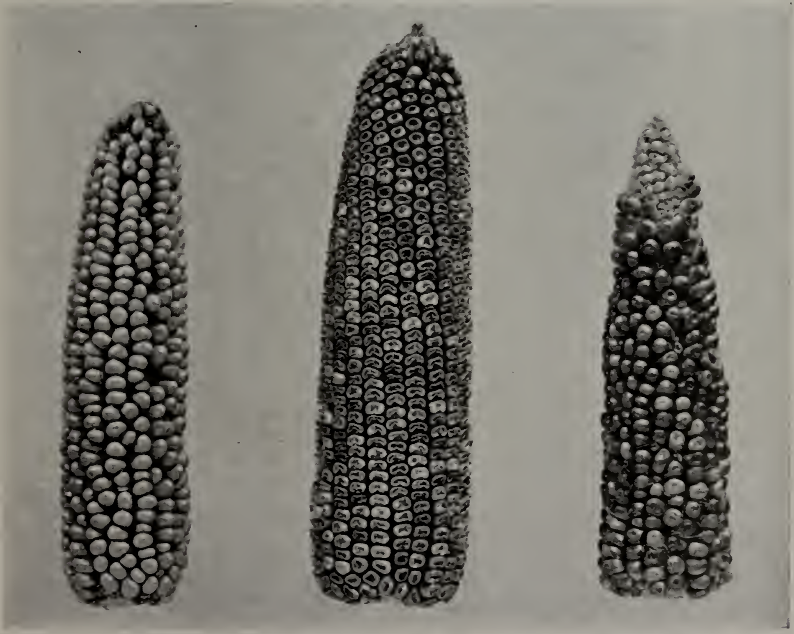


a. Two fully developed tassels on the left and two partially sterile tassels on the right characteristic of four different inbred strains of maize. From left to right they are, 20A-8-5-10; 1-9-1-2; 1-6-1-3; 21-3-13-9.



b. Representative ears from the corresponding strains shown in the illustration above. The first strain on the left produces fully developed tassels and moderately developed ears. The second produces the best developed tassels and the poorest ears. The other two have poorly developed tassels and moderately well developed ears.

a. Two inbred strains of dent corn, No. 1-6-1-3 at the right and No. 1-7-1-1 at the left and the first generation cross in the center. The three ears were grown under equal conditions and gathered on the same day to show differences in maturity.



b. Two inbred strains of dent corn, No. 1-7-1-2 at the right and No. 1-6-1-3 at the left and the first generation cross in the center showing the differences in maturity.

a. Two inbred strains of dent corn, No. 1-6-1-3 at the right and No. 1-7-1-2 at the left, and their first generation cross.

b. An inbred flint and an inbred dent corn compared with the first generation cross.

a. Seeds of two inbred strains of corn and the seeds produced upon the first generation hybrid plant in the center. The second generation plants grown from these large seeds have an advantage over either the parents or the first generation hybrid.

b. Two inbred strains and their first and second generation hybrids. From right to left they are: inbred strain No. 1-9-1-2, No. 1-7-1-1, (1-9 x 1-7) F_2 and F_1.

a. The same two inbred strains and their first and second generation hybrids as in IX b. From right to left they are: inbred strain No. 1-9-1-2, No. **1-7-1-1**, (1-9 x 1-7) F_2 and F_1.

b. Same as above—ten plants of each.

a. Selfed, reciprocally crossed and out-crossed seeds obtained by pollinating plants of three different strains with a mixture of yellow and white-carrying pollen from the plants which bore the two ears shown below, showing the ratio and distribution of the two different kinds of seeds produced on each ear.

(The seeds resulting from the "yellow" pollen were colored by hand on all three ears.)

b. Seedlings showing the rate of growth and the amount of germination of selfed and crossed seeds from the same ears from five different plants.

a. The first generation cross of an inbred strain which lacks brace roots but has the habit of branching freely from the base of the plant (shown at the right) with an inbred strain (shown at the left) which has well developed brace roots but does not branch at the base. The three lots of plants have resulted from three seeds each.

b. A closer view of the roots of the plants shown in the above illustration.

HEREDITY OF QUANTITATIVE CHARACTERS IN WHEAT

GEO. F. FREEMAN
Société Sultanienne d'Agriculture, Cairo, Egypt

Submitted to the Faculty of the Bussey Institution of Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Science, April 30, 1917.

Reprinted from Genetics **4**: 1-93, January, 1919

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

GENETICS is a bi-monthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume, and $7 per volume for completed volumes until the edition is exhausted. Canadian subscribers should add 25 cents for postage. To all other countries 50 cents should be added for postage. Single copies will be sent to any address postpaid for $1.25 each.

All subscriptions, notices of change of address, and business correspondence should be sent to the Princeton University Press, Princeton, New Jersey, and all remittances should be made payable to the Princeton University Press.

Entered as second-class matter February 23, 1916, at the post office at Princeton, N. J., under the act of March 3, 1879.

THE HEREDITY OF QUANTITATIVE CHARACTERS IN WHEAT

GEO. F. FREEMAN
Société Sultanienne d'Agriculture, Cairo, Egypt

[Received May 15, 1918]

TABLE OF CONTENTS

INTRODUCTION

This paper forms a report on certain phases of a series of investigations in wheat breeding under the supervision of the writer, in the Department of Plant Breeding of the ARIZONA AGRICULTURAL EXPERIMENT STATION. The work was initiated by the making of a number of reciprocal crosses between an Algerian white macaroni wheat, an Algerian red bread wheat and two local white bread wheats, Early Baart and Sonora. The original hybridizations were made at Yuma, Arizona, in the spring of 1913, the F_1 was grown at Tucson in 1913-'14 and the F_2 and F_3 on the experimental farm at Yuma in 1915, 1916, respectively. The data concerning time relations, width of leaf, height, rust resistance, etc., were, of course, taken in the field. At the time of ripening, the heads of each plant were harvested and placed together in a paper bag, care being taken to label each bag so that it could be completely identified. All other data were taken in the laboratory of the Department of Plant Breeding at the UNIVERSITY OF ARIZONA at Tucson. The summation and analysis of this data begun some months earlier, has been continued throughout the present year by the writer while on sabbatical leave from the UNIVERSITY OF ARIZONA. The writer here wishes expressly to thank the officers and management of the BUSSEY INSTITUTION for laboratory and library facilities throughout the year and especially Dr. E. M. EAST for many valuable criticisms and suggestions. He also wishes to recall with appreciation the assistance rendered by Mr. DONALD F. JONES who made the original crosses, by Mr. LEONHARDT SWINGLE to whose careful and accurate work may be credited a large proportion of the field and laboratory notes of the second generation, and finally, by Mr. W. E. BRYAN in his efficient assistance with the field and laboratory notes for the third generation.

Since the re-discovery and publication of MENDEL's original papers, the question of paramount interest among geneticists and plant and animal breeders has been that as to whether or not the principles involved in the discoveries of MENDEL are of limited or universal application. Practically all real progress in the study of heredity has arisen through experiments and observations designed to test the validity and universality of MENDEL's laws.

At the present time, the inheritance of a large number of characters, including those both of a qualitative and quantitative nature, in a wide series of both plants and animals, are almost universally considered to be best explained by the Mendelian hypothesis. These include all characters which in the F_2 and subsequent generations, show definite, discontinuous segregation. Most of the cases of peculiar and unusual ratios have been satisfactorily explained as due to multiple factors, lethal factors, gametic coupling, gametic selection, partial sterility, etc.

There are cases, however, which admit of explanation by hypotheses other than those based upon Mendelian principles. Examples may be cited among characters which may be expressed quantitatively. In many such cases the F_1 is more or less intermediate between the parents, and the F_2 and subsequent generations show segregation, but such segregation as does occur is perfectly continuous. Where a sufficiently large number of variants are grown, there is found every degree of size from the lowest to the highest extreme of the hybrid distribution. The extremes of this distribution may or may not reach or extend beyond the extremes of the parental races.

There are some geneticists who believe that such a type of inheritance is not Mendelian. They advocate the application of the Mendelian principles in many cases, but maintain that we have no proof that Mendelism is universal and that cases such as those described above may be just as easily explained by assumptions other than those of gametic purity and unchanged segregation.

The literature on the subject of the inheritance of quantitative characters has been collected by SHULL (1914) and MACDOWELL (1914), and has been summarized with excellent clearness by these writers. It is therefore not necessary to re-summarize these earlier papers. The results of original research bearing upon the inheritance of quantitative characters which have appeared since SHULL'S and MACDOWELL'S summaries may now be reviewed briefly.

NILSSON-EHLE (1914) shows a genetic linkage between a factor for yellow glume color and an inhibitor which shortens beard length in oats.

PHILLIPS (1914) crossed Rouen and Mallard ducks which differ greatly in size. The F_1 was intermediate in size between the parents and not more variable than the most variable parent. The F_2, while still intermediate in average size, was markedly more variable than either the F_1 or the parents.

PUNNETT and BAILEY (1914) in crosses of bantam with larger breeds of fowl found the F_1 intermediate and the F_2 highly variable, transgressing the extremes of both parents. Small F_2 fowl bred together gave an F_3 all of small size; large F_2 individuals bred *inter se* produced altogether large offspring. The F_3 obtained by mating intermediate F_2 individuals was highly variable. They interpret the results as being due to the segregation of Mendelian unit factors and give a factorial scheme to account for the phenomena observed.

HAYES and EAST (1915) crossed flour corn with a flint variety and found that the endosperm character was determined by the mother only, although it was proved that endosperm character, first visible in the next generation could be inherited through the pollen. The authors conclude that this behavior is due to the fact that the endosperm is produced from a union between two female polar nuclei and one male cell and that the presence of two factors dominates one in either the direction of starchy or flinty endosperm. In other flint-starchy crosses, the ratios were not so definite, due possibly to the difficulty of classifying the seed. It was thought, however, that the same principles were involved as in the previous crosses. Crosses involving grains of different shape were made between rice pop corn, pearl pop corn and a dent corn. The results of these experiments indicated that several factors were involved which segregated in a Mendelian fashion in the F_2 and F_3. Parental types when once recovered bred true.

East (1916 a) records the crossing of *Nicotiana Langsdorffii* and *N. alata* which differ markedly in corolla length. The F_1 was intermediate and no more variable than the more variable parent. The F_2 also had an intermediate average but the variability was much higher than in the F_1. There was a wide range in the variability of the different F_3 races but they were all lower than in F_2. He showed by F_3 pedigrees that segregation had occurred in F_2 but did not attempt to determine the number of factors.

East (1916 b) in a second paper reports the results of crossing a variety of *Nicotiana longiflora* having the corolla about 93 mm long with another variety of the same species having a corolla length of about 40 mm. He carried the study through the first, second, third, and in a few races as far as the fourth generation, with sufficient numbers to calculate the coefficients of variation in the separate races. The author lays down eight conditions which he assumes the data must fulfill in order to be interpreted as complying with the conditions of Mendelian inheritance. Tables and distributions with the calculated constants are given in detail and the conclusions are that no single phenomenon has occurred which cannot be interpreted as Mendelian.

Phillips (1915) after a study of the results of color inheritance in various duck crosses and pheasant crosses says that "it is almost certain that the ordinary subspecies of the ornithologist is very far from being a unit variation."

Since the work of Johannsen on the effect of selection in beans, there has been no similar work with plants which can compare in volume and significance with that of Fruwirth (1915). Fruwirth followed the system of pure line selection as practiced by Johannsen. Choosing a variety of *Lens esculenta* with flecked seed, he endeavored through selection to bring about greater flecking on the one hand and the diminution of the flecks on the other. After 13 generations he had made no progress in either direction. Chevrier beans (*Phaseolus vulgaris*) produce seeds which, for the most part, have seed coats of a slightly greenish color rather than creamy white but a few seeds are white on one or both sides. It was attempted, through selection within a pure line, to secure complete inheritance of the green type. Though carried out for 14 generations no change was produced. In a race of vetch which produced both green and cream-colored seeds on the same plant, he tried for 10 generations to fix the green coloration by selection but made no progress. Likewise two years selection of yellow seed made no progress in the direction of fixing the type. In a Victoria pea variety with yellowish green and yellow seed three years of selection was without effect. In a variety of Soja bean having lighter and darker brown seed, three years of selection could make no progress in either direction of darker or lighter seed coats. In a certain variety of *Pisum arvense* the seeds are variable in color. They may be pure yellowish green, or yellowish green with violet flecks or bands, or the violet color may be so extended as to leave the yellowish green appearing only as flecks, or finally the violet color may prevail altogether. FRUWIRTH endeavored by selection to increase the amount of violet color in the seeds on the one hand and to reduce it on the other. In the selection for more violet color in the seed coats, 10 generations produced no results. The results of the selection in the opposite direction can best be given in FRUWIRTH's own words as follows (FRUWIRTH 1915, p. 200):

"In beiden JOHANNSEN'SCHEN Linien 1 und A ist die Anlage zur Ausbildung violette Farbe der Samenschale vorhanden, die Anlage ist aber stark modifikabel und ausserdem sind beide Linien geneigt spontan Zweige abzuspalten, in welchen diese Anlage ihre Wirksamkeit ganz (in 1 die Zweige II von Ernte 1909, und IV von 1910 Ernte) oder fast ganz (in 1 der Zweig III der von Ernte 1908 abgeht und die Auslese A) eingebüsst hat. Eine Neigung rein violettsamige Zweige abzuspalten, besteht nicht."

"In beiden JOHANNSEN'SCHEN Linien ist die Anlage zur Ausbildung violette Farbe in der Hülsenschale vorhanden, und zwar ist die Anlage—sowie jene violetter Farbe der Samenschale—stark modifikabel. In beiden Linien ist die Neigung vorhanden, spontan Zweige abzuspalten, in welchen die Wirkung der Anlage durchschlagend, ohne Modification auftritt, so dass dann nur violette Hülsen gebildet werden. Violette Färbung der Samenschale ist ganz unabhängig von violetter Färbung der Hülsenschale."

"Auslese nach grüner Farbe der unreifen Hülse ist wirkungslos, Auslese nach violetter Farbe derselben nur dann—und dann sofort—von einer

Wirkung begleitet, wenn spontan ein violetthülsiger Zweig abgespaltet worden ist."

In a selection carried out upon a variety of lupine (*Lens esculenta*) having mottled seed, FRUWIRTH sought by selection to produce both dark- and light-seeded strains. Six years selection in one direction and eight years in the other produced some divergence in the selected lines but was not effective in producing either self-colored dark- or light-seeded races.

In a variety of vetch which normally produced either greenish or cream-colored seed (see selection experiment described above) after five generations of self-fertilization, there appeared in the harvest of 1910, 2 plants having mottled seeds. In 1912 after 7 generations of self-fertilization and selection the same line produced 4 plants having mottled seeds. Finally, "trat diese Variation auch als Variation einer ganzen Pflanze bei 5 Individuen der Ernte 1910 auf, nach 9 Generationen aus Selbstbefruchtung, fünf in der Linie, vier während der vorangegangenen Massenauslese." All mottled seed bred true.

In selection work with Soja beans one or two spontaneous variations were observed. All effects of selection (from a mass lot), however, were produced in the first year. The spontaneous origin of a white-flowered vetch is also noted.

White mustard (*Sinapis alba*) with which FRUWIRTH worked, produces both yellow and brown seed. After eight years of selection of close-fertilized seed, he was unable to fix the type or even materially to diverge the tendency in one direction or the other.

In extensive selection experiments with oats which for some characters were carried through ten generations he decides that selection within pure lines is without effect.

FRUWIRTH (1915, p. 450) finally sums up by saying:

"Bei einer Reihe von äusseren Eigenschaften zeigte sich durchweg, dass in einer JOHANNSEN'SCHEN Linie bestimmt gerichtete Auslese auch bei Fortsetzung durch eine grössere Zahl von Generationen keine Änderung des Liniencharakters mit sich bringt."

MACDOWELL (1915) has reported the results of selection experiments upon a race of Drosophila which possessed more than the normal 4 bristles on the thorax. The average number of bristles increased for 6 generations of selection. The same selection was carried on for 5 more generations without additional effect. The author concluded that there were several accessory factors limiting extra bristles which were gradually eliminated by selection. MACDOWELL has also shown a very strong correlation of extra bristles with body size. The present writer strongly suspects that the real factors here concerned were size factors and that MacDowell's extra bristle selection was merely an indirect means of selecting for larger size.

The paper by Yuzo Hoshino (1915) on the flowering time of peas and rice has been the subject of much interesting recent comment. Hoshino crossed early- and late-blooming varieties of peas. He found that the variation behaviors of the F_1, F_2, F_3 and F_4 races (detailed distributions of which are given) could for the most part be interpreted by assuming the Mendelian segregation of two allelomorphic pairs, A and a, which determined early- and late-blooming respectively and two modifiers B and b. Those variation behaviors which could not be explained by these factors, he supposed to have been caused by a "contamination" of genes. What he means by contamination of genes is not clear for he distinctly states that he does not refer to such a contamination as is assumed by Castle in rodent crosses. He suggests "secondary factors." This is the same as assuming additional factors of secondary importance such as are assumed by Nilsson-Ehle in the report of his *compactum*-squarehead-Landweizen wheat crosses.

Hoshino has also shown a gametic coupling of early-blooming with white flowers and late-blooming with red flowers. This coupling is broken (by physiological interference or crossing over) approximately 1 time in 7.

In crossing early- with late-shooting rice varieties he finds the F_1 intermediate, the F_2 showing strong segregation. The behavior of the F_3 and F_4 races were such as would be normally expected of segregating Mendelian factors.

Castle (1917) has re-stated certain data and conclusions previously published (Castle 1912, pp. 163-168). In crossing + variants of hooded rats with wild rats he found that "wild" was dominant in F_2 and that the hooded extractives of the F_2 were often higher in hood grade than were their hooded grandparents. In crossing "mutant" hooded rats (a race which suddenly appeared with a very high + hooded condition) with wild rats, the F_1 was of the wild type but the hooded extractives of the F_2 did not drop lower than the range of the original "mutant" race. Castle concludes that these facts cannot be interpreted as Mendelian and must be explained as the results of changes in a single unit factor.

The present paper is offered as the first in a series of further contributions to the knowledge of the inheritance of quantitative characters. Wheat has proved an especially favorable subject for such an experiment inasmuch as its small size renders feasible the production of large numbers without prohibitive expense and the fact that it is close-pollinated greatly simplifies the genetic analysis of the F_2 and subsequent generations.

The characters here studied are the date of the appearance of the first head on each plant, the total height of the plants measured in centimeters from the ground to the top of the tallest head (not including beards) and the width of the broadest leaf.

MATERIAL AND METHODS

A brief description of the four varieties of wheat used may be given as follows:

Algerian macaroni (No. 1)

Late, tall; stems large, stiff; leaves broad, dark green, medium width; heads large, cylindrical, flattened, long; glumes bearded, pubescent, light straw yellow; grain large, mostly translucent light amber, and very hard, but with some grains having spots of opaque starch in the endosperm. Originally obtained from R. MARIE, Algiers, Algeria.

Algerian red bread (No. 3)

Late, tall; stem medium in size; leaves medium in width and color; heads medium size, square; glumes bearded, smooth, light straw yellow; grain red, medium soft, opaque. Originally obtained from R. MARIE, Algiers, Algeria.

Early Baart (No. 34)

Early, low; stem medium in size; leaves medium width, medium green; heads medium size, square; glumes bearded, smooth, light straw yellow; grain white, medium soft, medium size, opaque. Originally obtained locally.

Sonora (No. 35)

Early, low; stem medium in size; leaves broad, light green; heads cylindrical, square, medium size; glumes beardless, pubescent, reddish brown; grain white, opaque. Soft. Originally obtained locally.

All planting was done with a nursery row machine by which each grain was covered 2 inches deep and spaced 3 inches in rows 10 inches apart. There were fifty hills in each row. Strips of barley were planted on either side of the plot in order that the end plants should not have more space than those within the plots. All plants of the pure varieties grown in 1914 were from mother plants which were selected from the 1913 general mass cultures as true to the types of their respective varieties. Of these selected 1913 plants there were 14 of macaroni (No. 1), 3 Algerian red bread wheat (No. 3), and 5 early Baart. The head records for Sonora (No. 35) in 1914 came from 12 typical heads of this variety selected from a mass culture. In 1915, of the 9 nursery rows of pure macaroni (No. 1), 6 were plant rows from the previous year's culture and 3 were from a mixture of seeds resulting from threshing together a number of typical heads of this variety selected from a field culture. The 3 nursery rows of No. 35, 1 of No. 3 and 1 of No. 34 were plant rows from the previous year's harvest. In 1916, 5 of the nursery rows of No. 1 came from a single mother plant in 1915 (No. 52-4-1-4) and the remaining 2 from a single other 1915 mother plant (No. 3-12-1-5). The 5 nursery rows of each of the other varieties originated from single plants in 1915 as follows: No. 35 from No. 35-11-1-4; No. 3 from No. 32-2-38; No. 34 from No. 1-13-3-1-24. In all of the discussions, the word culture is used in the sense of a group of plants, grown in a single nursery row and originating from a single mother plant of the previous season. This applies alike to the pure varieties and hybrids. The exception in the case of the 3 nursery rows of mass-selected macaroni, grown in 1915, has been noted. The expression "pure race" is often used to distinguish plants belonging to one of the parental varieties from those of hybrid origin.

