PATROGENESIS

A Form of Inheritance with the Characters of the Female Parent Completely Excluded—A Cross Between Two Genera of Grasses, Tripsacum and Euchlaena[1]

G. N. COLLINS AND J. H. KEMPTON
Bureau of Plant Industry, U. S. Department of Agriculture, Washington, D. C.

INTRODUCTION

A FERTILE hybrid between *Tripsacum dactyloides* L. and *Euchlaena mexicana* Schrad., was reported by the writers in 1914. The behavior of the single first generation plant was at that time described and its close resemblance to the male parent noted.[2]

It is now possible to report the behavior of the progeny of this hybrid plant, which have been grown for two seasons, and to make comparisons with the first generation plant and with the parents.

The parental stocks were *Tripsacum dactyloides* and *Euchlaena mexicana*. Tripsacum is a perennial grass native in many parts of eastern United States and is of no economic importance. Euchlaena is an annual grass native in Mexico and frequently grown in the United States for forage under the name of "teosinte." These species not only belong to different genera, but are placed in separate groups of the tribe Maydeae. The two genera, together with Maize or Indian corn, are the only American representatives of the tribe. The plants differ profoundly in general appearance, as well as in structural details, as the illustrations show.

The list of contrasted characters given on the opposite page will serve to indicate the more conspicuous differences.

The plant of Euchlaena used as the male parent in the hybrid was from seed received from Dr. H. V. Jackson, of Durango, Mexico. Euchlaena is reported as a wild plant about Durango. It is also cultivated in the same region. The cultivated form, at least, is much hybridized with maize. Plants representing all stages from what appears to be pure Euchlaena to those that closely resemble pure maize have been grown from original seed received from that region.

The fact that the particular plant used as pollen parent of the cross was grown in the greenhouse, where Euchlaena plants never behave normally, made it difficult to determine whether this plant shared any of the frequent contamination with maize. The plant was stunted and somewhat abnormal, but no maize characters could be observed, and there has been a similar absence of maize-like characters in the pure seed progeny of the hybrid plant. It is, therefore, believed that the male parent of the hybrid represented a relatively pure form of Euchlaena.

DESCRIPTION OF SUPPOSED HYBRID

The original cross was made in March, 1913, in a greenhouse of the Department of Agriculture at Washington, the Euchlaena pollen being placed on the stigmas of a plant of Tripsacum. Precautions were taken to guard against foreign pollen, although no other Tripsacum plants were growing in the greenhouse and no pollen was yet being produced on the plant that was fertilized, Tripsacum being decidedly proterogenous. The cross was such a violent one that there was little expectation of success, but four seeds developed and these were planted as soon as mature. When a sprout appeared above

[1] Read before the twelfth annual meeting of the American Genetic Association, at Berkeley, Cal., August 6, 1915.

[2] Collins, G. N., and Kempton, J. H., A Hybrid between Tripsacum and Euchlaena. *Journal Washington Academy Science*, Volume IV, No. 5, pp. 114-117, March 4, 1914.

TRIPSACUM DACTYLOIDES	DURANGO EUCHLAENA
Plant perennial.	Plants annual.
Staminate and pistillate flowers in the same inflorescence.	Staminate and pistillate flowers in different inflorescences.
Terminal inflorescence with from 1 to 3 branches.	Terminal inflorescence with from 8 to 20 branches.
Branches of terminal inflorescence erect.	Branches of terminal inflorescence drooping.
Branches of terminal inflorescence without pulvini.	Branches of terminal inflorescence with pulvini.
No secondary branches in terminal inflorescence.	Secondary branches in terminal inflorescence equalling or more numerous than the primary.
Staminate spikelets in pairs both sessile.	Staminate spikelets in pairs one sessile, the other pedicelled.
Staminate spikelets in alveolae.	Staminate spikelets not in alveolae.
Pistillate inflorescence naked.	Pistillate inflorescence enclosed in bracts.
Outer glume of pistillate inflorescence completely exposed.	Outer glume of pistillate inflorescence partially enclosed by the rachis.
Stigmas about 2 cm. long.	Stigmas from 10 to 15 cm. long.
Stigmas divided to the base.	Stigmas divided for about 3 mm.
Inflorescence basipetal.	Inflorescence acropetal.
Fruit trapezoidal.	Fruit triangular.
Rachis not constricted between the seeds.	Rachis constricted between the seeds.
No branches in axils of prophylla.	Branches in the axils of prophylla.
Leaf blades about 50 times as long as wide.	Leaf blades about 10 times as long as wide.

