THE ALLOPLOID MODEL IN AVENA*

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Sixty years ago NILSSON-EHLE reported triplicate genes in wheat and oats. Twenty years later STADLER considered these genes as indicators of homoeology of the triplet chromosomes, although, it was HUSKINS who invented the term homoeology a few years later. As STADLER phrased it: ". . . some genes would be identical in all groups and other genes would not; and we have at present no sound basis for estimating the proportion of genes in each class." Two decades later the sound basis was beautifully demonstrated by his associate, DR. E. R. SEARS. The wheat aneuploids and the demonstration of homoeologous groups initiated the intellectual renaissance of cytogenetics, providing new insights into the evolution and meiotic regime of alloploids. These were my thoughts when I was honoured with the invitation, for which I am truly grateful, to address the Third Stadler Genetics Symposium.

I have deliberately chosen alloploidy as my subject for a meeting at this University. Most of the grass species I have been working with are alloploids. I have always been fascinated by the complexities of their evolution and stimulated by the unfolding story of wheat.

I shall draw heavily on the oat species, because these I know best and because oat cytogenetics is just an upstart in the distinguished group of other alloploids such as wheat, cotton and tobacco. Only passing references will be made to cotton and tobacco, since GERSTEL (1963) last discussed the cytogenetics of these alloploids. No one could, of course, neglect wheat in discussing alloploidy, although it was recently reviewed by MORRIS and SEARS (1967) and SEARS (1969). Wheat is an obvious model for cytogenetic research in oats. Both genera consist of cereal species with great economic importance together with wild and weedy species. Both genera are assumed to have originated in the Middle-East; some of the wheat and oat species are Mediterranean, others conquered the temperate zones. Species in both genera are inbreeding annuals, form polyploid series from 2x to 6x, and the polyploids are bivalent forming alloploids. Thus, it is convenient to relate similarities and differences between the cytogenetic architectures of wheat and oats which may lead to a more generalized picture of alloploidy.

Although half of the flowering plants are estimated to be of alloploid origin, the bulk of our knowledge related to alloploidy comes from a few economically-important species. This is no surprise if the amount of work invested in these few groups is considered. This leads me to believe that these groups will have to serve as models from which to extrapolate and generalize for a vast number of natural alloploids, giving added importance to the similarities and differences between these model architectures.

THE DIPLOIDS

It is convenient to begin with the diploid oat species, since in a polyploid series some of these should have served as building elements of the architecture of the polyploids (Table 1). There are some 7 or 10 diploid species, depending on the taxonomic treatment.

Table 1. Genomes of Avena species cited.

Diploids (2n=2x=14)		Tetraploids (2n=4x=28)	
A. hirtula	A_s	A. barbata	AB ($A=A_s$, B=A mod.)
A. longiglumis	A_l	A. magna	AC (?)
A. pilosa	C_p	Hexaploids (2n=6x=42)	
A. ventricosa	C_v	A. sterilis	ACD
		A. sativa	ACD

KARYOTYPES.
The diploid species fall into two very distinct groups: one has isobrachial, the other heterobrachial chromosomes (Figure 1). The former group was designated A and the latter C (RAJHATHY and MORRISON 1959, RAJHATHY 1966). Each of these groups can be further subdivided by small yet definite structural differences, giving a total of six well defined karyotypes. This array of distinct karyotypes at the diploid level suggests divergence through structural rearrangements and hints at isolation barriers between karyotypes due to irregularities.

REPRODUCTIVE ISOLATION.
All attempts to produce hybrids between any of the members of the A and C karyotype groups have failed thus far. A strong cross-incompatibility barrier is obvious even if hybrids will be obtained later by finding compatible genotypes. Within the subgroups, As is isolated from Al and Cp from Cv by hybrid sterility.

SYNAPSIS.
As was predicted from the karyotypes, sterility in hybrids is due to structural differences. Multivalents indicate interchange differences; anaphase bridges with acentric fragments indicate inversions (Figure 2). Homologies of the genomes in both AsAl and CpCv hybrids are clearly indicated, however, by the notable absence of univalents (RAJHATHY 1961).