The statistical methods used in these investigations were those commonly employed by biometricians. The constants used were the arithmetical mean, standard deviation and coefficient of variation. The means were calculated to the nearest unit employed in the taking of the original data. The standard deviations were calculated from the mean class as a mean, i.e., with the middle of the mean class as the assumed mean, no correction being made for the true mean. This was considered sufficiently accurate in view of the fact that different plant rows of the same pure race (pure line originating from a single mother plant) often showed more difference in standard deviation in the same season than could possibly arise from failure to correct for the true mean. An example will suffice. All of the plantings of pure No. 3 (Algerian red bread) arose from the seeds of a single plant in 1914. In 1916 there were 5 plant rows of this culture grown in different parts of the experimental plots for comparison with the various hybrids into which this culture entered. The data for height and the statistical constants calculated therefrom by various methods are given below. The original measurements were made to the nearest centimeter and in the summation of the data the classes were made to include 5 cm with the middle points at 2.5 and 7.5, thus 62.5, 67.5, etc.

TABLE I A

Height of pure No. 3, 1916, in centimeters.

Row No.	45 to 49	50 to 54	55 to 59	60 to 64	65 to 69	70 to 74	75 to 79	80 to 84	85 to 89	90 to 94	95 to 99	100 to 104	105 to 109	110 to 114	115 to 119	120 to 124	125 to 129	130 to 134	135 to 139	140 to 144	145 to 149	150 to 154
105A ...	1*												1	3	3	19	8	8	2			
105B ...															2	2	4	10	13	15	3	
105C ...															1		2	12	21	10	3	1
105D ...															1	8	18	14	6	1		
105E ...																	7	13	9	10	6	5

* Not used in calculation of constants given in table I B.

TABLE IB

Statistical constants.

Row No.	Number of variants	True mean (A)	Mean used in the calculation of σ used in the discussions (B)	Approximate mean given in the tables and discussions	Standard deviation calculated on (A)	Standard deviation calculated on (B)
105A	44	122.85	122.5	123	6.4	6.4
105B	49	135.00	137.5	138	7.0	7.3
105C	50	137.40	137.5	138	5.8	5.8
105D	48	129.50	127.5	128	5.2	5.5
105E	50	138.50	137.5	138	7.7	7.7
Averages and totals	243	132.65	132.5	133	8.5	8.6

Now the greatest difference in standard deviation arising from different methods of calculating was .3 or about 3.5 percent of the average standard deviation, whereas the greatest difference between the different lines was 2.5 (that between 105D and 105E) or 29.4 percent, a little over eight times the error introduced by the different methods of calculation. In view of such facts it was not considered worth while to waste time in accuracy of calculation which could not possibly add any significant value to the constants so obtained.

Although the probable errors of a large proportion of the constants here given have been calculated they are not given in the text on account of lack of space and the difficulty of placing them in complicated tables of distribution, etc. In nearly every case, however, in which the reader is interested, the probable errors can readily be calculated from the data given. In the F_2 hybrids most of the cultures had from 85 to 95 individuals and in the F_3, from 40 to 48.

It has been necessary to devise some means of comparing the variability of a series of hybrid races with their pure line parents, each of which may perhaps be grown in several different plant rows in different parts of the experimental plots. Moreover, if we accept high variability as a measure or indication of heterozygosity, it will be of interest to compare the variability of second generation hybrids with the third generation (F_3). In close-pollinated plants like wheat, as the average of heterozygosity certainly decreases from generation to generation, the average variability of plant populations (populations arising from single mother plants) should also decrease. This average increase in homozygosity with respect to any one character is, however, not uniform in all lines. The recombinations may be such that an F_2 plant is just as heterozygous with respect to the factors governing height, for instance, as was its F_1 parent and the same may be said of certain individuals in the comparison of the F_3 plants with their F_2 parents. We will therefore have some F_2 plants just as heterozygous as their F_1 parents that will give rise to cultures of F_3 which are just as variable as were the F_2 cultures, but the majority of the F_2 plants will be less heterozygous than their F_1 parents and will therefore give rise to F_3 cultures less variable than were the F_2 cultures. Now since the quantitative characters concerned, as well as the variability of the same, are subject to environic modification (see behavior of pure lines in table 1) there must be some means of comparing statistically the variability of the F_3 cultures with the F_2 cultures in order to demonstrate this general decrease of variability in the succeeding hybrid generations.

Three methods are available as follows:

(a) Throw all the cultures of a given generation into a single population and calculate the standard deviation of the same.

(b) Superimpose the means of the several hybrid cultures, sum the equal deviations on each side of this mean and calculate therefrom a standard deviation for the whole series.

(c) Calculate the standard deviation and coefficient of variation of each hybrid culture separately and show the average and distribution of these constants.

These methods and the value of the constants so obtained will now be discussed in order:

(a) The standard deviation calculated by this method from a population consisting of several plant rows of a single pure line is always greater than the average of their standard deviations taken separately. This is caused not necessarily by differences in the standard deviations of the plant rows entering into the total population (these may be all identical) but by differences (environic) in the means of the several rows whereby the distribution of the population as a whole is much broadened. The distribution of this total population and the standard deviation derived from it are therefore measures of the total effects of the given different environments in modifying the character concerned. If now we are dealing with an F_2 generation all of which originated from genetically equivalent F_1 plants, part of the differences in the F_2 plants would be due to environic effects and part to the effects of genetic recombination. The distribution and standard deviation of a hybrid population calculated by method (a) would therefore give the total combined effect of environment and recombination in producing variability. When now we come to consider an F_3 population arising from genetically unequal F_2 plants we simply re-measure (if we plant all the seeds of all of the F_2 plants or a sufficiently large random sample) the influence of the same factors as were measured in the F_2, i.e., the sum of the effects of environment and all of the factors entering the cross from the original parents. We cover up the possibility of discovering any decrease in the heterozygosity of the F_2 plants since differences in the means of the F_3 cultures, due to the genetically different parents, will have the same effect in broadening the distribution of the total population, as differences in the individuals of a single highly variable culture.

(b) The method of superimposing the means introduces a small but unavoidable mathematical error where the standard deviation is used as a measure of the average variability of a number of separate cultures. It is well known, however, that where the means differ, the standard deviation is not a good measure of comparative variability. In order to overcome this difficulty and obtain abstract numbers which may be compared, the coefficient of variation has been devised. This is the percentage which the standard deviation is of the mean. It is therefore apparent that a given deviation from the mean has more weight in the determination of the coefficient of variation when it is a deviation from a small mean than when it is a deviation from a large mean. When now we superimpose small means and large means we give equal values to deviations which are of unequal value in determining the coefficient of variation. Hence if our data have to do with cultures differing widely in their means, where the coefficients of variability rather than the standard deviation must be used in the comparison of variabilities, we are not justified mathematically either in averaging standard deviations or superimposing means. As a matter of fact, however, it may be said that the error introduced by this means is not large. Taken alone, however, the method of superimposing the means has one serious fault. It covers up wide differences in the variability of different individual F_3 cultures. For the purposes of genetic analysis it is necessary to know whether all of the F_3 cultures have decreased in variability or whether this decrease is confined to the offspring of certain only of the F_2 plants. It is therefore necessary to calculate the standard deviations and coefficients of variation of each of the cultures separately.

(c) Since, as just stated, a knowledge of the distribution of the coefficients of variation of a series of hybrid cultures is probably even more important than a single general expression of the average variability as a whole, method (c) which gives all of these details is usually to be preferred.

In general the coefficient of variation was used as a measure of variability. In time relations, however, this is difficult on account of the necessity of selecting arbitrarily some point from which to estimate the means. In the case of the date of first heading, if some date in March, say the first or fifteenth were chosen, it was feared that the differences in means would be so great as to unduly distort the coefficients of variation. One may readily see that the later such a basal date be chosen the greater will be the distortion on this account. On the other hand, if the chosen date be moved backward, the various means, in comparison with each other, approach unity, and the coefficient of variation becomes then more and more dependent upon the size of the standard deviation. Although all of the plots were planted within a period of seven days in the fall and all came up at approximately the same time, it would be questionable whether the total vegetative period would be the best basis of a determination of the variability of date of first heading on account of the fact that some strains were more active in winter than others and were therefore given unequal starts in the rapid vegetative period of spring. In view of these difficulties it was decided to use the standard deviation (expressed in days) alone as the measure of variability in all time relations.

In the studies on size relations, the coefficients of variation only are given.

Where averages of a series of standard deviations are given, or standard deviations are calculated from artificial populations produced by superimposing the means of different races, such fact has been expressly stated, but it must not be understood that the writer would infer that these are strictly comparable mathematically to an average of a series of coefficients of variability, for reasons already given. Rather than true arithmetical averages, such means should be considered as foci around which the distribution of the given series of constants (here standard deviations) cluster, and therefore form, as it were, a locus for thinking specifically.

DATE OF FIRST HEAD

The dates of the first head of the parents and the F_1 plants in 1914 were not taken.

Macaroni × bread wheat crosses. Algerian macaroni (No. 1) × Sonora (No. 35)

In 1915, 3 pure races of No. 35, 9 pure races of No. 1, and 37 cultures of (1 × 35) F_2, were grown at Yuma. The following results were obtained:

TABLE 2 A

Date of first head in F_2 of cross 1 × 35 and in the parent strains, 1915.

	Number of cultures	Number of individuals	Average dates of first head	σ of population	Average σ of cultures
Pure No. 35...	3	168	March 17	2.14	1.66
(1 × 35) F_2...	37	2546	" 27	4.00	3.56
Pure No. 1...	9	650	" 31	3.30	1.87

TABLE 2 B

Distribution of standard deviation of cultures.

	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75
Pure No. 35............		1	1	1							
(1 × 35) F_2..........				2	7	12	5	8	2	1	
Pure No. 1............		1	5	2		1					

The 37 hybrid cultures were from the seed of the 37 F_1 plants secured in 1914 which were sown in plant rows in 1915. It should here be noted that the standard deviation of the whole population is markedly higher than the average standard deviation of the plant rows taken separately. This was also true of the pure races and can be attributed in part to the place variation of the different plant rows. Part of this difference may also be due to slight differences in the genetic composition of the individuals of the parental varieties used in the original cross. However, these individuals, although not all belonging to one pure line, in their respective varieties, were carefully selected as belonging to the type of the variety which they were to represent. The differences between the average standard deviation of the pure lines taken separately and of their respective populations is therefore an approximation of the error introduced by place varation (modification) and whatever genetic differences there might have been in the several individuals of the parental cultures.

The greater variability of the hybrid cultures as compared with the parental varieties is in accordance with what would be expected from the recombination of genetic factors in the F_2 generation. The mean of the hybrid cultures was 3 days later than the mean of the parents and 4 days earlier than the late parent. The heading dates of both parents and of the F_2 cultures may be summarized as follows:

TABLE 3

Date of first head in (1 × 35) F_2, 1915.

Cultures	March									April									
	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21
Pure No. 35..........	25	85	47	7	4														
(1 × 35) F_2..........	4	18	74	21	403	796	306	403	266	98	86	42	17	8	1	2			1
Pure No. 1............						11	78	153	132	134	81	54	5	2					

Means of cultures.

Cultures	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21
Pure No. 35..........			2	1															
(1 × 35) F_2..........					1	7	17	12											
Pure No. 1............							1	4	1	2	1								

From the 2546 F_2 plants, 230 were selected and planted in plant rows at Yuma in the fall of 1915. These selections were, for the most part, based upon economic characters. However, the dates of first heading of the plants in the spring of 1915 varied from March 15 to April 9 and thus furnished material for the study of the segregation of the factors relating to time of heading.

For comparison of the parental varieties with these F_3 hybrids, 7 pure cultures of No. 1 and 5 pure cultures of No. 35 from plants selected as types from these same varieties of the previous year, were grown. The results may first be summarized as follows:

TABLE 4

Date of first head in (1 × 35) F_3, 1916.

Culture	Number of cultures or plant rows	Number of individuals	Average date of first head	σ of total population	Average σ of culture
Pure No. 35...	5	247	March 25	1.34	1.27
(1 × 35) F_3...	230	9772	April 11	6.24	3.14
Pure No. 1....	7	343	April 15	1.99	.91

Distribution of standard deviation.

Culture	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
Pure No. 35.......	1	3	3												
(1 × 35) F_3)......		2	9	20	38	35	45	41	17	8	9	4	1		1
Pure No. 1........		2	1	1	1										

The increase in the variability of the F_3 population of hybrids over the F_2 population is striking and surprising. Knowing that only selected individuals of the F_2 were planted, one, at first thought, might be inclined to attribute this to the selection of extremes from both ends of F_2 as parents, but observation of the column showing number of cultures in table 4 will show that the distribution of F_2 parents forms practically a normal curve. One can therefore only attribute this increase to climatic differences in the two seasons which emphasized the effects of extreme combinations more in 1916 than in 1915, or else to the following, which probably accounts for the greater part of the increase. It will be noted that the standard deviations of both the populations and cultures, averaged separately, of the parental varieties, was less in 1916 than in 1915, and also that the same was true of the average standard deviation of the separate cultures of F_3 as compared with that of the separate cultures of F_2. These facts indicate that the season of 1916 did not emphasize the extremes either in the pure cultures of that year or in the F_3 cultures taken separately, or at least that in the latter case the increasing homozygosity of the F_3 over the F_2 was a little more than able to offset this effect and thereby reduce the variability of the F_3 cultures as compared with the F_2 cultures taken separately. Now in this increase in homozygosity of the F_3 cultures probably lies the increase in variability of the population as a whole. We have already seen that the heterozygotes here tend to take an intermediate position. Hence as the percentage of heterozygous forms decreases with the approach toward homozygosity, the percentage of intermediate types will grow less, i.e., the curve will be flattened, and the standard deviation of the population, thereby slightly increased.

TABLE 5

Date of first head in (1 ×35) F_3, 1916.

	Number of cultures	March								April															May				Number of individuals
		15	17	19	21	23	25	27	29	31	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	2	4	6	
		16	18	20	22	24	26	28	30	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	1	3	5	7	
Pure No. 35…………	5				1	3	8	161	69			4																	246
(1 × 35) F_3…………	230		3	26	46	43		267	136	356	432	767	693	863	2	2893	2156	578	103	355	103	69	48	20	1	3		1	9772
Pure No. 1…………	7															88	164	84	6	2									344

Average dates of heading of separate plant rows.

Pure No. 35…………	5							4	1																				
(1 × 35) F_3…………	230						3	2	4	6	8	13	17	21	33	58	38	8	13	3	3								
Pure No. 1…………	7															2	3	2											

A summary of the distribution of the dates of first head in the plants of the parental cultures and the F_3 hybrids is shown in table 5.

It should now be noted that, considering individual plants, there were among the hybrids, 29 plants earlier than the earliest of No. 35 and 293 plants later than the latest of pure No. 1. Moreover, considered as cultures, there were three cultures whose average date of first head was earlier than the earliest average of any of the cultures of pure No. 35 and that there were 19 cultures averaging later than the latest pure culture average of No. 1. There were in fact three cultures whose average date of first head was later than the latest individual of pure No. 1. Does this indicate that by recombination we may be able to isolate races which are earlier than the early parent and later than the late parent?

Table 6 shows the distribution of the F_3 individuals and cultures arranged according to the date of first heading of the parent F_2 plants. + = the date of the first head on the selected F_2 parent. O = the average date of the population arising from such parents (reading horizontally). In the same grouping of cultures there are also shown the distribution of the means of the F_3 cultures taken separately and the distribution of the standard deviations of these cultures. The first vertical column at the left shows the number of F_2 plants (hence F_3 cultures) in each category. In a vertical column are also shown the average of the standard deviations of the cultures taken separately in that category.

Table 7 shows the distribution of the F_3 individuals and cultures arranged according to the means of the F_3 cultures. O = the average date of first head of the cultures going to make up the population in that group (horizontal). This table also shows the distribution of the selected F_2 plants which were the parents of the several cultures making up the corresponding culture groups. The distribution of the standard deviations of the several races taken separately which make up its corresponding category is given. The vertical columns are the same as in table 6.

Table 6 shows us that the differences observed in the date of first heading of the individual plants of F_2 were largely genetic, since their offspring (F_3) exhibits but little regression toward the general mean. Again the same thing is perhaps better shown in table 7 where the F_3 cultures are grouped and arranged in accordance with their own means. We then have the distribution of the parents of these groups of F_3 cultures. It will be observed that in no case does the distribution of the parents, for any group of F_3 means extend beyond the normal limits of

TABLE 6

Date of first head in (1 × 35) F_3, 1916. Distribution based upon date of first head of the selected F_2 parents.

	F₃ individuals																								
	March								April																May
Number of cultures	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23	24 25	26 27	28 29	30 1	2 3
1	+		11	9	8	O	13	1		1	6														
5		+ 3	12	25	25		O 81	25	28	8	10	2							1						
7			+ 3	10	9		88	O 51	54	32	14	11	6		10	1									
41				2	+ 1		81	46	163	225	O 348	210	226		363	93	18	1	4		1	1			
60					1	+	4	9	102	144	235	268	336	O 1	867	504	88	11	29	9	5	6			
37							+	3	3	12	92	116	78		O 362	233	55	3	39	9	12	6	3		1
40								+ 1	6	10	54	61	85	1	630	O 580	153	21	95	30	17	8	6	1	2
28									+	1	8	22	27		333	O 214	128	40	113	31	34	16	6		1
6										+		3	1		5	105	O 71	7	38	7	17	2	4	1	
2											+					49	O 8		22	1	1	2			
2												+				3	18	13	17	O	31	6	3		5/6 = 1
1													+			1	17	O 3		15	1				

+ = Selected F_2 parents.
O = Mean of F_3 group.

		Means of F₃ cultures														
		March			April											
Number of cultures	Average σ of F₂	25 26	27 28	29 30	‘31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	5.21	1														
5	3.88	3		1	1											
7	3.83		1	2	3	1										
41	3.39			1	2	5	10	7	7	5	3	1				
60	3.00					3	3	7	10	14	15	7	1			
37	3.21							3	3	8	16	6			1	
40	3.00							1	1	6	14	10	5	3		
28	2.81										8	12	1	4	1	2
6	3.34											2	1	3		
2	2.78											1		1		
2	3.51														1	1
1	2.58													1		

TABLE 6 (continued)

Date of first head in (1 × 35) F_3, 1916. Distribution based upon date of first head of the selected F_2 parents.

Number of cultures	Standard deviation of F_3 cultures													
	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
1										1				
5					2		1		1		1			
7			1			2		3				1		
41			5	3	6	10	10	3		1	2			1
60	1	5	6	8	6	15	10	4	2	3				
37	1	2		7	6	5	10	4	1	1				
40		2	3	10	7	7	5	1	2	2	1			
28			5	9	3	3	5	1	2					
6				1	1	3				1				
2					2									
2					1			1						
1					1									

variation of the most variable parental culture. If the differences in the means of the F_3 cultures in tables 6 and 7 are due to genetic causes, one would expect the intermediate cultures to be more variable than the extremes, thus assuming that the extreme cultures are more nearly homozygous than those which are intermediate.

Now noting the distribution of standard deviations in the F_3 cultures as given in tables 6 and 7 and the average of the standard deviations for separate cultures as shown in the vertical columns, we are unable to discover such a decrease in variability toward the extremes. In the present material, however, this is not surprising for the following reason: No. 1 and No. 35 differ in so many genetic factors that there is an extremely wide range in the products of their recombination. As a matter of fact many of these recombinations are so radical and unbalanced that they are no longer automatic (i.e., are unable to give rise to a living organism). Hence there is a large percentage of sterility in the F_2 and later generations. Now the recombination of factors which govern (by their interaction) the time of heading in this particular cross are likely so many and so widely different that all of the possible recombinations would give a range of heading time far beyond (both toward the early and late extremes) the limit of physiological possibilities of a normal wheat plant. Hence in the range of variation observed in the F_2 or F_3 of this cross we have only a small section taken from some part of the larger theoretical curve. It would therefore appear much flatter than the corresponding curve of a pure race and there would be but little difference in the heterozygosity, hence, variability, i.e., standard

TABLE 7

Date of first head in (1 × 35) F_3, 1916. Distribution based upon the means of the F_3 culture.

	F_3 individuals																								
	March								April															May	
Number of cultures	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23	24 25	26 27	28 29	30 1	2 3
4		3	23	34	31	O	59	6	9	2	9	1							1						
1			1	4	6		O 18	13	6	1															
4				2	1		88	O 32	32	10	1				1	1									
6			2	4	3		62	40	O 65	45	20	11	9		7										
9				3			28	22	101	O 95	66	17	7		8	3									
13					1		15	12	75	117	O 187	73	43		50	13	1								
18								6	28	79	229	O 150	128		135	29	2	1	2						
21								5	10	38	161	159	O 209		288	64	5		1						
33								1	1	23	64	167	269	O 1	618	200	21	1	6	3	1				
56									1	8	32	110	166	1	O 1175	788	137	12	43	8	10	3	3		
39										1		10	17		545	O 768	230	27	78	30	9	6			1
8											1	7	1		28	153	O 46	33	43	5	9	6	1		
13											1	2	1		27	128	112	O 10	122	44	31	12	6	2	1
3															6	11	29	17	O 26	5	30	4	6		1
3																4	10	3	43	O 7	28	15	4		

O = Mean of group.

		Distribution of F_2 parents												
		March								April				
Number of cultures	Average σ of F_3	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9
4	4.84	1	3											
1	3.07			1										
4	2.70		1	2		1								
6	3.77		1	3		2								
9	2.80			1		5	3							
13	3.34					10	3							
18	3.43					7	7	3	1					
21	3.63					7	10	3	1					
33	3.31					5	14	8	6					
56	2.85					3	15	16	14	8				
39	2.59					1	7	6	10	12	2	1		
8	3.47						1		5	1	1			
13	3.56								3	4	3	1		1
3	4.14							1		1			1	
3	3.24									2			1	

TABLE 7 (continued)

Date of first head in (1×35) F_3, *1916. Distribution based upon the means of the* F_3 *culture.*

Standard deviation of F_3 cultures.