the surface of the ground our faith was still so small that the plant was dug up and the seed examined to make sure we were not rearing a "cuckoo." As the sprout was found to be growing from an unmistakable Tripsacum seed, it appeared certain that the plant was either a hybrid or a parthenogenetically developed Tripsacum. The second alternative was soon dismissed, for Euchlaena characters appeared with the first leaves, and the further stages of development were those of a nearly normal Euchlaena plant. Most careful scrutiny failed to disclose any characters that could be referred to Tripsacum, the female parent. The plant was not exactly like others that had been grown previously, but even under the most favorable greenhouse conditions, Euchlaena shows many deviations from the normal behavior. The deviations in this were not extreme or unusual, indeed the plant was more nearly like normal Durango Euchlaena than any Euchlaena we have ever been able to grow under greenhouse conditions.

Two points regarding this cross should be kept in mind: (1) the plant was known to have grown from a seed borne on a Tripsacum plant; (2) the plant resembled the *male* and not the female parent. These two facts taken together eliminate all questions of foreign pollen or faulty technique.

The plant was grown to maturity in the greenhouse, was carefully guarded and self-pollinated and produced a quantity of seed. Unfortunately no Tripsacum pollen was available at the time the first generation plant was in flower, October, 1913, but plants of a Florida Euchlaena were just beginning to shed pollen and this was applied to a number of the pistillate inflorescences. Two very late varieties of tropical corn were also in flower and pollen from them was similarly used. All the pollinations were successful, seed setting as readily with the corn and Euchlaena pollen as with the plant's own pollen.

THE SECOND GENERATION

A few seeds representing each class of pollinations were planted in the greenhouse in December, 1913. From this planting there were secured seven plants, with the following parentage: Three plants from self-pollinated seed of the first generation cross; one plant from the first generation cross pollinated with Florida Euchlaena; two plants of the first generation cross pollinated with a Liberian variety of maize; one plant of the first generation cross pollinated with a variety of maize from Bolivia. The last plant was soon eliminated as the result of a peculiar abnormality. The sheath of the first leaf instead of being open on one side and enclosing

FEMALE PARENT OF THE CROSS

Plant of *Tripsacum dactyloides*, a grass which is fairly common in the southeastern United States. When crossed with the grass shown in the following photograph, it produced seeds, but did not seem to contribute any of its own characters to these seeds. Photograph made at Lanham, Maryland. (Fig. 2.)

the succeeding internodes, was closed and solid, consequently the growth of the plant terminated with the first leaf.

During the early stages the remaining six plants all behaved much as did the first generation plant, the only observable difference being their more early branching and the fact that the branches were nearly prostrate for several months. Studies of Tripsacum seedlings disclosed no such tendency to produce horizontal branches from the lower nodes. Minor differences in the development and distribution of the hairs appeared, but these were not consistent even among the plants having the same male parents.

As the plants developed the diversity became more pronounced, although the variations were largely in the nature of abnormalities. With one exception the main axes of all the plants terminated their growth much earlier than is customary in Durango Euchlaena, only ten to fourteen internodes being produced. The branches from the lower nodes of all these plants greatly exceeded the main stalk in height and produced many more internodes. The exception noted was one of the plants having the Liberian maize for male parent. This plant produced 51 internodes, a larger number than has been recorded in Euchlaena, Tripsacum or maize.