THE TETRAPLOIDS

KARYOTYPES.
The four tetraploid species are classified into two groups by their karyotypes. Three of these share the one designated AB, and two features of this karyotype should be noted (Figure 3). The A is a replica of diploid As, and B appears to be a slightly modified form of A. This would suggest an autoploid or nearly autoploid origin of these tetraploids (SADASIVAIAH and RAJHATHY 1968). The other karyotype is found in the recently discovered tetraploid, A. magna
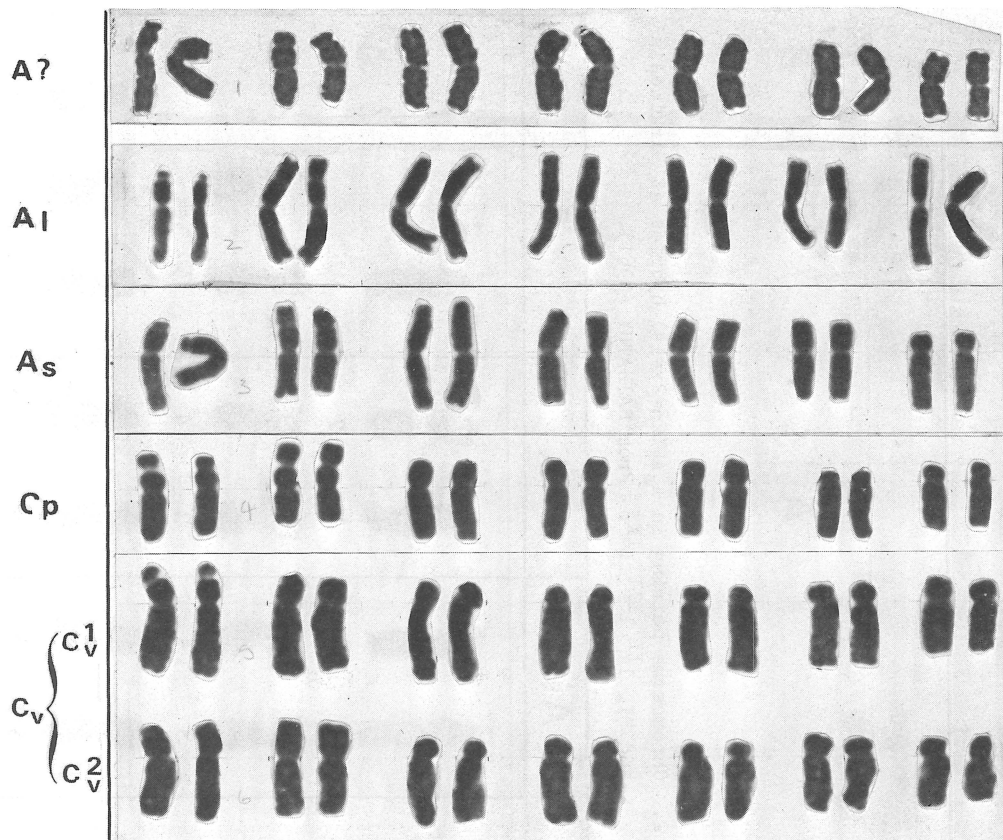
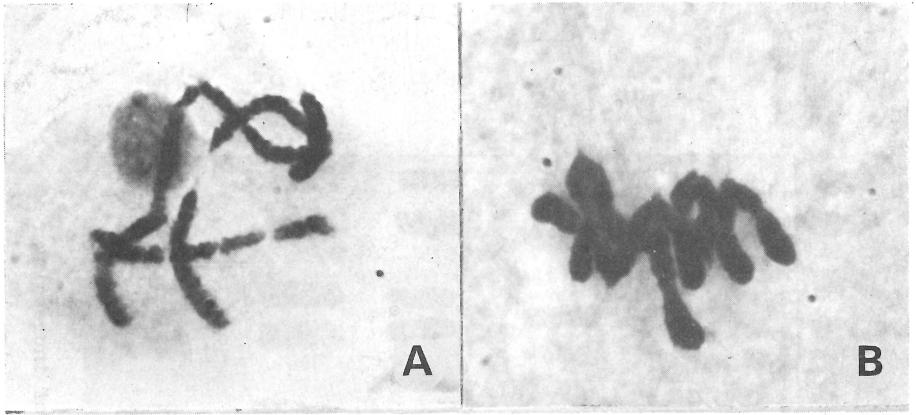Figure 1. Karyotypes in diploid Avena in order of increasing asymmetry from top to bottom.

Figure 2.   Chromosome pairing in $A_s A_1$ (2n=2x=14) hybrids at Diakinesis and MI, 1^{II} 1^{III} 1^{IX}. From RAJHATHY (1961).

Figure 3.   Karyotype prepared from an $A_s AB$ triploid (2n=3x=21) hybrid. From SADASIVAIAH and RAJHATHY (1968).