Number of cultures	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75	7.25
4							1		1	1	1			
1						1								
4			1	1	1			1						
6					2	2		1				1		
9	1	1	1	2		1	1	1			1			
13			3	1		3	3	1	1	1				
18			1	1	4	4	5	1	1	1				
21					3	8	5	3		1	1			
33			2	7	5	5	9	3	1					1
56	1	6	6	9	8	12	9	3	1	1				
39		2	5	12	10	5	3	1	1					
8				3		2	1			2				
13				1	3	3	1		2	1	1			
3					1			1		1				
3			1				1	1						

deviation, of the cultures arising from individuals selected from either the middle or extremes.

Bread wheat crosses. Red Algerian bread (No. 3) × *early Baart (No. 34)*

In 1915, 1 culture of pure No. 3, 1 culture of pure No. 34 and 6 plant rows of the F_2 of 3×34 were grown. These hybrid rows were from the 6 F_1 plants of this cross obtained in 1914. As noted above, dates of first heading were not taken in the F_1 plants. A summary of the results in 1915 is given in table 8:

TABLE 8

Date of first head in (3×34) F_2, *1915.*

	Number of cultures	Number of individuals	Average date of first head	σ of population	Average σ of cultures
Pure No. 3	1	42	March 28	1.60	1.60
(3×34) F_2	6	538	March 23	3.98	2.95
Pure No. 34	1	93	March 16	1.75	1.75

Distribution of σ of separate cultures.

	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75
Pure No. 3			1						
(3×34) F_2		1		1	1		2	1	
Pure No. 34			1						

As previously, it may be noted again that the standard deviation of the hybrids both as a population and as separate cultures was higher than that of the parental varieties. The mean of the F_2 hybrid population was only 1 day later than the mean of the parents. The heading dates of the populations of parental cultures and F_2 hybrids may be given in table 9.

TABLE 9

Date of first head in (3 × 34) F_2, 1915.

	March												April
	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3
Pure No. 3									2	24	10	6	
(3 × 34) F_2	1			18	33	61	136	47	62	130	40	8	2
Pure No. 34				53	33	6		1					

Means of cultures.

Pure No. 3										1			
(3 × 34) F_2							2	3		1			
Pure No. 34				1									

From these 538 F_2 plants 112 were selected, for economic reasons, for planting in the fall of 1915. For comparison 5 cultures of each of the parental varieties were also grown. These were selected from typical plants of the parental varieties of the previous season. The range of dates of first heading of the selected F_2 plants extended from March 10th to the 29th, thus covering 19 of the 23 days of total variation of the F_2. The first summary of results are given in table 10.

TABLE 10

Date of first head (3 × 34) F_3, 1916.

	Number of cultures or plant rows	Number of individuals	Average date of first head	σ of total population	Average σ of cultures
Pure No. 3	5	242	April 13	1.52	.82
(3 × 34) F_3	112	5321	April 5	6.43	2.95
Pure No. 34	5	244	March 25	3.10	2.17

Distribution of standard deviations.

	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25
Pure No. 3	2	2		1									
(3 × 34) F_3	2	2	7	14	15	15	7	10	14	8	9	4	3
Pure No. 34		1			2	1	1						

The general features of this table are the same as those for the other crosses, namely, that the average standard deviations for the cultures are less than those of their respective populations and that the hybrid cultures are much more variable than the pure lines. Moreover, as in the comparison of tables 1 and 4 we here note also an increase in the variability of the F_3 population of hybrids over that of the F_2. (Compare tables 8 and 10.) The failure of the average standard deviation of the hybrid cultures to decline from 1915 to 1916 should be noted. Does this indicate a lack of progress toward homozygosity?

Such an inference would be natural were it not for the peculiar behavior of the parental pure race No. 34.

It will be observed that the variability of this race was strongly increased in 1916 over 1915, although all of the 5 cultures belong to one and the same pure line, i.e., the single pure line grown the previous year, which had originated from a single plant in 1914. Perhaps the same factors which caused this increase in the variability of the pure line No. 34 were also able to increase the variability of the hybrid cultures which arose from No. 34 as one parent and that this influence upon the variability was sufficient to offset that of increasing homozygosity and thus maintain the variability for the two seasons at approximately the same figure.

The distribution of the dates of first head in the parental races and in the F_3 hybrids for 1916 is shown in the following table:

TABLE 11

Date of first head in (3 × 34) F_3, 1916.

	March								April										
	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
Pure No. 3.......										1	1		14	87	138	1			
(3 × 34) F_3......		12	17	43	139	415	761	675	597	842	391	195	157	30	1103	21	17	1	1
Pure No. 34......	1	30	41	56	23	74	17	1											

Means of cultures.

Pure No. 3.......														3	2				
(3 × 34) F_3......					1	12	9	14	15	21	9	6	10	7	8				
Pure No. 34......			1	1	2	1													

It is interesting to note here that no hybrid plant was earlier than the earliest individual of the early culture and that there were only 19 later than the latest of the late parent. Again considered as cultures, the means of the hybrid cultures all fall within the limits set by the extreme means of the parental variety cultures. Here recombination does not seem to have extended the variability definitely beyond the limits of the parents.

Tables 12 and 13 show the segregation of the F_3 to be just as marked in this cross as in the cross already discussed. The greater variability of the intermediate classes is also quite evident. This fact taken in connection with the fact that there was no indication of partial sterility among the hybrids seems significant. It is exactly what should be expected if the segregation of the F_2 plants and F_3 cultures were due to recombination. This should be contrasted with the absence of greater variability of intermediates in the semi-sterile hybrids of the bread wheat—macaroni wheat crosses.

TABLE 12

Date of first head in (3 × 34) F_3, 1916. Distribution based upon dates of first head of the selected F_2 parents.

Number of cultures	F_3 individuals																						
	March												April										
	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	+						1	2	1		13	O 11	14	5					3				
2				+						56	O 16			22									
7					+	2	6	37	16	O 172	47	30	3	21									
13						+		1	16	72	153	103	O 30	158	10	22	4	3	56	2	1		
38						10	+ 10	3	104	91	481	O 396	248	214	59	45	26		101	6			
13								+	2	3	49	85	121	O 170	37	26	15	12	84		5		
14									+	11	1	37	57	195	O 151	36	31	14	124	4	8	1	
21										+	1	13	24	57	134	O 56	80	1	619	2			
3											+					14	1		O 125	1			1

+ = Selected F_2 parents.
O = Mean of group.

Number of cultures	Average σ of F_3 cultures	Means of F_3 cultures														
		March			April											
		25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1	6.30				1											
2	1.47		1		1											
7	2.01	1	4	1	1											
13	3.79		1	3	1	3	5									
38	3.46		6	5	9	9	7	1		1						
13	4.02				1	3	4	3	1	1						
14	3.82					1	3	4	3	3						
21	2.46						1	1	2	5	6	6				
3	2.03										1	2				

TABLE 12 (continued)

Date of first head in (3×34) F_3, *1916. Distribution based upon dates of first head of the selected* F_2 *parents.*

Standard deviations of F_3 cultures.

Number of cultures	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75
1													1	
2	1					1								
7			1	3	1	2								
13			1	1	2	1			5		1		2	
38			1	5	7	4	3	4	2	5	4	2		
13				2	1			2	2	1	3	1		
14				1		3	1	2	4	1	1	1		
21	1	2	3	1	4	3	3	2	1	1				
3			1	1			1							

TABLE 13

Date of first head in (3×34) F_3, *1916. Distribution based upon means of* F_3 *cultures.*

F_3 individuals

Number of cultures	March												April										
	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3	4 5	6 7	8 9	10 11	12 13	14 15	16 17	18 19	20 21	22 23
1						2	4	24	O	15	1												
12						8	9	16	79	O 200	214	38	1	1	1								
9							3		30	72	O 195	108	13	6	1				1				
14						1	1	2	20	40	157	O 222	101	92	7		3		17				
16									9	55	116	136	O 108	221	37	18	6	2	59	2			
20						1		1	1	20	78	136	192	O 291	58	24	31	2	101	8	1		
9										13	1	27	69	150	O 71	7	19	5	79		1		
6											1	1	9	52	84	O 45	26	7	52	3	5		
10													4	27	112	58	O 46	13	213		6	1	
7														2	19	40	24	O 1	248				
8															3	8	2		O 352	2	1		1

O = mean of group.

TABLE 13 (continued)

Date of first head in (3 × 34) F_3, 1916. Distribution based upon means of F_3 cultures.

		Selected F_2 parents												
		March											April	
Number of cultures	Average σ of F_3 cultures	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 1	2 3
1	2.55					1								
12	2.05				1	4	1	6						
9	2.05					1	3	5						
14	3.35	1			1	1	1	9	1					
16	4.18						3	9	3		1			
20	4.32						5	7	4		1			
9	4.18							1	3	4	1			
6	3.74								1	3	2			
10	3.63							1	1	3	5			
7	2.53										6	1		
8	1.21										6	2		

Standard deviations of F_3 cultures.

Number of cultures	.25	.75	1.25	1.75	2.25	2.75	3.25	3.75	4.25	4.75	5.25	5.75	6.25	6.75
1						1								
12	1		1	3	3	3	1							
9			2	2	4			1						
14				4	1	3	1		1	1	1	1	1	
16				1	1	1	1	1	5	2	2	1	1	
20		1		2	1			1	4	3	4	2	2	
9						2		2	1	2	2			
6						1	1	1	2	1				
10							4	4	2					
7				1	2	4								
8	1	1	4	1	1									

Summary; date of first head

In both crosses the parents had wide differences in heading dates and the averages of the F_2 and F_3 were in every case intermediate and nearer to the late parent. The range of the individual hybrid plants in no case extended significantly beyond the range of the early parent toward extreme precocity of heading. Toward the late extreme, however, in the macaroni—bread wheat crosses, there was a long extension of the range, much beyond that of the late parent. As a matter of fact many plants never headed, but remained as dark green, grass-like tufts until they were killed by the heat and dryness of the summer. Among the bread wheat crosses the extension of the range of date of first head beyond the extreme of the late parent was never marked and could, in fact, be accounted for by the normal extension of the curve due to greater numbers.

The same observations made above with regard to the relation of the means of the hybrid populations to their parental means, apply also to the distribution of the means of the hybrid cultures, as compared with their parents, in the F_2. In the F_3, however, the matter was somewhat different. In the macaroni—bread wheat cross there were 3 cultures whose average dates of first head were earlier than the earliest parental average and there were altogether 19 cultures averaging later than the latest parental average. Since there were 230 cultures concerned, 8.2 percent are thus seen to lie outside of the parental range. In the bread wheat cross, on the other hand, there was no case where the average of a hybrid culture was outside the range of averages for the parental varieties. As regards individuals in the F_2 the parental types were abundantly recovered in every case. As regards means of F_3 cultures (a better criterion of the genetic constitution of the F_2 plants) the parental types were also recovered in all cases.

In all cases where more than one culture was involved the standard deviations of the population were greater than the average of the standard deviations of the cultures taken separately and in all cases the standard deviations of the hybrids[1] were greater than those of either parent both as regards that of the populations and the averages of the cultures taken separately.

In comparing the standard deviations of the hybrid F_3 populations with their respective F_2 parental populations we may note the following observations: (1) the standard deviation of F_3 populations are so dependent upon the range of F_2 parents chosen, that conclusions drawn from the calculation of this constant should be carefully guarded. The standard deviation of the F_3 population of both crosses was greater than that of the F_2 population. Since heading time appears to be imperfectly dominant in these hybrids, the number of intermediate types will tend to be reduced as the population approaches homozygosity. If therefore we assume a Mendelian inheritance, whenever the selected F_2 parents practically cover the range of distribution of the F_2 population and form a random sample thereof, we would expect the F_3 population to have a higher standard deviation than the F_2 population.

When we come to compare the average variability (here measured by standard deviation) of the F_3 cultures taken separately with the average

---

[1] It should be remembered that the F_1 is not here included.

variability of the F_2 cultures we are not hampered in our conclusions, to so large an extent as mentioned above in comparing the variability of the F_2 and F_3 populations. With a Mendelian interpretation there is no genetic reason why any F_3 culture should be significantly more variable than the most variable F_2 culture. Moreover, the average variability of the F_3 should be equal to or less than that of the F_2, whatever the mode of selection. We may now observe as follows: (1) In the macaroni—bread wheat cross, 1 × 35, the average variability of the F_3 cultures was significantly below that of the F_2 cultures. (2) In the bread wheat cross some complications arose. The average standard deviations of the F_2 and F_3 cultures of the 3 × 34 were the same (2.95). This, however, cannot be assumed as evidence of a lack of progress toward homozygosity, for the following reasons: It will be observed that the variability of pure race No. 34 was strongly increased in 1916 over 1915 (2.17 and 1.75, respectively) although all 5 of the cultures grown in 1916 came from the 1 culture grown in 1915, which in turn came from a single plant in 1914. Perhaps the same factors which caused this increase in the variability of the pure line No. 34 were also able to increase the variability of the hybrid cultures which were grown from No. 34 as one parent and that this influence upon the variability was sufficient to offset that of increasing homozygosity and thus maintain the variability for the two seasons at the same figure.

The strongly fluctuating nature of the variability of date of first head is shown by a study of the distribution of the standard deviations of the F_2. In every case the range of distribution of the standard deviations of the F_2 overlapped the range for one or both parents. This could be explained by assuming a partial-blending inheritance and assuming that in some F_1 plants the blend was more complete than in others. If this were true the F_3 cultures grown from these low-variable F_2 cultures should also show a low variability. The results are given in table 14.

TABLE 14

Number of F_2 cultures as little variable as one parent	Number of F_3 cultures arising from these	Average σ of these F_3 cultures	Number of F_2 cultures more variable than either parent	Number of F_3 cultures arising from these	Average σ of these cultures
22	148	3.12	21	194	3.05

It is thus seen that the low-variable F_2 cultures gave rise to the higher-variable F_3 cultures. This is what would be expected upon a Mendelian interpretation if we assumed that the low variability of the F_2 cultures in question were so because but few of the extreme combinations chanced to occur. It must be admitted however that the difference shown is not large enough to be significant. We may therefore safely conclude that the differences in standard deviations of the F_2 cultures were wholly fortuitous and without genetic significance.

In the F_3 generation, in all cases, cultures occurred with as low variability as that of the parents, i.e., there were cultures which, insofar as variability is concerned, appeared as nearly homozygous as the pure lines.

With a Mendelian interpretation we are accustomed to expect those F_2 plants which take a position relative to the parents similar to that occupied by the mode of the F_1, to give rise to F_3 cultures which are more variable than the F_2 plants otherwise located. In the macaroni—bread wheat crosses we are not able to observe any relation of this kind. This fact, however, does not argue the absence of Mendelian segregation for the following reasons: The macaroni and bread wheats here crossed, differ in so many genetic factors that there is an extremely wide range in the products of their recombination. Many of these recombinations are so radical and unbalanced that they are no longer automatic. Hence there is a high percentage of sterility in the F_2 and later generations. Such sterility may have the effect of flattening the distribution curve of the F_2 or perhaps even limiting it to one end or the middle or even the extremes of a curve which would be formed by all of the recombination possibilities. As already pointed out many of the F_2 plants never got beyond the rosette stage and many plants which made a robust vegetative growth were completely sterile. The study of sterility in these crosses will be reserved for a future paper. In circumstances such as these it is apparent that there may occur very little difference in the heterozygosity, hence variability, of the cultures from individuals selected from either the middle or extremes of the fertile F_2 of such a population. In the 3 × 34 cross there is a very apparent greater variability of the cultures arising from the modal F_2 plants (see tables 12 and 13). It should be noted that here there was complete fertility and the F_2 selections covered nearly the whole of the range of the F_2 population. A glance at tables 6 and 12, where the F_3 individuals are grouped with reference to the heading date of the F_2 parents, yields abundant evidence that some sort of segregation has occurred. The F_2 plants were not alike genetically. All of the phenomena observed can be explained by assuming that heading date is governed by three or more Mendelizing unit factors. No attempt has been made to determine the number of factors in any case but the fact that many of the intermediate groups (see tables 6 and 13) show cultures with low variability would indicate that the number of factors concerned was rather large, thus providing the possibility of securing several genetically different but still homozygous types.

HEIGHT

Macaroni—bread wheat crosses. Algerian macaroni (No. 1) × Sonora (No. 35)

In this study all height measurements were made from the ground to the top of the highest head (not including the awns). Lengths were taken to the nearest centimeter and expressed in the summaries to the nearest five centimeters. No pure No. 35 was grown in 1914 which was comparable with the pure No. 1 and the (1 × 35)F_1. The No. 1 grown in 1914 was not a single pure line but was from seed of several different mother plants of this variety. A summary of the results for 1914 is shown in table 15.

TABLE 15

Heights in centimeters in (1 × 35) F_1, 1914.

	Number of plants	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	Average	C.V.
Pure No. 1..........	151	1		1	3	9	26	43	49	18	1	134	10.0
(1 × 35) F_1.........	39				1		1	4	8	21	4	147	8.0

The F_1 was taller but no more variable than the parent given. Thirty-eight of these hybrid plants gave rise to hybrid cultures in 1915. The results are summarized in table 16.

TABLE 16

Heights in (1 × 35) F_2, 1915.

	Number of cultures	Number of individuals	Average height	Coefficient of variation	
				of population	of separate cultures
Pure No. 1..........	9	648	147	8.5	6.7
(1 × 35) F_2.........	38	2535	122	19.6	19.0
Pure No. 35.........	3	166	128	11.1	6.4

Distribution of the coefficients of variation of cultures.

	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Pure No. 1............		3	2	2	1					1											
(1 × 35) F_2...........													2	8	3	9	8	4	2	1	1
Pure No. 35...........	1		1			1															

It should be noted here that, whereas the F_1 was taller than No. 1, the tall parent, the average of F_2 (where all of the F_1 was planted) was lower than either parent. The high sterility of the F_2 plants has already been noted. As usual the hybrids were more variable than either parent. It should also be noted that the F_2 hybrids were much more variable than the F_1.

Table 17 gives the distribution of the populations and means of both parents and the F_2 hybrids as regards height.

TABLE 17

Heights in centimeters in (1 × 35) F_2, 1915.

	Distribution of individual heights																Distribution of means of cultures				
	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	110 119	120 129	130 139	140 149	150 159
Pure No. 1						1	4	4	4	25	89	155	217	139	10				2	3	4
(1 × 35)F_2	5	2	18	29	51	104	178	226	311	409	447	399	248	94	11	3	4	30	4		
Pure No. 35								8	25	29	52	38	13	1				1	1	1	

Only three of the hybrid plants were taller than the tallest individuals of the tall parent, but there were 95 lower than the lowest individual of either parent. No hybrid culture averaged as tall as the highest average for the low parent, but 4 cultures averaged lower than the lowest average of either parent. All recombinations so far obtained appear therefore to be less vigorous than the parental races. Since the F_1 plants showed considerable range in height, it would be interesting to know whether this was inherited to any degree in F_2, i.e., was the range in F_1 due solely to modification or were these differences partly genetic? Table 18 shows the F_2 cultures grouped according to the parental height. The class in which the parental height fell is marked **+**, and the mean of the population arising from such parents is marked **O**.

While the last class is 8 cm higher than the first class, considering the small number of races in each, this difference is not above the probable error. We may therefore safely conclude that for all practical purposes the F_1 plants were uniform genetically.

Two hundred and thirty of the F_2 plants were selected for planting in the fall of 1915 and gave rise to hybrid cultures which were measured just before ripening in 1916. For comparison 7 pure cultures of No. 1 and 5 pure cultures of No. 35 were grown. The first summary of results follow.

TABLE 18

Heights in centimeters in (1 × 35) F_2, 1915.

Number of cultures	Height of parent	Average height of offspring	Number of individuals	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
1	120 129	118	37				3		2	6		O 4	+ 6	10	3	3				
4	130 139	123	228	1		3		8	6	18	20	25	O 34	+ 48	38	21	6			
8	140 149	122	485	2		2	7	3	20	39	40	57	O 68	87	+ 78	51	27	2	2	
21	150 159	123	1488	1	2	11	16	37	65	98	143	199	O 249 O	253	223	+ 139	46 +	5	1	
4	160 169	126	297	1		2	3	3	11	17	23	26	52	49	57	34	15	4		

TABLE 19

Height in centimeters in (1 × 35) F_3, 1916.

	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	7	344	137	8.4	6.6
(1 × 35) F_3..	230	10084	118	20.3	15.4
Pure No. 35...	5	246	123	7.1	6.3

Distribution of coefficients of variation in (1 × 35) F_3, 1916.

	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
Pure No. 1...		4	2	1																					
(1 × 35) F_3..		6	15	24	35	38	28	21	20	19	11	3	4	3	1			1							1
Pure No. 35..	1	2	1	1																					

As usual it may be observed that the pure races are less variable than the hybrids and that the average coefficient of variation of the cultures is smaller than those of the populations. It should be further noted that the average coefficient of variation of the F_3 hybrid cultures is smaller than that of the F_2. This is to be expected in the case of increasing homozygosity.

Table 20 shows the distribution of the populations in 1916.

TABLE 20

Heights in centimeters in (1 × 35) F_3, 1916.

	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
Pure No. 1....								2	2	1	9	83	114	95	33	6			
(1 × 35) F_3..	1	12	15	62	127	217	404	496	862	1335	1723	1757	1435	1077	471	75	8	5	2
Pure No. 35...							1	3	1	10	72	141	17	1					

Distribution of means.

Pure No. 1....												2	2	3					
(1 × 35) F_3 ..						1	2	13	21	49	53	42	36	12	1				
Pure No. 35...											2	3							

Only 15 hybrid plants were taller than the tallest individuals of the tall culture. Considering the large number of hybrids in comparison with the number of No. 1, these few taller plants are without significance. At the other end of the scale, however, we find 474 plants lower than the lowest of the lower parent. Considering means we also note with interest that there were 86 hybrid cultures averaging lower than the lowest average for the low parent and one hybrid culture averaging lower than the lowest individual of the low parent.