The terminal inflorescence of these six second generation plants varied greatly, but none of the forms showed any approach to Tripsacum. One of the most striking abnormalities consisted in the replacement of the lower spikelets of the terminal inflorescence by little plants.[3] This abnormality occurred in the plant having the Florida Euchlaena for its male parent, in two of the second generation plants obtained by self-fertilization, and to a less extent in one of the plants having the Liberian maize for male parent. Several of these little plants which developed roots while still attached to the parent were removed and potted. They grew into plants resembling the larger branches or suckers of the parent plants and matured seed. Plants from some of the seed thus produced were grown during the past season (1915) and behaved like plants from self-pollinated seed of the second generation plants.

The diversities of the first lot of second generation plants, together with the occurrence of hitherto unobserved abnormalities, led us at that time to believe that although we could detect no indication of Tripsacum characters, the plants were something other than pure Euchlaena.

Further plantings from the original lots of seed secured from the first generation plant were made in the greenhouse in April, 1914. As soon as the weather permitted these were transplanted to the open and still other plantings were made directly in the open soil. We thus had second generation plants maturing in the greenhouse and others in the early stages growing in the open at the same time.

These later plantings, including both those transplanted and those planted in the open, developed none of the abnormalities observed in the first lot grown in the greenhouse. The straight second generation plants appeared to be pure Durango Euchlaena. The others were what might have been expected in first generation hybrids between Durango Euchlaena and the different types of maize used as male parents.

THIRD GENERATION

In the season of 1915 experiments were conducted near San Diego, Cal. The long growing season of Southern California afforded the first opportunity to allow plants of the hybrid to grow to maturity undisturbed. Small plantings were made of such second generation seed as had been obtained and the following plants were secured: ten plants from self-pollinated seed of three second generation plants of the hybrid; seventeen plants from self-pollinated seed of three plants of (Tripsacum x Euchlaena) X Liberian maize; five plants from self-pollinated seed of one plant of (Tripsacum x Euchlaena) X Florida Euchlaena. Plantings of Durango

[3] A similar abnormality has been observed in maize. See Collins, G. N., Apogamy in the Maize Plant. Cont. U. S. Nat. Herb., XII, Pt. 10, pp. 453-455, 1909.

MALE PARENT OF THE CROSS

Plant of Euchlaena, a grass which is grown to some extent for forage in the United States, under the name of teosinte. The variety here represented is that from Durango, Mexico; photographed at San Diego, Cal. In a cross with the grass shown in the preceding photograph, this Euchlaena proved so prepotent that the offspring cannot be distinguished from the male parent; while the female parent seems to have exerted no influence whatever on the heredity. This unusual type of heredity has been given the name of patrogenesis. (Fig. 35)

THE HYBRID RESEMBLES THE MALE PARENT

Compare this plant with the one shown in the preceding illustration, and you will see no real difference. Yet this is a hybrid, in the first generation from the Tripsacum x Euchlaena cross. The identity between the male parent and the offspring is so close that the female parent seems to have done nothing but furnish nourishment for the development of the seed. (Fig. 4.)

FLOWERS OF THE TRIPSACUM

The hairy threads in the lower part of the picture are the pistillate or female flowers, while above are the male or staminate flowers, their dark-colored anthers or pollen sacs hanging on very fine filaments. Photograph natural size. (Fig. 5.)

Euchlaena were also made for comparison. The seed was planted on March 16, and a second planting of Durango Euchlaena was made on June 11. The third generation plants of the cross, with the exception of those that had been crossed with maize, all developed as normal Durango Euchlaena, free from any of the abnormalities observed in the second generation plants grown in the greenhouse. Early in the season the branches showed the prostrate habit characteristic of the first and second generation plants, but the Durango Euchlaena plants also showed the same habit. Curiously enough, the first planting of Durango Euchlaena developed a series of abnormalities almost exactly paralleling those of the second generation hybrid plants grown in the greenhouse. Of eighteen Durango Euchlaena plants, twelve produced aborted main stalks that matured with nine to thirteen leaves. Four of the eighteen plants produced apogamous plants in the place of spikelets. All of the abnormal plants produced numerous suckers that grew normally and were indistinguishable from the main stalks of normal Durango Euchlaena plants. The later planting of Durango Euchlaena was entirely free from these abnormalities.

Table 1 gives the average measurements of plants grown at San Diego. It can be seen that there are no striking differences between the hybrid plants and the Durango Euchlaena, the hybrid plants being in many particulars intermediate between the two plantings of Euchlaena. Where significant differences occur they are not of a nature to suggest Tripsacum.

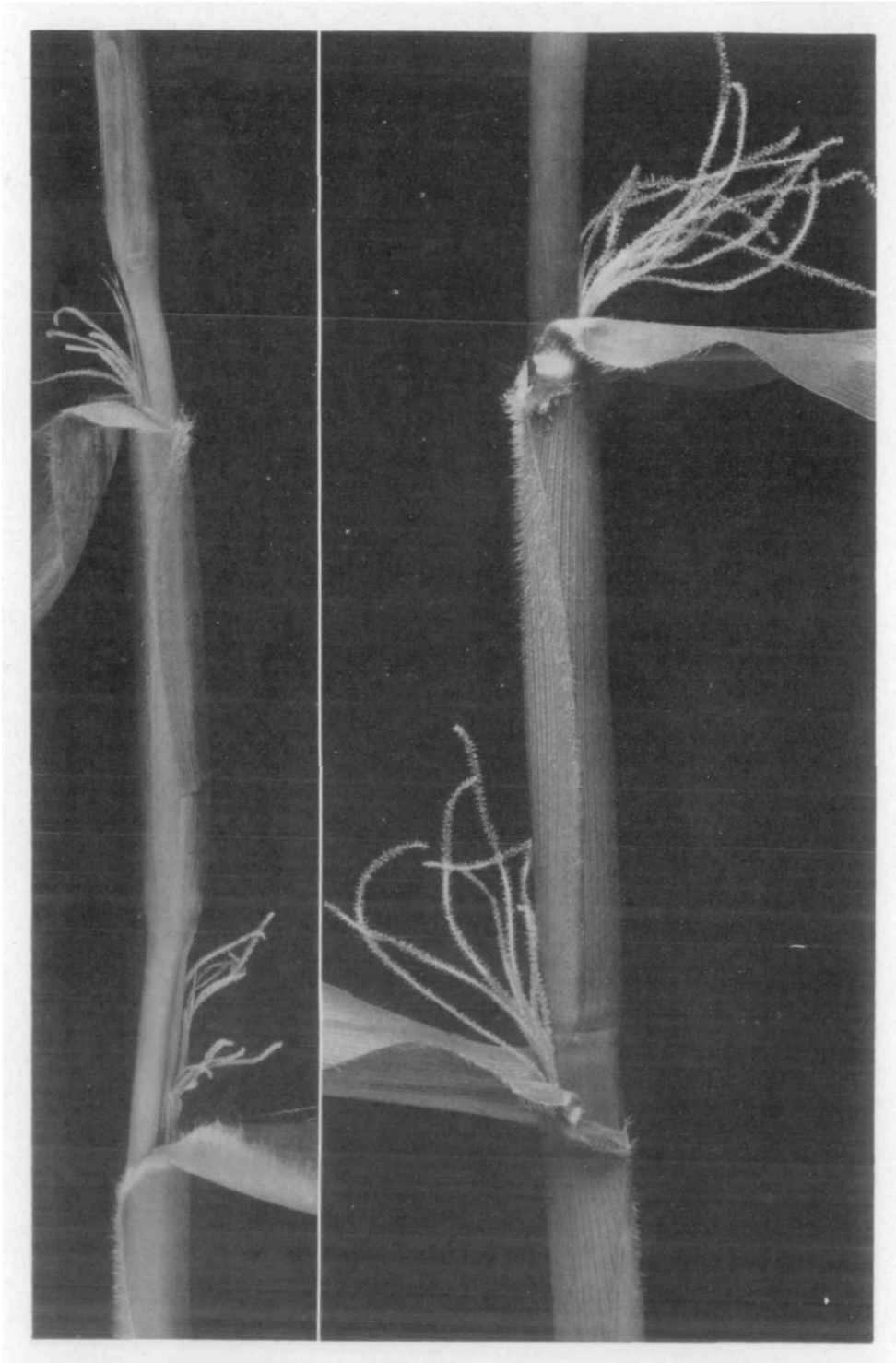
Several hundred plants from open pollinated seed of the different second generation hybrid plants were also grown and carefully examined for indications of Tripsacum, but no characters or abnormalities not attributable to Euchlaena or maize were observed.