TABLE 21

Heights in centimeters in (1 × 35) F_3, 1916.

Number of cultures	Arrangement of F_3 individuals grouped according to F_2 parents																		
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
3				9	12	13	11	+ 9	O 17	27	29	5							
8		1	2	3	5	11	32	30	+O 67	83	52	21	5	4	1				
12			1	2	11	13	21	35	65	O+ 96	123	62	31	22	3	1			
24		7	1	10	21	32	54	72	160	O 226	+ 240	128	71	21	6	1			
35		1		12	24	33	79	106	144	250	O 326	+ 304	168	56	16	2			
55	1	2	7	20	31	61	99	107	174	310	O 473	507	+ 328	223	89	6	2		
48			4	5	12	36	62	76	124	186	271	O 428	423	+ 351	138	15		2	2
40		1		5	5	21	38	47	92	141	178	O 282	385	354	+ 174	41	5	2	
4				1	4	2	8	11	11	11	15	O 19	21	39	31	+ 3	1		
1													1	27	O 17	5	+		

Number of cultures	Distribution of means of F_3 cultures										Average coefficient of variation
	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	
3	1				2						16
8			1	2	4	1					18
12			3		5	3		1			16
24		1	2	6	7	8					17
35			3	4	11	10	5	2			15
55		1	3	4	11	17	11	6	2		16
48			1	4	5	7	14	14	3		14
40				1	3	8	10	13	5		14
4					1	1			2		18
1									1		5

Number of cultures	Distribution of coefficients of variation																									
	1 2	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
3						2						1														
8						1	1	2	1	1	1	1														
12			1	2	1		2	2	1		2								1							
24			1	1	2	3	4	2	4	3	1			2												1
35				2	4	4	5	8	2	2	6		2													
55				2	9	10	9	3	5	4	4	3	1	2	2	1										
48			2	3	7	8	6	6	4	7	3	1			1											
40			1	5	1	6	11	3	5	3	1	4														
4						1		1			1	1														
1			1																							

TABLE 22

Heights in centimeters in (1 × 35) F_3, 1916.

Number of cultures	Distribution of F_3 individuais																		
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	180 189	190 199
1				9	12	O 12	7			1	1								
2		4	1	12	10	7	O 6	5	4	4	4	3	1	1	1				
13		4	3	10	23	46	73	O 74	93	55	32	13	5	3					
21		1	5	15	31	51	90	125	O 207	176	134	55	20	7	1		1		
49		2	2	12	13	56	118	175	292	O 534	526	292	91	27	5				
53	1			7	10	27	70	66	144	375	O 627	625	280	95	23	5			1
42			4	2	7	15	30	30	71	131	269	O 481	484	264	75	12	1	2	
36					1	6	9	13	35	47	96	234	O 470	493	183	17	1	2	1
12					1		2	5	6	8	17	43	81	O 180	172	35	6		
1													1	27	O 17	5			

Number of cultures	Distribution of F_2 parents										Average coefficient of variation
	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	
1	1										24
2				1		1					41
13		1	3	2	3	3	1				23
21		2		6	4	4	4	1			21
49	2	4	5	7	11	11	5	3	1		17
53		1	3	6	10	17	7	8	1		14
42				2	5	11	14	10			14
36			1		2	6	14	13			11
12						2	3	5	2		11
1										1	5

Number of cultures	Distribution of coefficients of variation																									
	1 2	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52
1												1														
2															1											1
13									1	1	7	1		1		1			1							
21							1	5	1	5	1	3	1	2	2											
49			1		3	6	7	9	5	6	6	3	2	1												
53				6	7	10	8	6	6	4	4	2														
42				2	3	9	11	4	8	4	1															
36			3	5	9	7	8	2	1			1														
12			1	2	2	3	3	1																		
1			1																							

Table 21 shows the height of the F_3 plants grouped according to their F_2 parents, the means of the F_3 cultures and the coefficients of variation of these cultures, respectively, making up each population group. Table 22 shows the height of the F_3 plants grouped according to the means of the F_3 cultures, the heights of the parents giving rise to these groups and the standard deviations and coefficients of variation of the F_3 cultures, respectively. It should be noted in table 21 that, while there was considerable regression toward the mean, there was a nearly uniform correlation between the height of the F_2 parent and the F_3 offspring. By comparing table 21 with table 20 it will be observed that the distribution of the means in any group of hybrids is no wider than the range of variation of the individuals in either of the parental varieties. Observing the averages and distribution of the coefficients of variation we note an irregular but yet fairly definite lessening of variability in the taller groups.

Again comparing table 22 with table 20 we note that for any F_3 group (in table 22) the distribution of the parents was not wider than the distribution of the individuals of the parental varieties. The differences in the heights of the individuals of these parental groups (which gave rise to cultures having the same mean) could therefore be assumed to be environmental modifications of plants of the same or equivalent heredity so far as height is concerned.

The column showing the average coefficient of variation and the distribution of these constants in table 22 shows a very decided decrease in variability of those cultures which have high means.

One conclusion stands out prominently from these tables. The factors for height were not uniform in the F_2 plants. Recombination had occurred so that on the average (i.e., excluding environmental modifications), tall parents gave rise to tall offspring and the grading of the parents into a series of ascending heights resulted in a slightly less marked but still regularly ascending series of offspring groups. The completeness of this series indicates that the number of factors was large.

Algerian macaroni (No. 1) × Algerian red bread (No. 3)

In 1914, 151 plants of pure No. 1 and six plants of pure No. 3 together with 5 plants of (1 × 3) F_1 were measured for height.

The following table shows the distribution of the heights of these plants and their means. Except for the pure No. 1, the numbers were too small for the calculation of the standard deviations with any degree of accuracy.

TABLE 23

Heights in centimeters in the (1 × 3) F_1, 1914.

	Number of plants	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	Mean
Pure No. 1....................	151	1		1	3	9	26	43	49	18	1	134
(1 × 3) F_1....................	5				2			1	2			124
Pure No. 3....................	6				2	1	2	1				118

The numbers are too small to give results of any particular significance, but it may be noted that the range of the F_1 hybrids lies within the range of the most variable parent and that the mean of the hybrids lies between the means of the two parent cultures.

The 5 F_1 hybrid plants gave rise to 5 hybrid F_2 cultures in 1915. For comparison in the same year 9 cultures of No. 1 and 1 culture of No. 3 were available. Table 24 gives a summary of the results.

TABLE 24

Heights in the (1 × 3) F_2, 1915.

Culture	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of the separate cultures
Pure No. 1....	9	648	147	8.5	6.7
(1 × 3) F_2....	5	406	118	21.1	20.4
Pure No. 3....	1	42	146	4.2	4.2

Distribution of coefficients of variation.

	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32
Pure No. 1...		5	3			1									
(1 × 3) F_2..				1			1		1			1			1
Pure No. 3...	1														

Whereas the F_1 hybrids were intermediate between the parent races, the F_2 averaged lower than either, the two parent races being of practically equal height. The variability of the hybrids was strikingly higher than that of the parental cultures.

Table 25 gives the distribution of the populations and the means of both parents and the F_2 hybrids as regards height.

None of the hybrid plants was taller than the tallest individual of the parental cultures but there were 29 lower than the lowest individual of the parents. It is striking that all of the means of the hybrid cultures save one were lower than the lowest parental mean. All recombinations, therefore, appear to be less vigorous than the parental cultures.

TABLE 25

Heights in centimeters in the (1×3) F_2, *1915.*

	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1....					1	4	4	4	25	89	155	217	139	10
(1×3) F_2....	7	5	8	9	17	27	39	57	61	87	34	27	8	
Pure No. 3....										3	18	21		

Distribution of means of cultures.

	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1....										2	3	4		
(1×3) F_2....							2	1	1	1				
Pure No. 3....											1			

Table 26 shows the F_2 cultures grouped according to the height of their respective F_1 parents. The class in which the parental height fell is marked + and the means of the population arising from such parents are marked O.

TABLE 26

Heights in centimeters in the (1×35) F_2, *1915.*

Number of cultures	Height of parent	Average height of offspring	Number of individuals	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169
2	100 109	105	82		2	4	5	4	9	10	O + 9	10	12	9	6	2	
1	130 139	110	54		3	1		2	4	3	5	O 9	9	+ 13	3	2	
2	140 149	126	270		2		3	3	4	14	25	38	O 40	65	+ 45	23	8

Although the range of each of these groups is practically the same, the distinct correlation between the height of parent and height of offspring cannot be disregarded. This would indicate that one or the other of the parental stocks was not pure as regards the factors influencing height and that the F_1 plants were, therefore, not all equivalent genetically in this respect. In order, therefore, to avoid complications, the subsequent discussion of this cross will be based upon the product of a single F_1 plant (145 cm high) in 1914 from which a culture (No. 32-1) was grown in 1915, of which the following data may be given:

TABLE 27

Heights in centimeters in the (1×35) F_2, *1915.*

Culture	Height of parent	Average height of offspring	Number of individuals	Average C.V.	Distribution of heights of individuals 70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169
32-1	145	130	71	15	1	1	4	10	7	11	9	13	10	5

From this culture 40 plants were selected as parents in 1915-'16. A first summary of the results may be given as follows:

TABLE 28

Heights in centimeters in (1 × 3)F_3, 1916.

Cultures	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	7	342	137	8.5	6.6
(1 × 3) F_3....	40	1758	123	20.6	14.2
Pure No. 3....	5	243	133	8.0	6.6

Distribution of coefficients of variation

Cultures	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
Pure No. 1...............		4	2	1																	
(1 × 3) F_3...............	1	6	3	5	5	3	3	2	5	2	2	1				1					1
Pure No. 3...............	2	1	1		1																

Again we perceive that the averages of the coefficients of variation of the cultures are less than the coefficients of variation of their respective populations, and that the pure lines are less variable than the hybrids. The average variability of the F_3 is markedly less than that of the cultures in F_2.

Table 29 gives the distribution of the populations and means of both the hybrid and parental cultures.

TABLE 29

Heights in centimeters in (1 × 3)F_3, 1916.

	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1..............					1	1	1	1	11	91	123	84	26	3	
(1 × 3) F_3..............	8	6	21	21	67	73	100	157	244	274	252	320	170	36	8
Pure No. 3..............		1			1			1	10	68	108	48	6		

Distribution of means.

	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 1..............										2	2	3			
(1 × 3) F_3..............						2	4	5	9	6	3	9	2		
Pure No. 3..............										3	2				

Observing tables 28 and 29 it is evident that on the average, height-vigor in the F_3 hybrids was again less than for the two parental cultures but that there were two hybrid cultures taller than the tallest average for the taller parent. On the other hand 20 hybrid cultures were lower than the lowest average of the low parent.

Table 30 shows a fairly uniform correlation between the height of the selected F_2 parent and the average height of its F_3 offspring. Table 31 exhibits rather strikingly the fact that the taller F_3 cultures are much less variable than those which averaged lower. Now if one will compare the distribution of the selected F_2 parents (table 30) with the total F_2 population as shown in table 25, it will be observed that the selections just cover the upper half of the range. As regards the variability of the F_3, therefore, table 31 and the accompanying column of average coefficients of variation might be assumed to represent only a half curve. The low selections were therefore really intermediate F_2 individuals. The higher variability of these lower F_3 cultures, and the very evident decline in variability as we approach the taller, real, extreme, can be interpreted as being in accord with the idea of hybrid recombination of height factors with the intermediate forms most heterozygous and hence more variable.

TABLE 30

Heights in centimeters in $(1 \times 3)F_3$, *1916.*

Number of cultures	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
2					1		4	7	13	+ 11	O 13	31	8	1			
3			2	1	6	4	12	17	O 16	19	+ 20	10	3	4			
7			1	3	4	5	19	16	22	42	O 87	+ 67	36	19	2		
9			3	2	6	7	20	17	21	47	O 66	81	+ 57	45	10	3	1
11			2		2	5	8	9	18	27	32	49	O 80	+ 147	89	27	7
6					1		4	7	9	10	22	30	O 54	72	+ 48	1	
2									1	1	4	7	14	O 32	21	+ 5	

+, Selected F_2 parents.
O, Means of F_3 groups.

Number of cultures	Distribution of means of F_3 cultures									Average coefficient of variation
	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	
2				1	1					15
3		1	1	1						25
7		1		1	3	2				16
9			2	1	2	3		1		17
11			1	1	1		3	3	2	11
6					2	1		3		12
2								2		10

TABLE 30 (continued)

Heights in centimeters in (1×3) F_3, *1916.*

Number of cultures	Distribution of coefficients of variation in F_3 cultures																				
	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
2					1			1													
3						1			1												1
7			1	1		1	1		1	1	1										
9			1	2		1	1		1	1	1					1					
11	1	3	1		4			1				1									
6		3					1		2												
2				2																	

TABLE 31

Heights in centimeters in (1×3)F_3, *1916.*

Number of cultures	Distribution of F_3 Individuals																
	10 19	20 29	30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
2			1	2	4	5	20	**O** 20	21	9	5	4					
4			4	3	11	10	17	11	**O** 20	18	17	24	6	7	1		1
5			2		1	2	10	18	25	**O** 49	55	32	10	2			
9					4	2	10	15	23	55	**O** 114	109	46	13	5		
6			1	1	1	2	8	6	8	20	38	**O** 73	66	38	5		
3							2	3	2	3	8	17	**O** 43	49	13	1	
9									1	2	7	15	77	**O** 194	108	10	
2										1			4	17	**O** 38	25	7

O, Means of F_3 groups.

Number of cultures	Distribution of F_2 parents							Average coefficient of variation
	100 109	110 119	120 129	130 139	140 149	150 159	160 169	
2		1	1					22
4		1		2	1			31
5	1	1	1	1	1			16
9	1		3	2	1	2		15
6			2	3		1		15
3					3			12
9				1	3	3	2	6
2					2			7

TABLE 31 (continued)

Heights in centimeters in (1 × 3) F_3, 1916.

Number of cultures	Distribution of coefficients of variation in F_3 cultures																				
	3 4	5 6	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44
2									1		1										
4									1			1				1					1
5						1	2	2													
9			1	1	2	1			2	2											
6				2		1	1		1		1										
3					3																
9	1	5	1	2																	
2		1	1																		

Height in bread wheat crosses, 3 × 35

No pure No. 35 was grown in 1914 for comparison with the pure No. 3 and the F_1 hybrids of 3 × 35. The following table summarizes the data for the pure No. 3 (6 plants, not a pedigree line) and the (3 × 35) F_1 hybrids.

TABLE 32

Heights in centimeters in (3 × 35) F_1, 1914.

Culture	Number of plants	Average height	Distribution of heights of individuals							
			100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 3	6	118	2	1	2	1				
(3 × 35) F_1	18	142			1	5	8	3	1	

The hybrids are thus seen to be taller than the pure No. 3 and the range is slightly greater, but not more than would be expected with the larger number of individuals grown, i.e., one could not infer that the hybrids were more variable than the pure race.

Each of the 18 F_1 plants gave rise to an F_2 culture in 1915. For comparison 3 cultures of No. 35 and one of No. 3 are available. Table 33 summarizes the results for 1915.

TABLE 33

Heights in centimeters in (3 × 35) F_2, 1915.

Culture	Number of cultures	Number plants	Average height	Coefficient of variation of the population	Average C.V. of separate cultures	Distribution of C.V.			
						3 4	5 6	7 8	9 10
Pure No. 3	1	42	146	4.2	4.2	1			
(3 × 35) F_2	18	1611	148	7.4	6.0		15	1	2
Pure No. 35	3	166	128	11.1	6.4	1	1		1

It is here interesting to note that the hybrids are somewhat taller than the tall parent.

Table 34 gives the distribution within the populations of F_2 hybrids and parental races. In the hybrids, the cultures are arranged in groups with regard to the height of their F_1 parents.

TABLE 34

Heights in centimeters in (3 × 35) F_2, 1916.

	Number of cultures	Parental height	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 3	1									3	18	21		
(3 × 35) F_2	1	120 129				1		1	+ 4	8	O 40	30	2	
"	5	130 139	1				1		14	+ 46	144	O 169	65	9
"	8	140 149				1	2	3	18	80	+O 236	286	93	3
"	3	150 159				2	1	1	5	12	57	+O 105	55	4
"	1	160 169							2	5	13	O 52	+ 20	
(3 × 35) F_2 Totals	18		1			4	4	5	43	154	O 508	663	235	16
Pure No. 35	1						8	25	29	52	38	13	1	

Distribution of means of cultures.

			60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179
Pure No. 3											1			
(3 × 35) F_2										1	6	11		
Pure No. 35									1	1	1			

+, Selected F_1 parent.

O, Mean of group.

No appreciable correlation between the height of the F_1 parent and the average of the F_2 offspring is apparent. We may therefore consider that so far as the height factors are concerned, the F_1 plants were all equivalent. The range of distribution of the hybrid population slightly exceeded that of the most variable parent in both directions but no more than would be expected considering the larger number of plants grown.

From the above F_2 hybrids 80 selections were made for growing in 1915-16. These ranged from 118 to 173 cm high, thus covering all of the upper but not quite all of the lower end of the range of the F_2. For comparison with these, 5 cultures of each of Nos. 3 and 35 were grown. A first summary of the results are shown in table 35.

TABLE 35

Heights in centimeters in (3 × 35) F_3, 1916.

Culture	Number of cultures	Number of individuals	Average height	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 3....	5	243	133	8.0	6.6
(3 × 35) F_3...	80	3849	143	8.4	6.3
Pure No. 35...	5	246	123	7.2	6.3

Distribution of coefficients of variation.

	3 4	5 6	7 8	9 10	11 12	13 14
Pure No. 3.......	2	1	1		1	
(3 × 35) F_3......	8	43	21	4	3	1
Pure No. 35......	1	2	1	1		

It should here be noted that the average height of the hybrids is again greater than that of the taller parent and that there is no diminution in the variability of the F_3 from the F_2. Moreover, the hybrids are no more variable than the pure races.

Table 36 gives the distribution of the populations of the hybrids and their parental races as well as the distributions of the means of the cultures of each.

TABLE 36

Heights in centimeters in (3 × 35) F_3, 1916.

	Distribution of individuals														Distribution of means of cultures				
	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	110 119	120 129	130 139	140 149	150 159
Pure No. 3..	1			1			1	10	68	108	48	6				3	2		
(3 × 35) F_3.				1	3	1	37	164	519	1045	1350	611	104	14		12	26	34	8
Pure No. 35.				1	3	1	10	72	141	17	1				2	3			

That we should here have 42 hybrid cultures (slightly more than half) whose average heights were higher than the highest average for the tall parent is somewhat surprising. Especially is this so when we reflect that the variability of the hybrids is no greater than that of the pure lines.

From table 37 we observe that the regression of the offspring of extreme selections is quite strong, but it is not complete. The difference between the means of the offspring of selected extremes is greater than between the means of the parental races (compare table 35). Comparing the distribution of selected F_2 parents forming the groups in table 38 with the distribution of the individuals of their parental varieties in table 34, we will note that they are not more widely distributed. They can therefore be assumed to be environic modifications of individuals representing equivalent genetic combinations so far as height is concerned. There was a fairly well marked decrease in the variability of the taller cultures.

Table 37

Heights in centimeters in (3 × 35) F_3, 1916.

	Arrangement of F_3 individuals grouped according to F_2 parents										
Number of cultures	69 78	79 88	89 98	99 108	109 118	119 128	129 138	139 148	149 158	159 168	169 178
1				5	+ 11	O 10	5	15	3		
2				2	13	+ 12	O 21	24	23	2	
9	1	2		7	43	110	O+ 79	96	73	19	1
20			1	15	33	188	O 265	+ 314	132	17	2
35			1	7	53	148	484	O 669	+ 273	43	10
12		1		1	12	48	176	O 212	98	+ 23	1
1						2	15	O 24	9		+

Number of cultures	Distribution of means of F_3 cultures				Average C.V. of F_3 cultures	Distribution of coefficients of variation of F_3 cultures					
	119 128	129 138	139 148	149 158		3 4	5 6	7 8	9 10	11 12	13 14
1	1				12.0					1	
2	1		1		8.0		1			1	
9	3	2	4	1	8.2		4	1	3		1
20	4	6	9	1	6.1	2	10	7	1		
35	3	13	15	4	5.9	4	23	7		1	
12		5	5	2	5.9	2	4	6			
			1		5.0		1				

Red Algerian bread (No. 3) × early Baart (No. 34)

In 1914 there were grown 6 plants of pure No. 3, 12 plants of pure No. 34 and 6 plants of (3 × 34) F_1. These numbers are too small to warrant the calculation of coefficients of variation but the distribution and averages may well be given.

TABLE 38

Heights in centimeters in (3 × 35) F_3, 1916.

Number of cultures	F_3 individuals arranged in accordance with the means of the F_3 cultures										
	69 78	79 88	89 98	99 108	109 118	119 128	129 138	139 148	149 158	159 168	169 178
12	1	1	1	25	108	O 242	150	46	6		
26		2	1	10	43	213	O 542	402	45	1	1
34				2	13	61	231	O 797	390	32	2
8						3	22	105	O 170	71	11

Number of cultures	Distribution of F_2 parents							Distribution of coefficients of variation of F_3 cultures						
	109 118	119 128	129 138	139 148	149 158	159 168	169 178	Average C.V. of F_3 cultures	3 4	5 6	7 8	9 10	11 12	13 14
12	1	1	3	4	3			8.1		4	4	1	3	
26			2	6	13	5		6.3	1	14	9	1		1
34		1	3	9	15	5	1	5.8	7	17	8	2		
8			1	1	4	2		5.8		8				

TABLE 39

Heights in centimeters in (3 × 34) F_1, 1914.