TRIPSACUM POLLINATED BY MAIZE.

To repeat the original cross in the late plantings has been impossible, through a failure to bring Euchlaena and Tripsacum into flower at the same time. In 1914, however, maize pollen of several varieties was available at the time the Tripsacum plants were in flower. Numerous attempts to fertilize Tripsacum flowers with maize pollen resulted in a small quantity of viable seed. A number of plants from these seeds have been grown, but instead of resembling the male parent, all are apparently pure Tripsacum. These crosses were made with such precautions against accidental pollinations and have been secured in such numbers that there can be little doubt regarding the parentage of the plants. Euchlaena and maize are so nearly related and have behaved so much alike in the perjugate generations of our original cross with Tripsacum that we fully expect to secure similar results

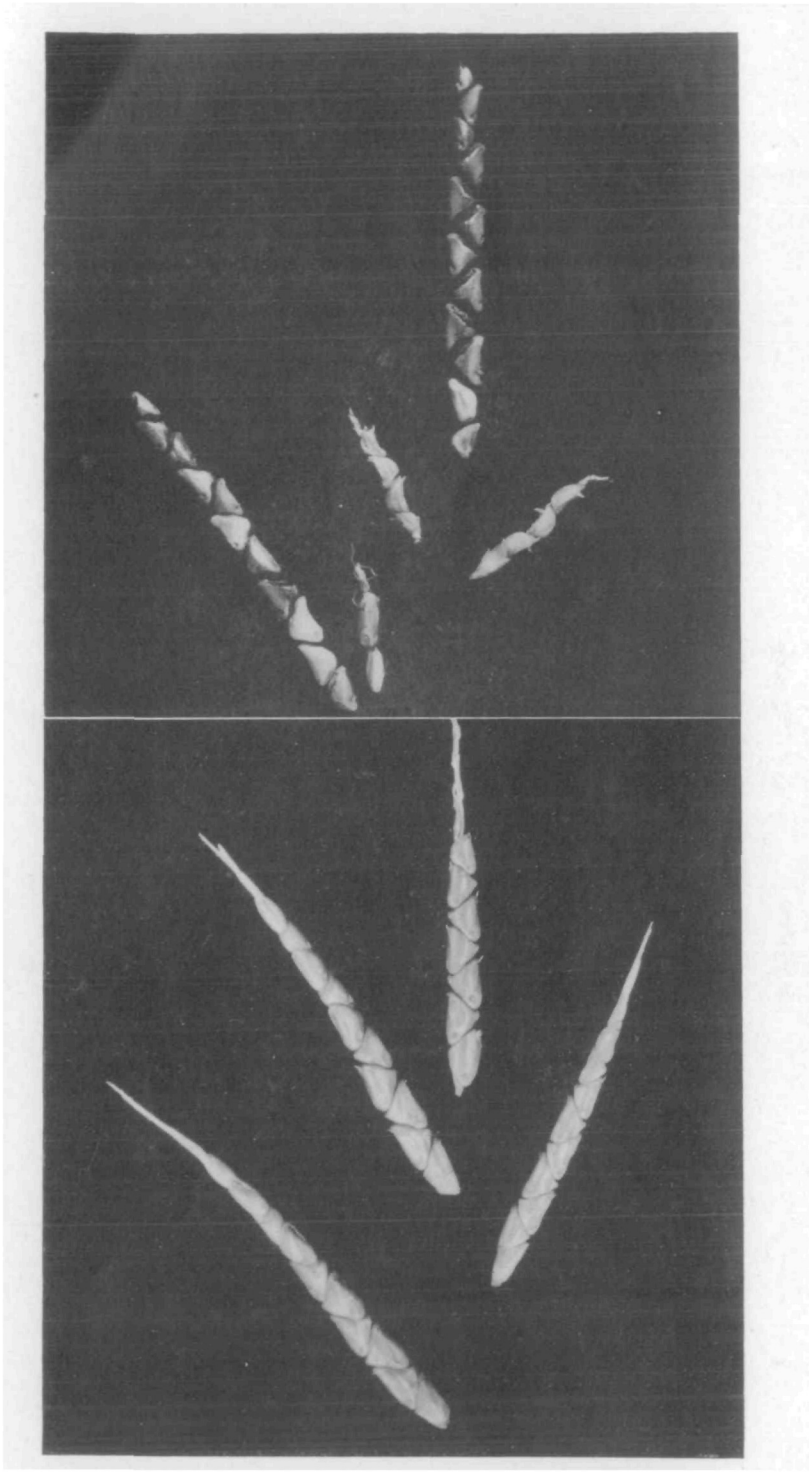
TABLE 1.—COMPARISON OF TWO PLANTINGS OF DURANGO EUCHLAENA WITH TRIPSACUM X DURANGO EUCHLAENA, GROWN AT CHULA VISTA, CAL., 1915

	Durango Euchlaena planted March 16	*Durango Euchlaena planted June 11*	*Tripsacum X Euchlaena third generation*
Height in centimeters	313.0± 8.25	202.0±5.51	200.0± 8.15
Exsertion of tassel in centimeters	6.6± .94	3.0± .48	1.7± .59
Branching space in centimeters	7.9± .45	11.1± .52	10.1± .31
Length of central spike in centimeters	13 8± .84	10.6± .44	8.2± .23
Length of lowest tassel branch in centimeters	17.5± .64	15.8± .72	11.0± .56
No. branches	10.1± .37	13.8± .64	12.3± .42
No. secondaries	16.0± 1.71	29.2± .36	27.2± 1.35
Length of longest leaf in centimeters	80.3± 2.01	67.8±1.47	67.7± .87
Width of longest leaf in centimeters	4.2± .13	6 0± .20	4.0± .08
Nodes above longest leaf	9.6± .19	8 8± .39	10.3± .66
No. suckers	18.8± 1.48	8.1± .76	11 0± .95
Height of tallest sucker in centimeters	300.0±10.10	195.0±2.79	199.0±10.90
No. exserted internodes	6.9± .26	7.7± .39	4.7± .37
Diameter of stalk in centimeters	2.2± .57	2.8±1.27	3.2± .59



THE MALE PARENT AND THE HYBRID: FLOWERS

At the left are pistillate flowers of the Durango Euchlaena, while on the right are shown pistillate flowers of the cross between Euchlaena and Tripsacum. They are alike in almost every particular, and the flowers of the hybrid shown no influence of the parent—compare with fig. 5. Photographs natural size. (Fig. 6.)