Cultures	Number of plants	Average height	100 109	110 119	120 129	130 139	140 149	150 159	160 169
Pure No. 3....	6	118	2	1	2	1			
(3 × 34) F_1...	6	123		1	1	4			
Pure No. 34...	12	150				1	2	7	2

The F_1 is here seen to be intermediate in height between the parents and with a smaller range of variation than either.

Each of the 6 F_1 plants gave rise to an F_2 culture in 1915. For comparison, one culture of No. 3 and one of No. 34 were available. Table 40 gives first summary of the results.

TABLE 40

Heights in (3 × 34) F_2, 1915.

Culture	Number of cultures	Number of plants	Average height in centimeters	Coefficient of variation of the population	Average C.V. of the cultures	Distribution of C. V.	
						3 4	5 6
Pure No. 3..	1	42	146	4.2	4.2	1	
(3 × 34) F_2.	6	537	150	7.1	5.0	1	5
Pure No. 34.	1	92	137	4.1	4.8		1

As in the last bread wheat cross (No. 3 × 35) and unlike either of the bread wheat × macaroni wheat crosses (1 × 35 and 1 × 3) the average height of the F_2 is greater than the mean of the parents, in fact greater than either of the parents. As usual the coefficient of variation of the F_2 taken as a population was greater than the average of this constant for the separate cultures and the average coefficient of variation of the hybrid cultures was greater than that of the pure parent cultures.

Table 41 gives the distribution of height in the parental races and the F_2 hybrids of this cross.

Table 41

Heights in centimeters in (3 × 34) F_2, 1915.

Culture	Distribution of individuals										Distribution of means of cultures		
	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	130 139	140 149	150 159
Pure No. 3.......						3	18	21				1	
(3 × 34) F_2......	1			1	6	26	151	232	111	9		2	4
Pure No. 34......					2	29	55	6			1		

That we should have 4 hybrid cultures averaging taller than the tall parent is interesting, but may be ascribed to hybrid vigor.

The following table (table 42) gives the distribution of the F_2 population grouped according to the height of the F_1 parents, + being the height of F_1 parent, and O the mean of F_2 individuals arising from such parents:

Table 42

Heights in centimeters in (3 × 34) F_2, 1915.

Number of cultures	Parental height	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159	160 169	170 179	Average height
1	110 119				+ 1	6	6	O 41	27	9		147
1	120 129					+	4	29	O 42	12		152
4	130 139	1					+ 16	81	O 190	99	9	155

There is thus seen to be a slight correlation between the height of the F_1 parents and the height of the F_2, indicating a possibility of some genetic differences in the F_1 in respect to height. In all further discussion of this cross, as regards height, it will be necessary to segregate the data into groups so as to consider at one time only plants originating from a single F_1 parent. Since nearly all of the F_3 population arose from one or the other of the original F_1 plants, Nos. 25-1 and 44-2, all F_3 cultures except such as originated from these two will be excluded from this study, and these will be kept separate. The distribution of the F_2 of these two cultures were as follows:

TABLE 43

Heights in centimeters in (3 × 34) F_2, 1915.

Culture	Parental height	Number individuals	Average height	Distribution of individuals						Average C.V.
				120 129	130 139	140 149	150 159	160 169	170 179	
(44-2) F_2, 1915	120	87	152	1	3	29	42	12		4.5
(25-1) F_2, 1915	135	90	155			12	42	33	3	4.9

The selections for the F_3 covered the full range of both of these parents. Table 44 gives a summary of the results in F_3.

TABLE 44

Heights in centimeters in (3 × 34) F_3, 1916.

Culture	Number of cultures	Number of individuals	Average height
Pure No. 3	5	243	133
(3 × 34 F_3 (44-2)	50	2408	133
(3 × 34) F_3 (25-1)	50	2396	131
Pure No. 34	5	243	121

Coefficient of variation

Culture	Population	Average of separate cultures	Distribution of C.V.						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
Pure No. 3	8.0	6.6	2	1	1		1		
(3 × 34) F_3 (44-2)	9.8	6.5	9	23	10	4	2		2
(3 × 34) F_3 (25-1)	7.7	5.9	10	26	10	3	1		
Pure No. 34	7.4	6.2		3	2				

In 1916, it will be observed that the average height of the F_3 is practically the same as the taller parents. The coefficient of variation of the hybrid population is greater than that of the populations of either parent but the average coefficient of variation of the hybrid cultures taken separately was not significantly below that of the pure cultures.

The distribution of the heights of the individuals of the F_3 population and the parental cultures and also of the means of the separate cultures are given in table 45.

Whereas the ranges of the hybrid populations extend beyond the limits of the parents, this is here not surprising considering the much larger

TABLE 45

Heights in centimeters in (3×34) F_3, *1916.*

Culture	Distribution of individuals														Distribution of means of cultures					
	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150-159	160-169	170-179	100-109	110-119	120-129	130-139	140-149	150-159
Pure No. 3......	1			1			1	10	68	108	48	6					3	2		
$(3 \times 34)F_3$ Total			5	12	13	29	87	453	1570	1819	1068	292	13	1	1	3	41	50	14	3
$(3 \times 34)F_3$ (44-2)			3	8	8	18	50	215	652	769	493	179	13		1	2	15	23	8	1
$(3 \times 34)F_3$ (25-1)			2	4	5	9	31	184	770	934	428	29				1	21	24	4	
Pure No. 34.....			1			2	22	85	119	14						1	4			

numbers used. It is interesting, however, to note that 17 hybrid cultures had average heights higher than the highest average for the parental cultures.

Table 46 shows the distribution of the F_3 grouped according to the selected F_2 parents. In table 47 the F_3 is grouped according to the means of the F_3 cultures. Table 46 shows a definite correlation between the height of the selected F_2 parent and the mean of the F_3 classes, but there is a strong regression, especially in the higher groups. The F_2 selections, it may be noted, covered practically the entire range of the F_2 population. The distribution of the parents in the F_3 groups of cultures having equal means, was not greater than the normal distribution of individuals in a pure culture. They could therefore be assumed to be modifications (environic) of genetically equivalent individuals.

TABLE 46

Heights in centimeters in (3×34) F_3, *1916.*

Number of cultures	Arrangement of F_3 individuals grouped according to F_2 parents												Distribution of means of F_3 cultures, 1916					
	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150-159	160-169	170-179	100-109	110-119	120-129	130-139	140-149	150-159
(44-2)					O		+											
1	2	2	1	9	15	5	10	1	1				1					
							O	+										
8		1	1	2	10	93	171	91	14					1	5	2		
								O	+									
16		3	3	4	11	71	218	233	180	53	4			1	7	4	4	
								O		+								
23	1	2	3	3	11	42	218	410	281	124	9				3	15	4	1
								O			+							
2					3	5	35	34	17	2						2		
(25-1)																		
							O		+									
4		1			5	23	86	54	19						3	1		
								O		+								
22	1	2	2	5	13	97	382	410	129	6				1	9	12		
								O			+							
22	1	1	3	4	13	64	279	423	254	20					9	10	3	
								O				+						
2							23	47	26	3						1	1	

+, Selected F_2 parent.
O, Mean of F_3 group.

Table 46 (continued)

Heights in centimeters in (3×34) F_3, *1916.*

Number of cultures	Mean of F_3	Average C. V. per cent	Distribution of coefficients of variation of F_3 cultures						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
(44-2)									
1	107	16.0							1
8	125	5.8	3	2	2	1			
16	130	6.3	3	8	2	1	2		
23	137	6.4	3	12	5	2			1
2	132	7.0		1	1				
(25-1)									
4	122	6.3	1	1	2				
22	130	6.3	1	15	3	3			
22	133	5.6	7	9	5		1		
2	136	4.0	1	1					

Table 47

Heights in centimeters in (3×34) F_3, *1916.*

Cultures	Arrangement of F_3 individuals grouped according to means of F_3 culture											Distribution of selected F_2 parents					
	69 60	79 70	89 80	99 90	109 100	119 110	129 120	139 130	149 140	159 150	169 160	129 120	139 130	149 140	159 150	169 160	179 170
(44-2)																	
1	2	2	1	9	O 15	5	10	1	1			1					
2			1	1	7	O 47	39	2					1	1			
16		5	6	8	18	129	O 340	207	34	2			5	7	4		
22	1	1			9	35	257	O 504	235	25			2	4	14	2	
8					1		6	52	O 206	130	6			4	4		
1								3	17	O 22	7				1		
(25-1)																	
1					1	O 22	23	1							1		
21		1	3	4	23	129	O 517	296	28					3	9	9	
24	2	3	1	1	7	32	225	O 629	287	12				1	12	10	1
4						1	5	58	O 113	17						3	1

TABLE 47 (continued)

Heights in centimeters in (3 × 34) F_3, 1916.

Cultures	Mean of F_3	Average C. V.	Distribution of coefficients of of variation of F_3 cultures						
			3 4	5 6	7 8	9 10	11 12	13 14	15 16
(44-2)									
1	107	16.0							1
2	118	6.0		2					
16	123	7.6	2	3	6	2	2		1
22	134	6.0	1	16	3	2			
8	147	4.5	6	1	1				
1	153	5.0		1					
(25-1)									
1	120	4.0	1						
21	126	6.2	2	12	6	1			
24	135	5.8	6	12	3	3			
4	142	5.3	2	1	1				

Summary; height

The number of F_1 plants grown were too small to give significant results except in the case of the 1 × 35 and 3 × 35 crosses. In both of these cases the F_1 averaged taller than the tall parent. In the other two cases the F_1 was intermediate. In the two macaroni—bread wheat crosses (1 × 35 and 1 × 3) the F_2 and F_3 averaged below both parental races. In the two bread wheat crosses (3 × 34 and 3 × 35) the F_2 averaged taller than either parent and the F_3 of the 3 × 35 cross was taller than either parent, but in the 3 × 34 cross the average of the F_3 was 1 cm shorter than the taller parent. The distribution of heights in F_1 did not go significantly beyond the limits of the parental cultures in any case except that of 3 × 35 in which the whole distribution was pushed upward about 24 cm. The range of distribution of the individual heights of the F_2 and F_3 in neither case of the macaroni—bread wheat crosses extended significantly above that of the parents, but in both cases extended markedly below the parental range. On the other hand in the bread wheat crosses the range in both cases extended distinctly above, but not significantly below, the parental ranges in F_2 of both crosses and the F_3 of the 3 × 35 cross, but in the F_3 of the 3 × 34 cross it did not extend significantly either above or below the parental range. The same observations made with reference to the distribution of the individual heights of the F_2 and F_3 of both kinds of crosses also apply with perhaps greater emphasis to the distribution of the means of the F_2 and F_3 cultures taken separately.

Now, referring to the appropriate tables, note that the average height of F_1 in one of the species crosses (macaroni—bread wheat) was above the tall parent and in the other intermediate between the parents. We must therefore assume that the maximum heterozygosity of these crosses will give plants at least taller than the low parent. In both the F_2 and F_3 of these crosses, however, the average F_2 and F_3 height was below the parent. We are therefore compelled to conclude that recombination and not antagonistic heterozygosis is the cause of the low averages of the F_2 and F_3. A complete double set of macaroni factors, a complete double set of bread wheat factors, or the combination of one complete set of factors from each species, was able to produce a plant of standard vigor, but a large majority of the recombinations of these factors where a complete set from one of the species was lacking, resulted, through failure of coördination, in the production of plants of reduced vigor.

Now it should be noted that no F_2 plant, tall because it was completely heterozygous, could give rise to an F_3 culture which had a high average height, for the reasons above given. Hence the majority of tall F_3 cultures must have arisen from F_2 plants, tall because they were genetically completely, or nearly completely, like one of the parents. Now this is in harmony with the fact (see tables 22 and 31) that the taller F_3 cultures were markedly less variable than were those with a less average height. Now let us remember that the completely heterozygous F_1 plants of the 1 × 35 cross were tall plants with wrinkled seeds. If we examine the F_2 plants selected and pick out all of those which were taller than the average of the low parent and which also had wrinkled seed, thus again resembling the F_1 plants we find that the average height of the F_3 cultures arising from these were 110 cm with an average coefficient of variation of 19.5 percent, whereas the average height of the offspring of all of the remaining selected F_2 plants taller than the average of the low parent was 123 cm with an average coefficient of variation of 14.1 percent. Again, if we pick out all of the selected F_2 plants which were taller than the average of the low parent and which also had smooth seeds, thus resembling one or the other of the parents, we find that the average height of the F_3 cultures arising from these was 126 cm with an average coefficient of variation of 12.6 percent.

A similar study in the 1 × 3 cross gave for the F_1-like F_2 plants F_3 cultures with an average height of 131 cm and an average coefficient of variation of 12.9 percent, whereas the parent-like F_2 plants gave F_3 cultures with an average height of 143 cm and an average coefficient of variation of 6.6 percent.

While these facts coincide completely with the assumptions above made, the story does not end here. Returning to the 1 × 35 cross we found that there were 30 tall F_1-like F_2 plants and 73 tall parent-like F_2 plants. If now we cast the F_3 cultures arising from these two groups respectively into subgroups arranged according to the average heights of the F_3 cultures and find the average coefficients of variation of each subgroup we may tabulate the results as in table 48.

TABLE 48

Average heights of F_3 cultures in centimeters.

		70 79	80 89	90 99	100 109	110 119	120 129	130 139	140 149	150 159
30 F_3 cultures from tall F_2 plants hav- the wrinkled seed (F_1-like F_2 plants)	Distribution of heights	1	2	3	6	8	5	5		
	Average coefficients of variation	30.0	26.0	23.7	20.5	18.5	16.2	16.0		
73 F_3 cultures from tall F_2 plants having smooth seed (parent-like F_2 plants)	Distribution of heights		1	2	5	12	27	20	5	1
	Average coefficients of variation		23.0	16.0	15.6	13.7	13.8	10.0	9.4	5.0

With these results we must conclude that we have not yet succeeded in separating out genetically equivalent groups and that those F_3 plants which gave rise to tall F_3 cultures are genetically more nearly homozygous or else we must postulate some other cause for the suppression of variability in the taller F_3 cultures. This last analysis in no way interferes with the conclusions already drawn, for it clearly shows that in F_3 subgroups of equal height, those cultures arising from F_1-like plants were always more variable than those which came from parent-like plants.

Now turning to the bread wheat crosses we note that the average coefficients of variation of the F_2 and F_3 generations were in no case significantly higher than that of the most variable parental culture (see tables 33, 35, 40, 44). If, however, we consult tables 38 and 47 we shall observe a distinct lowering of the variability of the taller cultures. Let us also remember that the F_1, F_2 and F_3 of the 3 × 35 cross all averaged taller than the tall parent and note (table 38) that the reduction of the variability of the taller F_3 cultures was uniform, whereas the F_1 of the 3 × 34 cross was intermediate, the F_2 taller and the F_3 again intermediate, and while the reduction in variability of the F_3 cultures (table 47) was still apparent (with the exception of 1 erratic extreme) there was some indication that the intermediate F_3 classes (F_1-like) had a tendency to be a little more variable. There appears, therefore, to be two conflicting forces at work, one (heterozygosis) tending to make the cultures arising from the F_1-like F_2 plants more variable, and another which tends to suppress variability in the taller cultures.

A means of testing for the presence of a factor suppressing variability, which is independent of heterozygosity, is found in the F_2 cultures which came from supposedly genetically equivalent F_1 plants. In the F_2, the means and variabilities of the several cultures from any given cross should be the same. Where slight differences occur, they are in all probability environic. Nevertheless if the cultures be grouped according to these slight differences in the F_2 means, and the average coefficients of variation of these groups calculated, if there be a factor suppressing variability in the taller groups it should become apparent, provided there is a sufficient number of F_2 cultures to give valid averages. Such an analysis of the F_2 hybrid cultures for 1915 is given in table 49.

TABLE 49

Correlation between average height and coefficient of variation in F_2 hybrids.

		Total number	Average heights, 1915					
			100 109	110 119	120 129	130 139	140 149	150 159
(1 × 35) F_2	Number of cultures	38		4	30	4		
	Average C. V.			19.2	19.0	18.9		
(1 × 3) F_2	Number of cultures	5	2	1	1	1		
	Average C. V.		28.5	20.2	10.4	14.5		
(3 × 34) F_2	Number of cultures	6					2	4
	Average C. V.						5.5	4.8
(3 × 35) F_2	Number of cultures	18				1	9	8
	Average C. V.					7.0	5.9	6.0

The differences, while not large, are as uniform as could be expected from such small numbers and indicate the presence of a suppression factor of some sort which slightly reduces the variability of the taller cultures.

The presence of this suppression factor for variability in the taller cultures is even more strikingly shown in the pure races. Grouping the cultures according to their means (without regard to year in which they are grown) and calculating the average coefficient of variability for each group we have the result shown in table 50.

Having now shown that there is a factor which, independent of heterozygosity, may suppress the variability of the taller cultures, we may conclude as follows:

(1) Some factor for suppressing variability has been able to com-

TABLE 50

Correlation between average height and coefficient of variation in pure races.

		Total number	Average height				
			110 119	120 129	130 139	140 149	150 159
Pure No. 1	Number of cultures	16		2	4	6	4
	Average C. V.			7.5	7.5	6.5	5.5
Pure No. 35	Number of cultures	8	3	3	1	1	
	Average C. V.		6.7	6.7	6.4	3.9	
Pure No. 3	Number of cultures	6		2	3	1	
	Average C. V.			7.5	5.6	4.2	
Pure No. 34	Number of cultures	6	1	4	1		
	Average C. V.		6.9	6.1	4.8		

pletely mask the effect of heterozygosity in a cross where the F_2 and F_3 cultures averaged taller than the tall parent (3 × 34).

(2) This same factor has largely suppressed, but not entirely masked, the variability due to heterozygosity in a cross where the F_2 and F_3 cultures were approximately as tall as the taller parent (3 × 35).

(3) The factor for the suppression of variability in tall cultures is apparent in crosses where the averages of the F_2 and F_3 cultures are below those of the low parent, but was in no case able to obliterate the effect of heterozygosity (see 1 × 35 and 1 × 3).

The question as to the nature of this suppression factor will be reserved for future discussion. The fact that the average variability of the F_2 and F_3 cultures was not significantly higher than that of the pure-line parents in the bread wheat crosses might be cited as showing that a blending inheritance has occurred with the production of a single new race no more variable than the most variable of the parental races, were it not for the fact that tables 37 and 46 show a definite positive correlation between the height of the F_2 parents and the means of the F_3 cultures derived therefrom. A distinct segregation occurred in the formation of the gametes of the F_1 plants whereby the F_2 plants were different genetically and exhibited these differences in the means of their offspring, thus giving rise, not to one race, but to a number of distinct races. The theoretically expected greater variability of the F_2 and F_3 cultures are simply here suppressed, but in the macaroni—bread wheat crosses where this suppression factor was ineffective in masking the variability due to heterozygosis the variability of the F_2 and F_3 cultures in all cases averaged markedly above that of the pure-line parents.

In the F_3 of all crosses, cultures were secured having the parental types both as regards average height and variability. In the bread wheat crosses the average variability of the F_3 cultures was slightly larger than that of the F_2 cultures in both cases. This is in accordance with the circumstance that in both, the average height of the F_2 cultures was markedly greater than that of the F_3 cultures and thus called into more active effect the variability-suppressing factor already shown to influence the taller cultures. In the macaroni—bread wheat crosses, on the other hand, the average height of the F_2 was greater than that of the F_3 in one case and less in the other, but still the average variability of the F_2 cultures was markedly above that of the F_3 cultures in both cases. This is in harmony with the fact pointed out above that the variability-suppressing factor visible in all of the crosses was not sufficient to mask the influence of heterozygosity in macaroni—bread wheat hybrids.

Finally we may conclude that all of the facts observed in the study of the inheritance of height in the wheat crosses here considered are in harmony with the hypothesis of the segregation of a number of simple Mendelian unit characters and that there is present some factor (as yet unknown) which suppresses variability in the taller cultures of both pure lines and hybrids and that this factor is sometimes able to completely mask the variability which would normally be produced by heterozygosity.

WIDTH OF LEAF

In the following study of the inheritance of width of leaf in wheat hybrids, all measurements are given in millimeters. Averages are therefore given to the nearest millimeter.

Macaroni (No. 1) × Sonora (No. 35)

No pure No. 35 was available for comparison in 1914. The data with reference to the pure No. 1 and the F_1 hybrid plants are given in table 51.

TABLE 51

Width of leaf in millimeters (1 × 35) F_1, 1914.

	Number of plants	Distribution of individuals															Average	Coefficient of variation
		13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		
Pure No. 1	151	2	1	1	3	11	11	19	25	24	32	5	10	3	3	1	20	13
(1 × 35) F_1	39					2	1		4	4	8	9	9	1	1		22	9

We will here pause only to notice that both the range and variability of the pure No. 1 were greater than for the hybrid. The average leaf width for the hybrid was greater than for the pure No. 1, but since the No. 1 is here the more narrow-leafed parent we have as yet no indication as to whether or not we are dealing with imperfect dominance or hybrid vigor.

In 1915 there were available for comparison 4 cultures of No. 35, 9 cultures of pure No. 1 and 37 cultures of the (1 × 35) F_2. A summary of these data is presented in table 52.

TABLE 52

Width of leaf in (1 × 35) F_2, 1915.

	Number of head rows	Total number of plants	Average width of leaf	Coefficient of variation of the population	Average C. V. of cultures
Pure No. 1	9	651	17	13.0	10.3
(1 × 35) F_2	37	2537	15	30.2	29.3
Pure No. 35	4	169	20	13.5	13.0

Distribution of coefficients of variation

	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 20	31 32	33 34	35 36
Pure No. 1	1	5	1	1	1										
(1 × 35) F_2									2	6	6	9	8	5	1
Pure No. 35	1			1	2										

The average of the hybrids is below that of either parent. The standard deviations of the populations are greater than the averages of the standard deviations of the separate cultures making them up, and the variability of the hybrids is much greater than that of the pure cultures. All hybrid cultures were more variable than the most variable pure culture.

Table 53 gives the distribution of the several populations and the distribution of the means of the cultures.

Studying these distributions we note that there were 16 hybrid plants having leaves wider than the widest individual of the widest-leaved parent, but there was no hybrid culture averaging as wide as the most narrow average for Sonora, the wider-leaved parent. On the other hand more than half of the hybrid cultures averaged lower than the lowest average of any macaroni head-row and there were 121 hybrid plants having more-narrow leaves than the narrowest-leaved individual of the macaroni parent.

TABLE 53

Width of leaf in millimeters in (1 × 35) F_2, 1915.

	Distribution of widths in individuals																												Distribution of means of cultures							
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	14	15	16	17	18	19	20	21
Pure No. 1						2	1	2	1	2	6	28	62	75	117	130	107	78	26	11	3										4	1	2	2		
(1 × 35) F_2	3	11	25	46	36	63	93	119	85	198	190	193	260	229	174	190	146	171	103	69	40	39	29	8	9	4	2	1	3	22	11	1				
Pure No. 35							1			1	1	4	2	6	16	13	19	32	25	24	13	6	4	2										1	2	1

TABLE 54

Width of leaf in millimeters (1 × 35) F_2, 1915.

Width of parent in 1914	Number of cultures	Average width in 1915	Distribution of leaf widths in individuals																										
			3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
17	1	17		1	1					1	2			3	2	4	+O 3	3	3	6	2	4		1	1				
18	1	16			2		2		1	1	3	6	6	8	3	O 11	2	+ 4	5	2	2	3	2	1	1				
20	4	15		3	1	3	3	8	7	7	8	19	19	19	O 27	24	20	23	16	+ 12	8	3	4	5	2				
21	4	15		1	1	8	5	8	8	13	8	16	21	15	O 31	17	21	15	10	24	+ 11	6	4	3	2	5	3	1	1
22	8	15		4	6	9	6	15	27	32	22	55	43	49	O 68	54	36	41	29	41	16	+ 21	9	9	2	1	1	1	
23	8	15		4	8	12	13	12	18	27	19	44	46	49	O 58	54	33	48	31	37	30	13	+ 10	9	9	2	2		
24	9	16	1	2	4	11	6	17	28	23	18	48	45	42	55	O 53	46	47	44	40	29	16	9	+ 10	12		3		1
25	1	15				1		1	3	7	3	4	5	3	O 8	7	4	5	3	6	3	2			+			1	
26	1	15			2	1	1	2		5	4	6	4	6	O 9	5	9	4	5	3	2	1	2	1		+			

Referring to table 51 it will be observed that there was considerable variation in the width of leaf of the F_1 plants. Table 54 groups the 1915 F_2 plants in accordance with the leaf width of their F_1 parents in 1914.

A glance at this table is sufficient to show that there is no correlation whatever between the parental leaf width in 1914 and the average leaf width of the offspring in 1915. We may therefore conclude that all of the variation observed in the F_1 plants was nutritional and that they were all equivalent genetically so far as the factors governing width of leaf were concerned.

From these F_2 hybrids 230 selections were made which gave rise to a like number of F_3 hybrid cultures in 1916. For comparison with these there were available seven head-rows of No. 1 and five head-rows of No. 35. The selected F_2 plants used as parents ranged in width of leaf from 10 to 35 mm. The very wide-leaved individual was very striking in appearance and was nearly sterile. Table 55 gives a first summary of the results in 1916.

TABLE 55

Width of leaf in millimeters in (1 × 35) F_3, 1916.

Class	Number of cultures	Number of individuals	Average width of leaf	Coefficient of variation in the population	Average coefficient of variation of separate cultures
Pure No. 1....	7	344	16	12.0	10.1
(1 × 35) F_3...	230	10123	15	24.9	20.9
Pure No. 35...	5	246	17	15.2	14.0

Distribution of coefficients of variation

Class	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54
Pure No. 1.......	5	1	1																				
(1 × 35) F_3.....	1	3	24	35	31	42	29	11	17	5	11	5	7	1	3	3	1						1
Pure No. 35......			3	2																			

The average for the hybrids is less than either of the parents; in every case the coefficient of variation of the population is greater than the average for the pure cultures of the same class and the coefficient of variation for the hybrids is greater than for either parent. The coefficient of variation both for population and average of cultures among the hybrids was lower in 1916 than in 1915. This was also true of the pure

TABLE 56

Width of leaf in millimeters in (1 × 35) F_3, 1916.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Pure No. 1..											14	24	47	53	78	57	40	21	9		1									
(1 × 35) F_3..	4	27	41	64	53	151	161	255	467	642	1076	904	1208	1074	1151	755	751	383	370	217	196	75	64	15	12	4	2		1	1
Pure No. 35..									1		4	10	24	35	48	27	30	18	21	10	16	1	1							

Distribution of means of cultures

Pure No. 1..													1	1	4	1														
(1 × 35) F_3..							**2**		2	15	22	30	45	48	27	18	13	5	1	2										
Pure No. 35..															2	1	2													

cultures, and therefore may be in part environic. One thing, however, remains to indicate progressive increase in homozygosity among the hybrids. This is the much greater difference in the coefficient of variation of population and average of cultures, which was apparent in 1916.

Table 56 shows the distribution of the populations of pure cultures and hybrids of this cross in 1916.

The hybrid population shows a distribution far beyond both extremes of the parents. This is also true of the means of cultures. Part of this greater distribution is of course due to the normal extension of the curve from the much larger number of hybrids grown. That the curve of variation is more flat, however, is shown by differences in the shapes of the curves of variation which are rendered comparable by reducing each group class to a percentage of the total number in the population and disregarding all percentages less than one-half of one percent and expressing all percentages to the nearest integer (see table 57).

TABLE 57

Width of leaf in millimeters in (1 × 3) F_3, 1916.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pure No. 1								4	7	14	15	23	17	12	6	3					
(1 × 35) F_3	1	1	1	2	2	4	6	11	9	12	11	11	8	7	4	4	2	2	1	1	
Pure No. 35								2	4	10	14	20	11	12	7	9	4	7			

When reduced to equal areas the polygon of the F_3 hybrid distribution is thus seen to be limited by a curve much more flat and with more extended limits than either of the parent races. This indicates that the extension of the range of variations of the F_3 hybrids over the parental races is genetic. This is further shown in table 58 where F_3 cultures are thrown into groups or populations in accordance with the leaf width of the selected F_2 parental plants.

Though somewhat erratic at the extremes, these results show a very definite genetic segregation of leaf width in the F_2 as exhibited by the means of their offspring. The distribution of the means of the cultures in each of these groups is shown in table 59.

TABLE 58

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of F_3 individuals grouped according to the leaf width of the F_2 parents.

Number of cultures	Leaf width of parent	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	35
3	10		3	2	3	2	8	8	10	+ 18	O 20	16	6	11	2	3	2	2	1	1												
2	11						1		3	10	+ 4	12	O 7	6	5	6	1	3						1								
4	12		4	3	3		7	3	16	14	23	O + 26	31	26	22	9	3				1											
14	13	1	9	10	14	10	15	13	32	44	79	O 96	+ 62	84	62	47	21	13	3	5	3											
10	14		1	1	2	2	3	6	11	30	51	84	O 60	+ 68	38	46	28	11	3	2												
23	15		1	5	3	4	16	24	34	79	87	113	118	O 125	+ 104	114	75	49	24	17	16	19	7	9	1	1	1					
19	16	1	1	3	6	4	14	14	33	36	51	105	98	O 107	88	+ 101	66	48	34	20	23	6	3	1	1							
24	17	1		7	11	10	24	19	31	53	92	127	91	O 130	118	114	+ 73	66	27	23	8	17	2	2								
28	18		8	2	6	7	17	24	16	57	81	157	119	O 172	144	135	79	+ 85	33	43	20	15	3	3			1	1				
12	19			1	4	5	8	5	12	20	23	69	55	O 54	73	78	40	41	+ 17	20	8	3	1	1								
32	20		2	1	2	3	10	12	24	36	54	119	101	176	O 167	181	132	153	82	+ 67	30	34	15	8		3	1				1	
22	21			2	1	2	15	10	11	28	33	54	65	107	112	O 123	94	96	57	58	+ 30	23	8	6	1	2						
13	22	1	3	3	3	1	4	4	9	14	15	27	39	66	53	O 67	38	54	30	39	23	+ 23	15	10	7	3		1				
4	23							2	1	5	2	17	10	8	14	22	O 24	34	15	9	8	3	+ 5	2	2							
8	24		2	1	4	2	5	15	3	13	10	23	14	31	O 36	61	34	35	15	13	25	9	3	+ 4								
7	25		3		2	1	4	2	5	6	6	17	15	19	23	32	O 37	45	25	32	12	21	5	5	+	1				1		
1	26									1			1	1	1	1	2	2	6	O 9	3	12	4	6	1	+						
1	27								2	2	7	8	9	O 4	4	1	1	2	4		2						+					
2	28								2	1	1	5	2	12	5	7	2	O 6	5	8	2	9	4	3		2		+				
1	35										2	1		1	3	3	3	6	O 2	4	3	2		3	2		1					+

+, leaf width of parent; **O**, mean of F_3 groups.

TABLE 59

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of means of F_3 cultures grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental leaf width in 1915	Mean of group in 1916	8	9	10	11	12	13	14	15	16	17	18	19	20	21
3	10	11	1		1			1								
2	11	13						2								
4	12	12				2	1	1								
14	13	12	1		1	1	6	2	2	1						
10	14	13				1	2	4	3							
23	15	14				3	3	3	6	4	2	1		1		
19	16	14				2	2	3	2	5	4	1				
24	17	14				4	1	5	4	7	2	1				
28	18	14					3	3	14	3	1	3	1			
12	19	14					2		4	3	3					
32	20	15				1	2	3	2	9	7	4	3			1
22	21	16						1	5	5	3	5	3			
13	22	16				1		1		4	2	1	3			1
4	23	17							1		1		2			
8	24	15						1	1	4		1	1			
7	25	17								2	2	1		2		
1	26	20													1	
1	27	14							1							
2	28	18								1				1		
1	35	19												1		

This table exhibits even more plainly than the preceding the correlation between the parental leaf width and the mean leaf width of the offspring.

In order to determine whether the offspring of narrow-, medium-, and wide-leaved F_2 mother plants exhibited any definite difference in their variability table 60 was constructed.

There is shown here an irregular but still evident diminution of variability among the offspring of the wider-leaved parents.

It may be suggested, moreover, that since width of leaf is highly influenced by the environment and there is therefore a strong regression of the mean of the offspring of extreme variants toward the general mean of the population, we may get a better idea of the segregation of leaf-width factors, by grouping the F_3 cultures according to their own means and then calculating the variability of these groups and observing the distribution of the parents which gave rise to them. We thus measure backward, determining the range of environic modification of individuals which are able to give rise to genetically equivalent progenies.

Table 60

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of coefficients of variation of F_3 cultures grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental leaf width	Average C. V. for group	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54	55 56
3	10	26.0							1	1					1											
2	11	23.0						1			1															
4	12	24.0		1						1			1	1												
14	13	25.6			1	1	2		4			1	2		1		1								1	
10	14	18.5				3	4	1	1		1															
23	15	20.3		1	1	2	3	7	5	1	1	1			1											
19	16	20.6			1	4	2	5	2	2	1		1					1								
24	17	22.0			4	4		1	3	3	4		1	2	2											
28	18	21.5			4	2	2	8	4	2	1		3					1	1							
12	19	20.1			2	1	3	2	1		2			1												
32	20	18.3		1	2	9	10	3	1	1	4	1														
22	21	19.9	1		4	4	1	7			1	1			1	1		1								
13	22	21.5			3	1	2	2	1			1	1		1		1									
4	23	17.8			1	1		1	1																	
8	24	22.9					1	2	2		1		2													
7	25	22.1			1	1	1	1	1					1			1									
1	26	15.0				1																				
1	27	22.0							1																	
2	28	18.5				1			1																	
1	35	20.0						1																		

Table 61

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of F_3 individuals grouped according to the means of the F_3 cultures. **O** = *mean of group.*

Number of cultures	Mean width	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
2	8	1	7	4	4	2	9	**O** 6	5	3	3	2	2	1			2		1												
2	10		1	6	6	2	2	3	7	**O** 15	20	15	3	5	1	4	1														
15	11	3	7	9	13	3	31	36	55	85	**O** 95	123	44	50	43	14	8	3	1	1											
22	12		6	5	9	8	25	28	73	83	158	**O** 165	129	115	75	48	25	15	4	4	3										
30	13		8	2	7	10	21	33	39	98	114	240	**O** 152	182	129	121	34	38	16	13	6	5		1							
45	14		3	6	10	13	34	30	38	94	130	256	248	**O** 327	254	232	135	110	44	31	16	8	4	3				1			
48	15		4	4	12	12	21	17	21	53	83	166	194	197	**O** 277	329	185	177	87	64	42	27	9	5	2	1				1	
27	16		1	5	3	3	5	12	11	18	21	59	72	126	155	**O** 213	168	160	73	61	37	27	8	2	1						
18	17						2	1	2	12	16	34	36	71	70	120	**O** 110	134	52	77	40	36	11	5	2	1					
12	18						1	2	2	4	6	6	11	28	51	49	50	**O** 76	60	64	37	32	15	9	4	4	1	1			1
6	19							2	2	1	4	6	10	5	14	20	27	30	**O** 28	35	20	37	10	19	2	3	2				
1	20									1			1	1	1	1	2	2	6	**O** 9	3	12	4	6	1						
2	21										1		1		4		8	5	9	10	**O** 11	11	13	12	3	3	1				

TABLE 62

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of F_2 parents grouped according to the means of the F_3 cultures.

Number of cultures	Mean of F_3 cultures	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
2	8			1			1																						
2	10			1			1																						
15	11					2	1	1	3	2	4			1		1													
22	12					1	6	2	3	2	1	3	2	2															
30	13			1	2	1	2	4	3	3	5	3		3	1	1		1											
45	14						2	3	6	2	4	14	4	2	5		1	1			1								
48	15						1		4	5	7	3	3	9	5	4		4	2			1							
27	16								2	4	2	1	3	7	3	2	1		2										
18	17								1	1	1	3		4	5	1		1	1										
12	18											1		3	3	3	2												
6	19								1									1	2			1							1
1	20																			1									
2	21													1		1													

TABLE 63

Width of leaf in millimeters in (1 × 35) F_3, 1916. Distribution of coefficients of variation of F_3 cultures grouped according to the means of the F_3 cultures.

Number of cultures	Means of F_3 cultures	Average C.V. of F_3	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	39 40	41 42	43 44	45 46	47 48	49 50	51 52	53 54
2	8	43.5													1										1
2	10	30.5								1							1								
15	11	25.6		1			2	2		2	2		1	2	1		1	1							
22	12	22.9				1	5	2	3	2	4	2	2		1										
30	13	22.2		1	1	4	5	4	5	2	2		3		1			1	1						
45	14	21.4			3	6	3	10	10	2	4	1	2	1	2			1							
48	15	20.8			10	6	8	8	4	1	3	1	3	2		1	1								
27	16	18.4	1		4	6	4	8			2	1			1										
18	17	17.4		1	2	5	2	4	3	1															
12	18	17.4			2	4	1	3	2																
6	19	18.6			1	1	1	1	2																
1	20	15.0				1																			
2	21	14.5			1	1																			

It is interesting to note in table 61 that practically all of the curves of group distribution are skew, i.e., they slope more abruptly toward the upper limit.

While the parental groups in table 62 exhibit considerable range, a comparison of tables 62 and 56 will show that this is not wider than occurs in the nutritional variations of a pure line.

Algerian macaroni (No. 1) × Algerian red bread (No. 3)

For this cross the F_1, grown in 1914, had too few individuals to give significant results. As a matter of record, however, the results obtained are given in table 64.

TABLE 64

Width of leaf in millimeters in (1 × 3) F_1, 1914.

Class	Number of plants	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	Average
Pure No. 1....	151	2	1	1	3	11	11	19	25	24	32	5	10	3	3	1	20
(1 × 3) F_1....	5	1	1		1				1			1					21
Pure No. 3....	3						1		1			1					20

From this material there were grown in 1915, 9 plant rows of No. 1, six plant rows (two being taken from one of the mother plants) of 1 × 3 and one plant row of pure No. 3.

Table 65 summarizes the results obtained.

TABLE 65

Width of leaf in millimeters in (1 × 3) F_2, 1915.

Class	Number of cultures	Number of individuals	Average width	Coefficient of variation of the population	Average C.V. of separate cultures
Pure No. 1....	9	651	17	13.0	10.3
(1 × 3) F_2....	6	406	14	27.6	25.8
Pure No. 3....	1	42	16	11.2	11.2

Distribution of coefficients of variation.

Class	7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30
Pure No. 1..............	1	5	1	1	1							
(1 × 3) F_2.............								1		3	1	1
Pure No. 3..............			1									

The average leaf width of the hybrids is below that of either parent. The coefficient of variation of the populations are greater than the averages of the separate cultures and the variation of the hybrids is greater than that of the most variable pure culture.

Table 66 gives the distribution of the individuals of the several populations and the distribution of the means of the separate cultures.

Table 66

Width of leaf in millimeters in (1 × 3) F_2, 1915.

Class	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Pure No. 1					2	1	2	1	2	6	28	62	75	117	130	107	78	26	11	3			
(1 × 3) F_2	2	1	3	7	15	13	20	30	30	33	37	49	44	32	30	17	19	9	6	4	1	3	1
Pure No. 3									1	1	2	7	11	8	9	1	1	1					

Distribution of means of cultures.

Class	13	14	15	16	17	18	19
Pure No. 1				4	1	2	2
(1 × 3) F_2	3		2	1			
Pure No. 3				1			

We first note that, notwithstanding the fact that there were nearly 200 more individuals in the population of No. 1 than in the hybrid population, still the range of leaf width among the hybrids extended markedly beyond the range of pure No. 1 in both directions, and this in spite of the fact that no single hybrid culture averaged greater than the narrowest-leaved culture of pure No. 1.

Now analyzing the relation of the F_2 hybrid cultures to their (F_1) parents we find that there is a possibility that there were some differences in the genetic constitution of the F_1 plants inasmuch as the narrow-leaved parents produced offspring with a lower average leaf width than did the wider-leaved parents. This is shown in table 67.

TABLE 67

Width of leaf in millimeters in (1×3) F_2, *1915.*

Plant No. 1914	Width of leaf, 1914	Average width of leaf of offspring, 1915	Distribution of leaf width in offspring, 1915																						
			4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
33-1	13	13	1			3	5	4	3	9	5	+O 6	3	7	8	4	3	1							
33-2	14	13				1	1	1	4	1	1	O 2	+ 4	1	2		1	1							
49-7	16	13			1	1	3	4	3	4	7	O 3	9	9	+ 3	1	3		1			1			1
32-1	20	15					4	2	2	5	4	4	7	O 9	7	8	7	3	+ 3		2	1	1	2	
52-2 (2nd head-row)	23	15	1	1	2	1	1	2	2	6	8	8	7	O 15	8	9	7	5	8	5	1	+ 1			
52-5 (1st head-row)	23	16				1	1		6	5	5	10	7	8	O 16	10	9	7	7	4	3	+ 1		1	

Now grouping these cultures according to their mean in 1915, table 68 gives the average and distribution of the coefficients of variation of these groups.

TABLE 68

Width of leaf in millimeters in (1 × 3) F_2, 1915.

Number of cultures	Average leaf width of culture in 1915	Average coefficient of variation	Distribution of C.V. of cultures				
			21 22	23 24	25 26	27 28	29 30
3	13	26.7			2		1
2	15	26.5			1	1	
1	16	22.0	1				

The coefficients of variation here show a strong decline in variability in the wider-leaved cultures.

In 1916 there were available for comparison 7 cultures of pure No. 1, 5 of pure No. 3 and 57 cultures of the F_3 hybrid 1 × 3. Table 69 summarizes the results obtained.

TABLE 69

Width of leaf in millimeters in (1 × 3) F_3, 1916.

Class	Number of cultures	Total number of plants	Average leaf width	Coefficient of variation of the population	Average C. V. of separate cultures
Pure No. 1	7	344	16	12.0	10.1
(1 × 3) F_3 (33-1)	9	406	12	21.3	18.1
(1 × 3) F_3 (49-7)	8	365	13	24.1	21.4
(1 × 3) F_3 (32-1)	40	1763	13	26.5	20.9
(1 × 3) F_3 (Total)	57	2534	13	25.3	20.5
Pure No. 3.......	5	243	14	12.2	11.4

TABLE 70

Width of leaf in millimeters in (1 × 3) F_3, 1916.

Class	Distribution of individuals																									
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Pure No. 1.........											14	24	47	53	78	57	40	21	9		1					
(1 × 3) F_3 (33-1)..		3		3	4	12	9	22	48	71	68	69	41	21	21	7	2	2	2							
(1 × 3) F_3 (49-7)..		4	4		2	6	6	17	23	66	38	47	38	37	30	27	9	7	4		1					
(1 × 3) F_3 (32-1)..	2	7	5	14	18	66	46	83	77	187	176	205	178	235	161	129	80	39	35	12	7					1
(1 × 3) F_3 (total)	2	14	9	17	24	84	61	122	148	324	282	321	257	293	212	163	91	48	41	12	8					1
Pure No. 3........								3	3	7	23	30	66	54	44	7	4	2								

Distribution of means

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Pure No. 1..............													1	1	4	1	
(1 × 3) F_3 (33-1).......									1	3	3		1	1			
(1 × 3) F_3 (49-7).......									1		2	3	1		1		
(1 × 3) F_3 (32-1).......								1	2	5	8	7	8	2	3	2	2
(1 × 3) F_3 (total)								1	4	8	13	10	10	3	4	2	2
Pure No. 3..............												1	3	1			

Distribution of coefficients of variation

	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38
Pure No. 1..............	5	1	1												
(1 × 3) F_3 (33-1).......	1	2	1		1		1	2				1			
(1 × 3) F_3 (49-7).......				1	3	1		2							1
(1 × 3) F_3 (32-1).......	2	9	12	6	3	2			2		1	1	1		1
(1 × 3) F_3 (totals)......	3	11	13	7	7	3	1	4	2		1	2	1		2
Pure No. 3..............	3	1		1											

A study of tables 69 and 70 will show that it is not worth while to treat separately the 1 × 3 hybrids originating from the different original pollinations, since their means and distributions were practically equal. They will therefore be treated together hereafter.