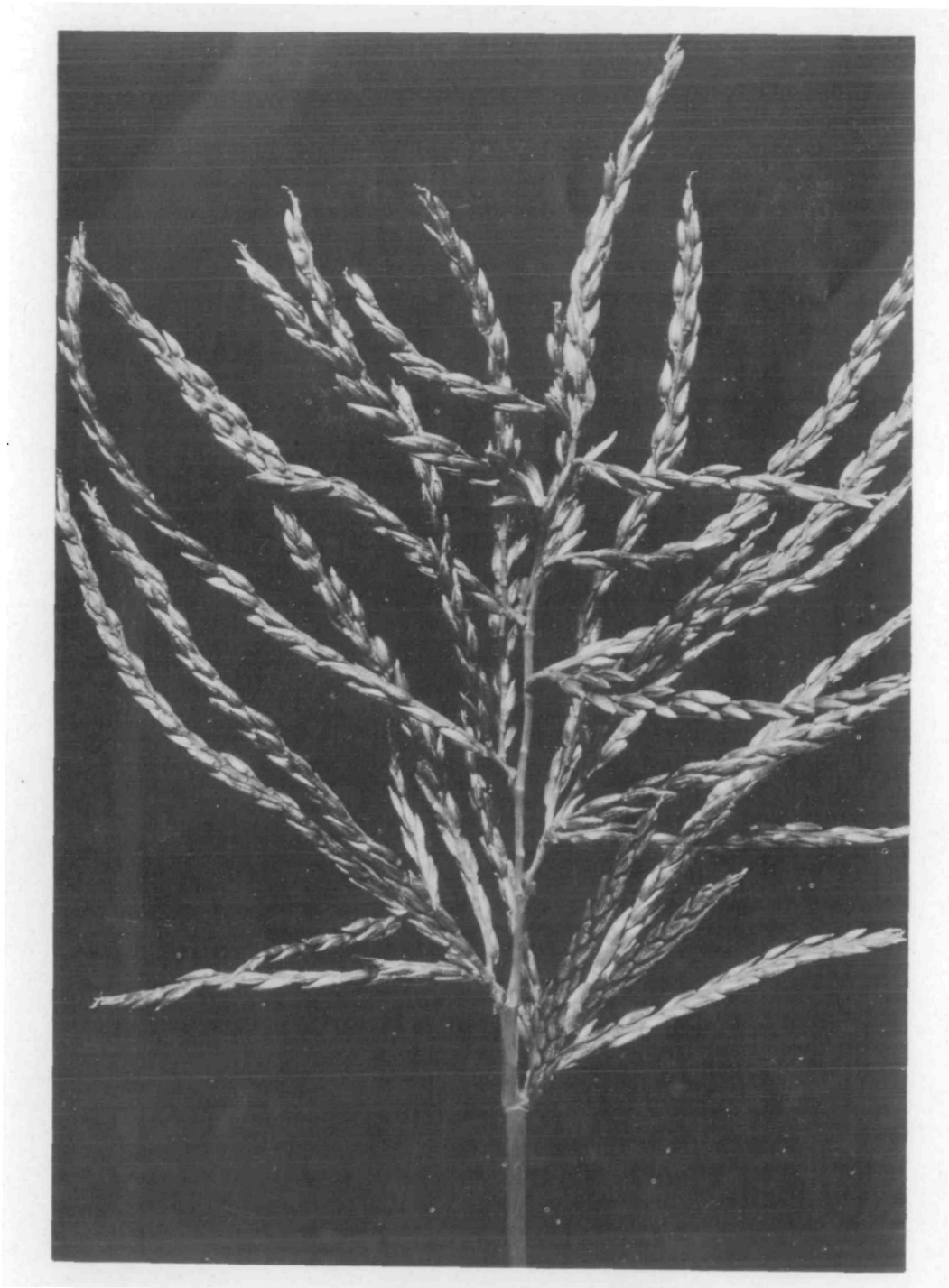


THE MALE PARENT AND THE HYBRID: FRUITS

Below are fruits of the Durango Euchlaena, nearly mature, and shown natural size. The spikes are arranged as they were borne on the branch. Above are the mature fruits of the Euchlaena x Tripsacum hybrid, likewise arranged as they were borne on the branch, and photographed natural size. The fruits of the male parent and hybrid offspring are similar in every respect. (Fig 7.)