In table 69 we observed that the average leaf width of the hybrids was below both the parents. The coefficient of variation was, however, as usual, markedly higher for the hybrids. From table 70 we note that the hybrid range in leaf width extends from a single case markedly above both parents to plants with almost filiform leaves. The different hybrid groups show practically the same behavior. Whereas 3 hybrid cultures showed as little variability (coefficients of variation) as the least variable parental culture, more than half were more variable than the most variable parental culture.

There were 8 hybrid cultures whose mean leaf widths were as great or greater than the mean for the wider-leaved parent. It is, moreover, interesting to note that from the hybrids of parents differing, on the average, only 2 mm in leaf width, there have segregated out races whose average leaf width differs by 9 mm. The fact that a large part of the differences in leaf width observed in the F_2 generation were genetic, is shown in table 70 which exhibits the F_3 cultures grouped according to their parental leaf widths.

There is a distinct correlation between parental leaf width and the mean of the offspring. Whereas the means show a marked range of distribution in each of the parental groups, this range is never wider

TABLE 71

Width of leaf in millimeters in (1 × 3) F_3, 1916.

F_3 individual plants grouped according to the heights of F_2 parents

Number of cultures	Leaf width of parent	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
2	8	1	3		4	7	9	+ 4	O 11	4	8	5	5	2			1		1								
1	9						6	3	+ 6	5	O 4	4	4	4	2	1											
1	11									4	+ 17	O 10	7	4		2		1									
4	13					3	3	5	10	7	38	O 31	+ 34	12	20	7	4	2	1	2		1					
5	14			1	2	3	4	5	13	7	36	36	O 33	+ 33	23	20	9	5		1							
11	15		6	6	2	7	22	14	23	35	74	O 66	71	44	+ 50	32	26	8	4								
12	16	1	1	1	4		18	14	35	35	72	55	O 59	70	76	+ 54	39	12	3	3		1					
6	17		1			1	8	3	6	14	29	28	O 43	32	46	18	+ 15	10		1	1						
6	18		2		1	1	8	8	13	25	38	36	O 34	29	25	19	17	+ 4	5	3							
2	19											1	11	9	24	O 19	15	7	+ 5	3	1						
3	20				4	2	4	5	3	5	4	6	6	9	O 6	6	9	15	17	14	+ 5	4					1
2	22		1	1			1		1	5	2	2	3	6	10	O 15	12	14	9	6	4	+ 1					
1	23						1		1	2	2	2	8	3	5	O 7	4	5	1	4		1	+				
1	25												3		6	12	O 12	8	2	4	1				+		

Means of cultures, 1916

Number of cultures	Mean of group 1916	9	10	11	12	13	14	15	16	17	18
2	9	1	1								
1	11			1							
1	12				1						
4	12			1	2		1				
5	13				2	2	1				
11	12		1	2	3	4	1				
12	13		1	2	1	3	3	1	1		
6	13				3		2	1			
6	13			2	1	1	1	1			
2	16								2		
3	15			1						1	1
2	16						1				1
1	16								1		
1	17									1	

+ = leaf width of parent O = average leaf width of offspring than the fluctuations of the individuals of a pure line. The coefficients of variation (see table 72) show a distinct though irregular decline toward the wider-leaved parental groups.

TABLE 72

Width of leaf in millimeters in (1 × 3) F_3, 1916. Coefficients of variation of F_3 cultures grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental leaf width	9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	Average C. V. of group
2	8													1		1	35.5
1	9								1								24.0
1	11			1													14.0
4	13				2	1					1						18.8
5	14				1	1	1	1		1							20.0
11	15	1				1	2		2	3			1			1	23.5
12	16	1	1	1	1	1	2	1	3			1					19.0
6	17			1	1	1	1			1	1						19.8
6	18	1	1			1	1					1	1				19.7
2	19		1	1													12.0
3	20	1								1					1		23.3
2	22	1									1						18.5
1	23						1										19.0
1	25	1															10.0

This study of variation is made much more distinct by regrouping the F_3 cultures according to their own means in 1916, as in table 73.

TABLE 73

Width of leaf in millimeters in (1 × 3) F_3, 1916. Distribution of F_3 individuals grouped according to the means of the F_3 cultures.

Number of cultures	Mean of culture	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	9	1	3		3	4	2	3	O 10	2	7	5	3														
4	10				1	8	15	9	19	O 27	40	13	11	4	2		1		2								
8	11		4		8	4	30	24	39	42	O 51	37	34	34	17	7	4	1	2			1					
13	12		4	5	1	6	18	12	29	45	130	O 100	93	40	46	20	12	6	3	1	1	1					
10	13	1	1	2	1	1	12	7	19	20	61	63	O 59	57	53	49	29	10	4	2		1					
10	14		2	2	3	1	6	4	6	10	41	38	71	O 63	84	57	48	18	3	5	2				1		
3	15									2	1	5	25	28	O 33	12	19	6	1	1							
4	16						1		1	2	2	3	20	20	46	O 35	27	15	7	8	1	1					
2	17							2		3		2	4	3	7	13	O 15	12	11	6	3	2					1
2	18								1					4	6	13	9	O 23	15	18	4	2					

TABLE 74

Width of leaf in millimeters in (1 × 3) F_3, 1916.

Number of cultures	Mean of F_3 cultures	Distribution of F_2 parents																	
		8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	9	1																	
4	10	1					1		1	1									
8	11		1						2	2		2		1					
13	12				1		2	2	3	1	3	1							
10	13							2	4	3		1							
10	14						1	1	1	3	2	1			1				
3	15									1	1	1							
4	16									1			2				1		
2	17													1					1
2	18													1		1			

Number of cultures	Mean of F_3 cultures	Coefficients of variation of F_3 cultures grouped according to the means of the F_3 cultures															Average C V. of group
		9 10	11 12	13 14	15 16	17 18	19 20	21 22	23 24	25 26	27 28	29 30	31 32	33 34	35 36	37 38	
1	9													1			33.0
4	10					1	1		1							1	29.8
8	11						1	1	2	1		1	1		1		26.1
13	12	1	1	2	1		2			3	2					1	21.1
10	13				1	3	1		3	1		1					21.2
10	14				3	2	2	1			1		1				19.9
3	15	1	1	1													11.7
4	16	1	1	1			1										13.0
2	17	1								1							17.5
2	18	2															10.0

A study of table 74 shows very plainly that there is a distinct and marked segregation of leaf-width factors in the F_2 which gives rise to F_3 cultures whose averages reach or exceed the parental means in both directions. As measured by the coefficient of variation, the variability of the hybrid cultures clearly decreased as the average leaf width increased. Does this mean that the wide-leaved cultures are more nearly homozygous (on the average) than the narrow-leaved segregates? If this were true it would follow that the factors tending to increase leaf width are recessive and that the genetically narrow-leaved plants were so on account of dominant inhibitors. This idea is, however, not supported by the fact that the leaf width of the F_1 plants (see tables 51 and 54) which had the maximum of heterozygosity, has leaf widths averaging as high or higher than either parent. If leaf-width inhibiting factors are dominant the maximum narrowness should occur in the F_1 plants. If on the other hand these factors exhibited imperfect dominance one would expect the medium races to have a higher variability than those approaching the extremes. Such, however, is not the case. We must therefore seek elsewhere for the explanation of this decrease in variability as the average leaf width of the cultures increases.

Inheritance of leaf width in bread wheat crosses, Sonora (No. 35) × red Algerian bread wheat (No. 3)

As previously mentioned no pure No. 35 was available for comparison with the F_1 generation in 1914. A comparison of the leaf width of pure No. 3 with the (3 × 35) F_1 hybrid plants is given in table 75.

TABLE 75

Width of leaf in millimeters in (3 × 35) F_1, 1914.

	Number of plants	18	19	20	21	22	23	24	25	26	Average leaf width
Pure No. 3	3	1		1			1				20
(3 × 35) F_1	18			4	2	4	3	4		1	22

While the numbers here given are too small to form the basis of definite conclusions, they at least indicate that the F_1 hybrids have leaves as wide as, or wider than, the parents.

These 18 F_1 plants gave rise to 18 plant rows of F_2 hybrids in 1915 and there were available for comparison with them 1 pure culture of No. 3, and 4 pure cultures of No. 35. The results may be summarized as in table 76.

TABLE 76

Width of leaf in millimeters in (3 × 35) F_2, 1915

Class	Number of cultures	Number of individuals	Average leaf width	Coefficient of variation of the population	Average C. V. of cultures	Distribution of C.V.				
						7 8	9 10	11 12	13 14	15 16
Pure No. 3	1	42	16	11.2	11.2			1		
(3 × 35) F_2	18	1620	18	13.9	13.4		1	2	12	2
Pure No. 35	4	169	20	13.6	13.0	1			1	2

The mean leaf width of the hybrids is intermediate between the parents. The average variability of the hybrids is only slightly above that of the pure cultures.

The distribution of the populations and means for this generation are given in table 77.

TABLE 77

Width of leaf in millimeters in (3 × 35) F_2, 1915.

	Distribution of individuals																					Distribution of means of culture					
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	16	17	18	19	20	21
Pure No. 3							1	1	2	7	11	8	9	1	1	1						1					
(3 × 35) F_2	1		3	2	3		7	17	74	113	191	256	259	225	213	127	70	31	22	5			2	14	2		
Pure No. 35				1			1	1	4	2	6	16	13	19	32	25	24	13	6	4	2				1	2	1

It is interesting here to note that the distribution of the means of the hybrids did not reach the extremes of the parents and that although the number of hybrids was many times that of No. 35, the range of variation of the hybrids toward wide leaves did not exceed that of its broad-leaved parent.

For the F_3 of this cross there were available 5 pure cultures of each of Nos. 3 and 35, and 80 plant rows of (3 × 35) F_3. The hybrid F_2 plants chosen for planting in the fall of 1915 included 11 of the 19 classes through which the population of F_2 was distributed. A first tabulation of the results follows:

TABLE 78

Width of leaf in (3 × 35) F_3, 1916.

Class	Number of cultures	Number of individuals	Average leaf width	Coefficient of variation of the population	Average coefficient of variation	Distribution of C. V.				
						9 10	11 12	13 14	15 16	17 18
Pure No. 3	5	243	14	12.2	11.4	3	1		1	
(3 × 35) F_3	80	3852	17	15.5	12.9	6	29	28	11	6
Pure No. 35	5	246	17	15.2	13.8			3	2	

One is surprised to find here the mean of the F_3 hybrids as high as the broader-leaved parent and the average coefficient of variation of the separate cultures of hybrids lower than that for the Sonora (No. 35).

The distribution of the individuals in the populations of hybrids and pure cultures is shown in table 79.

TABLE 79

Width of leaf in millimeters in (3 × 35) F_3, 1916.

	Distribution of individuals																				Distribution of means of cultures							
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	13	14	15	16	17	18	19	20
Pure No. 3				3	3	7	23	30	66	54	44	7	4	2							1	3	1					
(3 × 35) F_3	3	3	4	1	7	52	97	223	303	583	554	589	392	392	324	207	69	33	14	2		4	13	20	15	20	8	2
Pure No. 35					1		4	10	24	35	48	27	30	18	21	10	16	1	1					2	1	2		

It is particularly interesting to note here that there were ten cultures with means higher than the highest mean for the wide-leaved parent. We have here a suggestion that if there be some force limiting variability in the wider-leaved races it would more strongly affect these wide-leaved hybrid cultures and thus aid in reducing the average variability of the group. In this connection it may be remarked that the average coefficient of variability of these ten cultures is 11.4 percent, a figure well below the average coefficient of variability for pure No. 35, which is 13.8 percent.

It is also interesting to note that whereas in the macaroni—bread wheat crosses many cultures were grown, the average leaf widths of which were below that of the narrow-leaved parent, here we have no cultures lower, but there are eight above the wider-leaved parent.

The segregation and recombination of characters by which these markedly different races were isolated is shown in table 82 where the F_3 individuals are grouped according to the mean leaf width of the F_3 cultures.

TABLE 80

Width of leaf in millimeters in (3 × 35) F_3, 1916. Population grouped according to the leaf width of the F_2 parents.

Number of cultures	Parental width in 1915	Distribution of F_3 grouped according to leaf width of F_2 parents																					Average in 1916
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
2	14						3	6	17	+ 22	O 21	16	5	4	2								14.6
2	15	1				1	4	11	10	14	+ O 13	19	12	5	3	1							14.8
9	16		1			2	9	16	56	51	84	+ O 76	61	40	19	13	5	3					15.6
14	17	1		1			14	18	44	70	124	O 124	+ 115	72	47	32	14	2	3				16.1
11	18	1		3	1	1	11	16	30	41	96	65	O 82	+ 46	61	36	26	11	4				16.6
9	19						2	8	20	24	62	64	O 65	54	+ 49	38	32	6	2	2	1		17.2
15	20		1			3	6	18	25	59	102	113	O 104	71	78	+ 69	38	16	7				16.9
7	21							2	9	11	22	29	56	O 39	62	62	+ 29	9	4				18.1
6	22		1					1	6	8	26	21	49	O 33	36	43	36	+ 10	10	10	1		18.4
4	23						2		4		9	17	32	23	O 32	30	26	11	+ 3	2			18.5
1	24						1	1	1	3	14	O 10	8	5	3		1	1		+			16.1

This table shows a regular and nearly uniform correlation between the parental leaf width and the average leaf width of the offspring. The one exception at the wide extreme came from plant No. 21-5-2-1, a plant which stood at the end of the row and was very likely an extreme variant of about the 18 class (see range of this class in table 80).

TABLE 81

Width of leaf in millimeters in (3 × 35) F_3, 1916.

Number of cultures	Leaf width of F_2 parents	Distribution of means of F_3 cultures grouped according to leaf width of F_2 parents							Average coefficient of variation of F_3 cultures	Distribution of coefficients of variation				
		14	15	16	17	18	19	20		9 10	11 12	13 14	15 16	17 18
2	14	1	1						11.5		2			
2	15	1	1						15.5			1		1
9	16	1	3	4	1				13.3	1	2	3	2	1
14	17		4	5	4	1			12.5	2	5	5	1	1
11	18	1	3	1	2	3	1		13.4	1	4	3	1	2
9	19			3	3	2		1	12.6	1	4	3	1	
15	20		1	6	3	4	1		13.7		4	7	3	1
7	21				1	4	2		12.0	1	3	3		
6	22				1	2	2	1	13.2		3		3	
4	23					2	2		12.0		2	2		
1	24			1					13.0			1		

There is an indication of some decline in the coefficient of variation in the wider-leaved groups, but it is too much broken up by irregularities to be of any particular significance.

The study of variability of the F_3 is better made, however, by regrouping the F_3 cultures in accordance with their own means. This is done in table 82.

TABLE 82

Width of leaf in millimeters in (3 × 35) F_3, 1916. Population grouped according to the average leaf width of the F_3 cultures.

Number of cultures	Average leaf width of F_3 cultures	Distribution of leaf widths of individuals																			
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
4	14	1				3	12	19	31	O 36	40	31	15	3	1	1					
13	15			3	1	1	20	28	83	94	O 146	100	82	36	20	10	2				
20	16	1	2			2	14	31	59	94	209	O 170	164	83	70	33	23	8	1		
15	17		1				3	12	27	48	104	126	O 114	93	88	64	25	10	5		
18	18	1		1		1	3	6	21	27	64	95	150	O 118	136	129	80	26	7	1	
8	19									3	17	30	57	50	O 53	72	58	20	10	5	
2	20							1	1	1	3	2	7	9	14	O 15	19	5	10	8	2

O = means of F_3 groups.

Comparing tables 78 and 82 we note that, starting with cultures which differed on an average by 3 mm in leaf width, we have obtained cultures whose means differ by 6 mm.

TABLE 83

Width of leaf in millimeters in (3 × 35) F_3, 1916. F_2 parents of F_3 cultures grouped according to the means of the F_3 cultures.

Number of cultures	Mean of F_3 cultures	Distribution of F_2 parents											Average C. V. of F_3 cultures	Distribution of C.V. of F_3 cultures				
		14	15	16	17	18	19	20	21	22	23	24		9 10	11 12	13 14	15 16	17 18
4	14	1	1	1		1							13.8		2	1		1
13	15	1	1	3	4	3		1					13.4		5	6		2
20	16			4	5	1	3	6				1	13.6	1	5	7	5	2
15	17			1	4	2	3	3	1	1			13.1	2	2	8	3	
18	18				1	3	2	4	4	2	2		12.7	1	9	5	2	1
8	19					1		1	2	2	2		11.2	2	5	1		
2	20						1			1			13.5		1		1	

From table 83 we observe that the range of parents which may give rise to an offspring with a given mean is not greater than that of a pure culture.

When the coefficients of variation are calculated we find an irregular but still quite definite decline toward the wider-leaved cultures as usual (see table 83).

Algerian red bread (No. 3) × early Baart (No. 34)

This cross will be of special interest for comparison with the other crosses inasmuch as the two parents had practically the same width of leaf. The number of plants grown in 1914 are too small to furnish trustworthy averages but as a matter of record they may be given as follows:

TABLE 84

Width of leaf in millimeters in (3 × 34) F_1, 1914.

Class	Number of plants	Average leaf width	Distribution of leaf widths										
			14	15	16	17	18	19	20	21	22	23	24
Pure No. 3	3	19					1		1			1	
(3 × 34) F_1	6	20	1			1			1	3			
Pure No. 34	12	21					1	1	4	3	2		1

TABLE 85

Width of leaf in millimeters in (3 × 34) F_2, 1915.

Class	Leaf width of parent F_1	Average leaf width F_2	Distribution of individuals													Number of plants	C. V.
			10	11	12	13	14	15	16	17	18	19	20	21	22		
Pure No. 3	20	16			1	1	2	7	11	8	9	1	1	1		42	11
(3 × 34) F_2 (44-1)	14	15	1		8	4	28	23	9	10	3	3	2			91	12
(3 × 34) F_2 (44-2)	17	16			2	2	7	16	19	13	18	7	3			81	11
(3 × 34) F_2 (25-1)	20	18					1	5	6	18	22	16	18	5		91	9
(3 × 34) F_2 (28-1)	21	16			1	1	8	18	30	14	18	1				91	9
(3 × 34) F_2 (47-1)	21	18					1	2	5	16	21	25	13	5	1	89	8
(3 × 34) F_2 (47-2)	21	18					1	4	9	8	32	13	13	7	2	89	9
Pure No. 34	18	17			1	2	9	18	13	17	18	10	3	1		92	11
Averages and totals for (3×34) F_2	19	17	1		11	7	46	68	78	79	114	65	49	7	3	532	9*

* Coefficient of variation of hybrid population = 12.

TABLE 86

Width of leaf in millimeters in (3 × 34) F_3, 1916.

Class	Number of cultures	Number of individuals	Average width of leaf	C. V. of population	Average C. V. of cultures	Distribution of C. V.						
						7 8	9 10	11 12	13 14	15 16	17 18	19 20
Pure No. 3	5	243	14	12.2	11.4		3	1		1		
(3 × 34) F_3 (25-1)	50	2387	16	13.3	12.0	1	13	16	13	7		
(3 × 34) F_3 (44-2)	49	2336	15	12.9	11.8	1	11	21	14	1	1	
Pure No. 34	5	243	14	12.6	11.4			5				

These 6 F_1 plants gave rise to 6 plant rows of F_2 hybrids in 1915 and there were available for comparison 1 pure culture of each of Nos. 3 and 34. Since the F_2 cultures differed somewhat in accordance with the leaf width of the F_1 plants, the records will be given in full rather than being summarized as usual (table 85).

Here we have the average of the hybrids less variable than either parent. It should be observed that the one hybrid culture (No. 44-1) which was more variable than either parent had a mean lower than either parent and that the three cultures having means higher than either parent all had coefficients of variation well below either parent. The mean of all of the F_2 was equal to the wider-leaved parent and the total range of the F_2 was practically confined to the limits of the parental range. The means of the F_2 cultures varied on either side of the parental means but in such cases kept their total range inside of the parental range by narrowing their own variability.

In view of these rather marked discrepancies in the means of the F_2 cultures subsequent study is confined to the progenies of but two F_1 plants (44-2 and 25-1) and these are kept separate.

In 1916 there were available for study 5 plant rows of each of the parental cultures, pure No.3 and pure No. 34, selected from these strains of the previous season and for the hybrids 50 selections from the F_2 of 25-1 and 49 selections from the F_2 of 44-2.

Here the means of the hybrids are above the means of either parent but unlike the F_2 the coefficients of variation are slightly above that of the parental cultures. In table 87 we note that some of the hybrid cultures were more and some were less variable than certain of the pure

TABLE 87

Width of leaf in millimeters in (3 × 34) F_3, 1916. Distribution of the populations and means of cultures of hybrids and parents.

	Distribution of population																		
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pure No. 3..........			3	3	7	23	30	66	54	44	7	4	2						
(3 × 34) F_3 (25-1)..				7	24	69	119	327	405	555	297	321	109	98	38	14	3		1
(3 × 34) F_3 (44-2)..	2	1	2	15	61	188	249	447	514	451	178	154	48	20	5	1			
Pure No. 34........			2	6	25	37	34	67	47	16	7	2							
	Distribution of means of cultures																		
Pure No. 3.........							1	3	1										
(3 × 34) F_3 (25-1)..								2	13	19	13	3							
(3 × 34) F_3 (44-2)..							3	13	22	9	2								
Pure No. 34.........						1		4											

cultures. The differences obtained are, however, not large enough to have any especial significance.

In table 87, the most interesting feature is the distribution of the means. Here we have 46, approximately half, of the hybrid cultures with means higher than either of the parents. The same was true in the F_2 cultures (see table 85), As regards height, it will be recalled that the hybrids of this class also averaged as high or higher than the taller parent. The fact that so many races had average leaf widths so strikingly above either parent would suggest recombination with the production of races beyond the extremes of the parent. This, however, is made very doubtful by a study of table 88. There the F_3 cultures are grouped according to the leaf width of the F_2 parents. Moreover, seeds were planted from each of the plants of the F_2 of the populations of the cultures concerned (25-1 and 44-2). If therefore the variations in leaf width of the F_2 plants were partially genetic and partially nutritional (environic) the averages in the F_3 groups should show a correlation with their F_2 parents.

We do not seem to have any correlation whatsoever between the leaf width of the parent and offspring. We may therefore conclude that so far as this character is concerned the F_2 plants were all genetically equivalent and that all differences such as did arise were modifications.

A study of the distribution of the means of the F_3 cultures grouped according to their F_2 parents also confirms the conclusions already drawn that the F_2 plants were all equivalent genetically so far as leaf

Table 88

Width of leaf in millimeters in (3×34) F_3, 1916.

Number of cultures	Parental width F_2 1915	Average leaf width F_3, 1916	Distribution of individuals in F_3 cultures																			Distribution of means of F_3 cultures					
			7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	13	14	15	16	17	18
(25-1)																											
1	14	16						2	1	+ 3	7	O 12	8	12		2									1		
3	15	16				1	1	2	10	18	+ 22	O 24	26	26	8	5	1							1	1	1	
3	16	15					4	3	7	38	O 31	+ 45	9	9	1	1								3			
9	17	16				3	3	19	21	51	62	O 93	+ 63	54	17	23	8	2	1		1			1	6	2	
6	18	16				3	4	3	6	42	45	O 65	31	+ 36	17	16	9	4					1	1	2		2
10	19	16					6	18	25	76	79	O 125	48	68	+ 18	16	6	4					1	4		5	
14	20	16					5	17	38	81	126	O 145	88	90	35	+ 26	13	4	2					2	8	3	1
4	21	16					1	5	11	18	33	O 46	24	26	13	9	+ 1							1	1	2	
(44-2)																											
1	12	13					7	+ 11	O 10	12	5	1										1					
3	14	15				2	7	6	15	+ 30	O 29	25	14	5	2								2		1		
7	15	15				3	6	29	36	63	+ O 83	76	18	18	3	1							3	2	2		
11	16	15			1	3	13	46	72	111	O 138	+ 91	31	19	6	2							5	5	1		
7	17	15	1			4	7	32	27	58	O 74	61	+ 33	29	8	4						1		4	2		
12	18	15				1	12	30	41	115	O 119	135	41	+ 53	17	8	3	1					2	6	3	1	
5	19	15	1	1	1	2	8	21	32	36	O 48	28	29	14	+ 10	4	1					1	1	2		1	
3	20	15					1	13	16	22	O 18	34	12	16	2	+ 1	1							3			

+ = selected F_2 parents. **O** = means of F_3 cultures.

width was concerned. However, both tables indicate that the strain originating from the original hybrid plant 25-1 had slightly broader leaves than that originating from the original hybrid plant 44-2.

TABLE 89

Width of leaf in millimeters in (3 × 34) F_3, 1916.
Population grouped according to the average leaf width of the F_3 cultures.

Number of cultures	Average leaf width of F_3 cultures	Distribution of individuals																		
		7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
(25-1)																				
2	14				2	3	9	10	**O** 27	20	18	4	3	1	1					
13	15				1	11	30	50	133	**O** 132	148	55	53	6	6	1				
19	16				4	7	27	42	101	163	**O** 227	134	117	35	28	10	3	1		
13	17					3	12	16	59	74	144	**O** 84	122	53	40	13	6			1
3	18						1	1	7	16	18	20	**O** 26	14	23	14	5	2		
(44-2)																				
3	13				5	15	33	**O** 26	36	21	4	3	1							
13	14			1	8	24	75	92	**O** 156	135	95	25	10	2						
22	15	2	1	1	2	18	73	115	187	**O** 239	225	88	75	16	6	2				
9	16					4	14	12	62	104	**O** 111	44	58	17	6					
2	17						3	4	6	15	16	**O** 18	10	13	7	3	1			

O = means of F_3 groups.

In order better to study the variability of the F_3 generation of this cross, the plants were regrouped according to the means of the F_3 cultures in table 89, and table 90 gives the distribution of the F_2 parents and the coefficients of variation of the F_3 cultures in the same grouping.

The distribution of the F_2 parents in this arrangement appears entirely fortuitous without any correlation whatsoever with the means of the progenies to which they gave rise. These facts therefore form additional evidence that the F_2 plants were all equivalent genetically and that all variations of individuals in the F_2 or of means of cultures in the F_3 were due to non-genetic factors.

We are unable to detect any significant difference in the coefficients of

TABLE 90

Width of leaf in millimeters in (3 × 34) F_3, 1916. F_2 parents and coefficient of variation of F_3 cultures grouped according to the means of the F_3 cultures.

Number of cultures	Means of F_3 cultures	Distribution of F_2 parents										Average C. V. of group	Distribution of the coefficients of variation							
		12	13	14	15	16	17	18	19	20	21		7 8	9 10	11 12	13 14	15 16	17 18	19 20	21 22
(25-1)																				
2	14							1	1			13.5			1		1			
13	15				1	3	1	1	4	2	1	11.5		5	3	5				
19	16			1	1		5	2		8	1	12.1	1	4	7	4	3			
13	17				1		2		5	3	2	9.4		4	3	3	3			
3	18							2		1		12.3			2	1				
(44-2)																				
3	13	1					1		1			12.0		1		2				
13	14			.2	3	5		2	1			11.8		3	6	4				
22	15				2	5	4	6	2	3		12.0	1	2	11	6	1	1		
9	16			1	2	1	2	3				10.8		5	3	1				
2	17							1	1			13.0			1	1				

variation of the several groups, whether they be observed from the standpoint of averages or distribution. If, however, the two groups be combined and the columns be made to include 2 mm range in leaf width as is done in table 91 (see row for (3 × 34) F_3), we see a slight but definite decline in variability toward the wider-leaved groups.

Summary; width of leaf

In the 3 × 34 cross, the parents had essentially the same leaf width. The average of the F_1 was a little below either parent, the F_2 exhibited quite marked differences in the means of the different F_2 cultures but the average of the whole F_2 population was the same as that of the wider-leaved parent. In the F_3 the leaves of the hybrids averaged wider than those of either parent and there were again considerable differences in the means of the different hybrid cultures (see table 89). The differences observed, however, are not genetic differences, as is shown by the fact that there was no correlation whatsoever between the leaf width of the F_2 selected parents and the mean leaf width of their offspring (see table 88). In other words, the progeny of the different variants of the F_2 gave results such as would come from the fluctuants of a pure race. We may therefore justly conclude that so far as leaf width was concerned, the 3 × 34 hybrids formed a pure race. This, however, does not mean that these hybrids really formed a pure race in all characters for we have already seen that they segregated in both height and date of heading. A plant may easily be homozygous for one character and heterozygous for a number of others. We may assume therefore that the 3 × 34 hybrids received the same set of leaf-width factors from both parents. In the subsequent discussions of leaf width this group will be considered as a single pure variety.

Before proceeding with the summary and discussion of the other crosses we may first seek to discover whether or not a cause such as we found to suppress variability in the tall cultures of wheats was also operative in reducing variability in the wider-leaved cultures. Table 91 brings together all available data bearing on this point. The horizontal rows contain the data from plants or groups which were supposed to be genetically equivalent so far as leaf width is concerned.

The results obtained in table 92 are remarkably uniform and exhibit without doubt some general cause suppressing variability in the broader-leaved cultures. The nature of this suppression factor is not yet determined. Three possible explanations are suggested as follows:

(1) Can it be that the coefficient of variation is not a proper measure of the variability of quantitative characters in biology?

(2) Is it possible that even pure lines of wheat are still somewhat heterozygous and that the taller cultures are more homozygous than the others?

(3) Can there be some physiological limitation of growth in the higher classes which restricts the full development or expression of the plus combinations of factors?

The writer is inclined to attribute this suppression factor to a combination of suggestions (1) and (3). If a car be moving at rate A and we apply an additional force, say $F+m$, which gives an additional speed say $A+n$, it will require more force than $F+2m$ to give it a speed of $A+2n$.

The effect of a factor, environic or genetic, for increasing size, is probably much less in a combination which tends to produce a variant above the racial mean than in combinations, the product of which falls below the mean. We should have, as it were, a telescoping of variability in cultures with higher means. It is possible therefore that a better measure of the variability of quantitative characters would be a coefficient derived by dividing the standard deviation by some fractional power of the mean, thus $C_1 = \frac{\sigma}{M^x}$ where x is a quantity less than 1.

Returning to the macaroni—bread wheat crosses we remember that

TABLE 91

Correlation of average leaf width of culture and the coefficient of variation of the same in pure lines and genetically equivalent groups.

Culture		Total number	Leaf width in millimeters						
			9 10	11 12	13 14	15 16	17 18	19 20	21 22
Pure No. 1..................	No. of cultures	16			2	8	4	2	
	Average C. V.				11.0	10.6	9.9	9.0	
Pure No. 3..................	No. of cultures	4			2	2			
	Average C. V.				11.8	10.5			
Pure No. 34.................	No. of cultures	6		1	4		1		
	Average C. V.			12.0	11.3		11.0		
Pure No. 35.................	No. of cultures	9				2	3	3	1
	Average C. V.					14.5	13.7	14.7	8.0
(1 × 35) F_2.................	No. of cultures	37			5	31	1		
	Average C. V.				30.6	29.1	27.0		
(1 × 3) F_2..................	No. of cultures	6			3	3			
	Average C. V.				26.7	25.0			
(3 × 34) F_2.................	No. of cultures	6				3	3		
	Average C. V.					10.7	9.0		
(3 × 35) F_2.................	No. of cultures	18					16	2	
	Average C. V.						13.6	12.5	
(3 × 34) F_3.................	No. of cultures	99			18	63	18		
	Average C. V.				12.0	11.8	10.3		
F_3 cultures from tall F_2 plants having smooth seeds (parent-like) (1 × 35) F_3..........	No. of cultures	36			8	12	14	2	
	Average C. V.				19.1	17.9	15.6	14.5	
F_3 cultures from tall F_2 plants having wrinkled seeds (F_1-like) (1 × 35) F_3..........	No. of cultures	28		3	6	16	2		1
	Average C. V.			30.0	26.5	22.8	20.5		13.0
F_3 cultures from tall F_2 plants having smooth seeds (parent-like) (1 × 3) F_3..........	No. of cultures	9		1	2	3	3		
	Average C. V.			19.0	16.5	11.3	10.0		
F_3 cultures from tall F_2 plants having wrinkled seeds (F_1-like plants) (1 × 3) F_3.....	No. of cultures	9	1	4	3	1			
	Average C. V.		20.0	27.8	26.7	25.0			

the F_1 had wide leaves and wrinkled grains. The average leaf width of the F_2 was markedly below that of either parent but there were some F_2 plants having leaf widths as great or greater than the parental means. These wide-leaved F_3 plants were of three types, viz., (1) some had wide leaves and smooth grains (parent-like), (2) some had wide leaves and wrinkled grains (F_1-like) and a few had wide leaves and partially wrinkled grains (of uncertain classification). Now since the average of the F_2 was below that of the parents and the variability was much above the parental variability, we should expect the F_1-like F_2 plants to give F_2 cultures low in mean leaf width and high in variability, whereas the parent-like F_2 plants should give F_3 cultures high in mean leaf width and low in variability. Now disregarding the wide-leaved F_2 plants with partially wrinkled seed (on account of difficulty of classification) we find the results shown in table 92.

TABLE 92

	(1 × 35) F_3			(1 × 3) F_3		
	Number of cultures	Mean leaf width	Average C. V.	Number of cultures	Mean leaf width	Average C. V.
F_3 cultures from wide-leaved smooth-seeded F_2 plants (parent-like)	36	16.1	17.1	9	15.4	12.9
F_3 cultures from wide-leaved wrinkled-seeded F_2 plants (F_1-like)	28	14.9	23.8	9	12.4	26.2

No better agreement of the facts with the theoretical assumptions made, could well be expected. It is, of course, not here assumed that the parent-like F_2 plants were constituted genetically exactly like one or the other of the parents or that the F_1-like F_2 plants were completely heterozygous in every particular in which the F_1 plants were heterozygous, but it is assumed that the genetic agreement is close enough to give marked similarity in form and hereditary behavior. Where a number of factors are involved, as there probably are here, it would be extremely difficult, probably impossible, to pick out plants from the F_2 by inspection, which were exactly like either the parents or the F_1, genetically. This could only be done by judging the F_2 plants by the genetic behavior of their offspring. The facts developed seem to show that the wide-leaved F_2 plants fell into two groups, the one having a complete (or nearly complete) set of the factors from one or the other of the parental races, and that the other group contained plants which were heterozygous for all (or nearly all) of the characters in which the parents differed. Again therefore we have a situation where a complete double set of one or the other of the parental races or a complete (or nearly complete) single set from each of the two parents were able to produce wide-leaved plants, but that the large majority of the new recombinations of parental characters resulted in less vegetative development.

Now referring to table 92 we find that even in the offspring of these two groups of wide-leaved F_2 plants the factor for suppressing variability was apparent, but it was not sufficient to mask the effect of differences in heterozygosity because in the one case (those of the F_1-like parents) the means tended to be below that of the standard (pure line parents). Now when we turn to the 3 × 35 cross where the F_1, F_2 and F_3 all had average leaf widths larger than the more narrow-leaved parent, the suppression factor was able entirely to offset the theoretically expected increased variability of the heterozygous cultures. If in accordance with the F_1, the wide-leaved F_3 cultures were the more heterozygous and the more narrow-leaved the more homozygous we can easily see how the suppression factor might reduce the average variability of all of the F_3 cultures to a figure equal to or below that of the most variable parent especially in a case where the average of the leaf width of the F_3 cultures was equal to that of the wider-leaved parent.

One cannot here assume the formation of a single new blended race, for table 75 shows segregation in the F_2 with the formation of many distinct races in F_3, and moreover, in spite of the suppression factor and the fact that the F_2 had a larger mean than the F_3, the average variability of the F_3 was less than that of the F_2 (compare tables 76 and 78).

According to Mendelian expectation, the parental types of individuals in F_2 and culture means in F_3 were recovered in all cases. In 1 × 35, recombination formed individuals in F_2 and a number of cultures in F_3 whose means were significantly beyond, both above and below, the range of either parent. In 1 × 3 the range of individuals in F_1 and of means of cultures in F_3 were significantly below, but not above, the parental ranges. In 3 × 35 the range of individuals in F_2 and means of cultures in F_3 were not significantly above or below the parental ranges.

In the macaroni—bread wheat crosses the average variability of the F_2 and F_3 generations were markedly above that of the parents but in the F_3 many cultures were secured which were as little variable as either parent. In no case was there a single F_2 culture, however, which had as low a variability as the most variable parental culture.

The variability of the bread wheat crosses has already been discussed with sufficient fullness.

The segregation of simple Mendelian unit factors appears to suffice to explain all of the facts so far observed in the inheritance of leaf width in the wheat hybrids here discussed. No attempt has been made to determine the number of factors but the supposition is that there are several.

GENERAL SUMMARY

Detailed summaries of the three characters, date of first head, height, and width of leaf, may be found on pages 27, 52 and 87, respectively.

The F_1 of the macaroni—bread wheat crosses developed normally and were in every case equal or superior to the mean of the parents in vegetative vigor and they were no more variable in size characters or time of maturity than were the pure races. We may therefore conclude that a single complete set of macaroni wheat characters with a complete single set of bread wheat characters (the maximum of heterozygosis between the two varieties) will produce a perfectly normal plant.

In the second generation, on the other hand, many of the seeds would not germinate and those germinating produced plants differing in vegetative growth from those which were more vigorous than either parent to such as never got beyond the rosette stage. Moreover those which made a normal vegetative development exhibited every degree of sterility from completely sterile plants to those entirely normal in seed production. It would appear, therefore, that these facts alone refute any idea of blending inheritance, for if blending had taken place in the F_1, sterile or vegetatively deficient plants would be no more likely to occur in the F_2 than in the F_1. Hence we are compelled to predicate segregation and recombination in these quantitative characters. There is nothing to indicate even partial blending in any of the factors concerned.

In the use of the coefficient of variation as an indication of heterozygosity in hybrids involving quantitative characters, care should be exercised to make due allowance for the fact that races with high means resulting from increased vegetative growth, have their variability limited or reduced by the apparent law that size factors are more effective in producing variability in combinations tending to produce a result below the mean of the hybrid population than in combinations which tend to exceed this mean.

The suppression of variability in cultures with high means applies to pure as well as hybrid cultures. It appears to be a telescoping of variability as the mean approaches the upper physiological limit of growth rate for the species concerned.

LITERATURE CITED

Castle, W. E., 1912 The inconstancy of unit-characters. Amer. Nat. **46**: 352-362.

1917 Piebald rats and multiple factors. Amer. Nat. **51**: 102-114.

East, E. M., 1916 a Studies on size inheritance in Nicotiana. Genetics **1**: 164-176.

1916 b Inheritance in crosses between *Nicotiana Langsdorffi* and *Nicotiana alata.* Genetics **1**: 311-333.

Fruwirth, C., 1915 Versuche zur Wirkung der Auslese. Zeitschr. f. Pflanzenzüchtung **3**: 173 and 395.

Hayes, H. K., and East, E. M., 1915 Further experiments on inheritance in maize. Conn. Agric. Exp. Sta. Bull. 188, 31 pp.

Hoshino, Yuzo, 1915 On the inheritance of flowering time in peas and rice. Jour. College Agric. Tohoku Imp. Univ., Sapporo **6**: 229-228.

Mac Dowell, E. C., 1914 Size inheritance in rabbits with a prefatory note and appendix by W. E. Castle. Carnegie Inst. of Washington, Pub. No. 196, 55 pp.

1915 Bristle inheritance in Drosophila. Jour. Exp. Zoöl. **19**: 61-98.

Nilsson-Ehle, H., 1914 Über einen als Hemmungsfaktor der Begrannung auftretenden Farbenfaktor beim Hafer. Zeitschr. f. indukt. Abstamm. u. Vererb. **12**: 36-55.

Phillips, J. C., 1914 A further study of size inheritance in ducks with observations on the sex ratio of hybrid birds. Jour. Exp. Zoöl., **16**: 131-148.

1915 Experimental studies of hybridization among ducks and pheasants. Jour. Exp. Zoöl. **18**: 69-112.

Punnett, R. C., and Bailey, P. G., 1914 On the inheritance of weight in poultry. Jour. Genetics **4**: 23-39.

Shull, G. H., 1914 Duplicate genes for capsule-form in *Bursa bursa-pastoris.* Zeitschr. f. indukt. Abstamm. u. Vererb. **12**: 97-149.

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to the literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full,* and to indicate accurately in Arabic numerals, the volume number, the first and last pages and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Footnotes should be inserted immediately after the reference marks which refer to them, and should be separated from the text by lines. All footnotes should be numbered consecutively in a single series.

No limitation will be placed on the kind of illustrations to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS is 4⅝ × 7½ inches and all illustrations intended for use as single plates should not exceed 5 × 7¾ inches, or should allow of reduction to these dimensions. Double plates may be 12½ × 7¾ inches. Legends for all figures should be typewritten on a separate sheet.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page.

Contributors will receive 100 reprints of their papers, with covers, free of charge, and may secure additional copies at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, Dr. George H. Shull, 60 Jefferson Road, Princeton, N. J.

GENETICS, JANUARY 1919

TABLE OF CONTENTS

OUR FRONTISPIECE

On February 16, 1918, HUGO DE VRIES celebrated his seventieth birthday, and on June 13, 1918, he delivered his last lecture as Professor of Botany in the UNIVERSITY OF AMSTERDAM. In recognition of his long and distinguished career his birthday was marked by the presentation of an album containing the autographed photographs of his botanical friends and admirers the world over, and arrangements were made for the collection and reprinting in six large volumes, of all his contributions to scientific journals. It is particularly fitting therefore to present this portrait of HUGO DE VRIES at this time. The photograph used here is one of several taken by Elliott & Fry, Ltd., London, on the occasion of the DARWIN CENTENNIAL CELEBRATION in 1909. It is copyrighted by the photographers, from whom the right to publish here has been purchased. The editor is not aware that this photograph has been previously engraved; but one of the other two photographs taken at the same time, is used as frontispiece in the collected papers whose publication is mentioned above.

The reproduction of this portrait of Professor DE VRIES is made possible by a gift from Dr. LIBERTY HYDE BAILEY, who was for many years Director of the N. Y. STATE COLLEGE OF AGRICULTURE at CORNELL UNIVERSITY, and who is Author and Editor of many important works on horticulture and agriculture, including such works of special interest to geneticists, as *"Plant breeding"*, *"Survival of the unlike,"* *"Evolution of our native fruits,"* etc. In the title of the first of these books, first published in 1895, the expression "plant breeding" was used probably for the first time.