MALE FLOWERS OF THE EUCHLAENA

They are much like the familiar "tassels" of maize, to which the Euchlaena is closely related. But they are also so much like the staminate flowers of the Euchlaena x Tripsacum hybrid, shown in the next photograph, that no one could tell the difference. Photograph natural size. (Fig. 8.)



MALE FLOWERS OF THE HYBRID

There is nothing in this inflorescence which resembles the flowers of the mother (Tripsacum), shown in Fig. 5. But every detail resembles the corresponding detail of the male flowers of the paternal parent (Euchlaena), shown in the preceding illustration (Fig. 8). This similarity with the male parent, and exclusion of all the characteristics of the female parent, appear in all the traits of the hybrids, and have led to the belief that we are here dealing with a new type of inheritance, which has received the name of patrogenesis. Photograph natural size. (Fig. 9.)

with Euchlaena pollen. It appears, therefore, that the complete resemblance to the male parent, which we secured in the first cross, was exceptional. Crosses between Tripsacum and Zea, at least, usually show a complete resemblance to the female parent. It seems not improbable that the maize pollen served only to induce parthenogenesis in the Tripsacum parent. With the view of determining this point material for cytological study has been secured and is being investigated.

CONCLUSIONS

A cross between *Tripsacum dactyloides*, female, and *Euchlaena mexicana*, male, has been carried through three generations without exhibiting any indication of the characters of the female parent. In attempting to explain this complete absence of the characters of the female parent two alternatives may be considered. (1) The characters of the female parent have been completely masked by those of the male, or (2) the male nucleus developed in the ovary to the complete exclusion of the female, representing in a way the counterpart of parthenogenesis. In the three generations of the progeny of this hybrid at least 350 plants have been examined. This and the fact that a great variety of conditions has called forth great variation and induced many abnormalities without evoking any indication of Tripsacum characters has caused the first alternative to be dismissed. If the second alternative be adopted we are compelled to look upon the results of this cross as a special type of inheritance not previously recognized. Hybrids showing a predominance of the characters of the male parent have been described as patroclinous, but in this cross and its successive progenies no trace of the characters of the female parent has been detected. No true hybridization or conjugation between the two nuclei appears to have taken place. For this form of false hybridization the name patrogenesis is proposed. The term patrogenesis would also serve to place the phenomenon in proper contrast with parthenogenesis. This is rendered appropriate by the occurrence of what appears to be true parthenogenesis in Tripsacum, when pollinated with maize.

The Effect of War

WAR AND THE BREED, by David Starr Jordan. Pp. 265, price $1.35 net. Boston, The Beacon Press, 25 Beacon Street, 1915.

Twenty years ago the idea that war was an important factor in changing the inborn nature of the human race was a novel one recognized by few. Dr. Jordan is largely responsible for making this fact seem almost a truism at the present day. In the present book he has explained the thesis with a great wealth of illustration, and in a most readable way, prefacing the main discussion with a short and popular outline of the various methods in which evolution proceeds. The volume therefore makes an interesting elementary treatise on eugenics, and one that from its timeliness ought to have a wide circle of readers.

Reprints from the Journal of Heredity

To contributors of articles describing the results of research, the American Genetic Association will henceforth furnish, on request, 100 reprints without covers, gratis and post free. Additional reprints can be had at the following prices:

50 copies, 4 pages	$0.30
50 copies, 8 pages	.55
50 copies, 16 pages	.80

If covers are desired, they can be had at two cents each for the first hundred and one cent each for additional quantities.