(MURPHY et al. 1968). This is evidently different from and more asymmetrical than the AB karyotype (Figure 4). It resembles a combination of the A and C karyotypes.
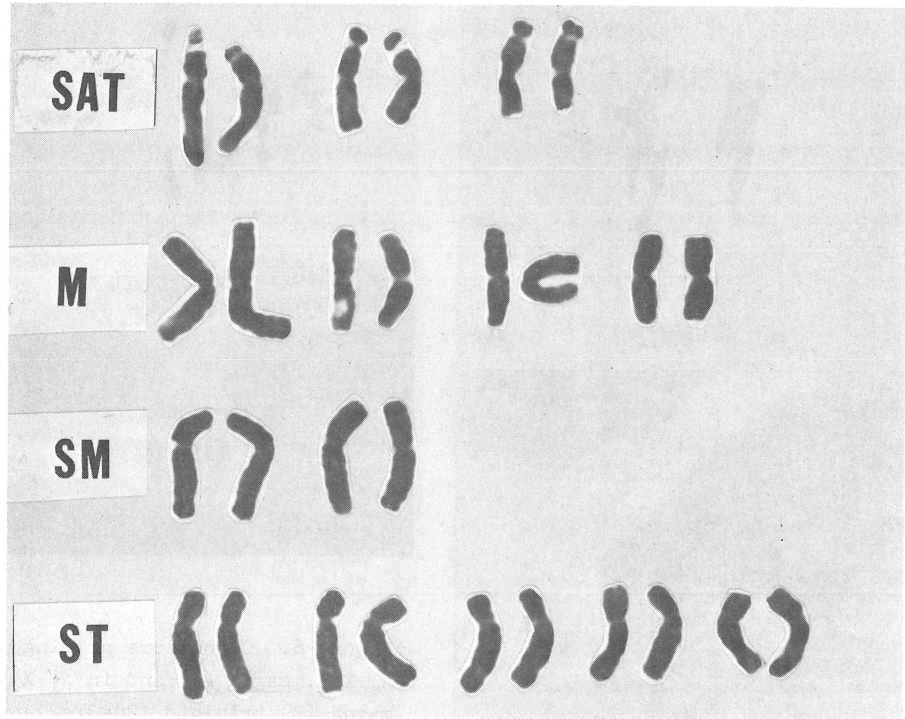

Figure 4.   Karyotype of A. magna.   Adapted from RAJHATHY and
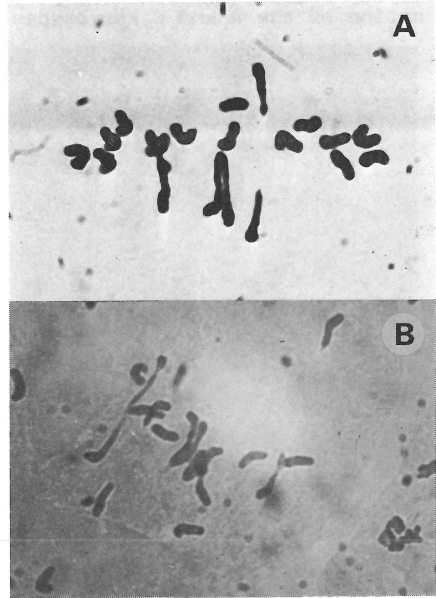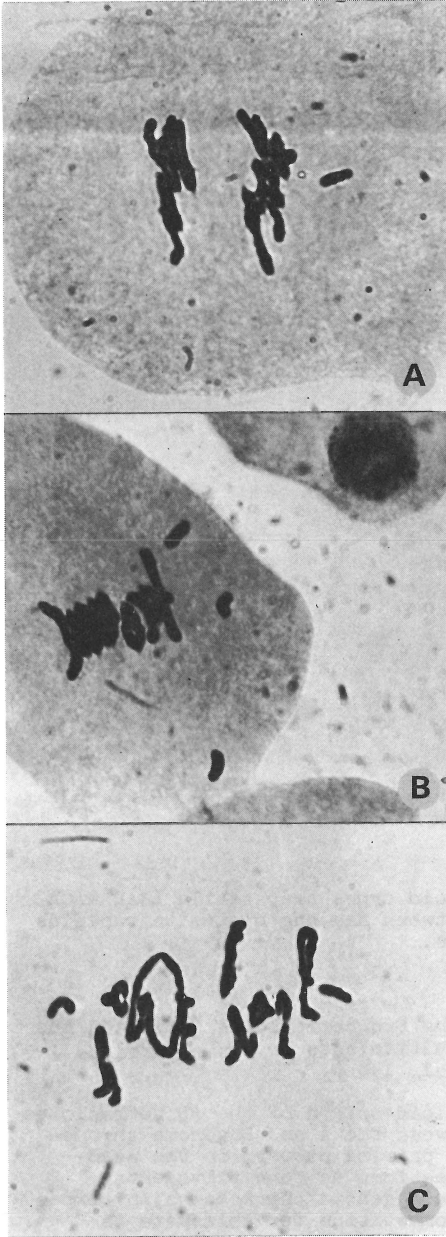   SADASIVAIAH (1968).

REPRODUCTIVE ISOLATION.
    Hybrids between the two tetraploid types are sterile (SADANAGA et al. 1968). So are the hybrids between any one of the tetraploids and any of the diploids or hexaploids.

SYNAPSIS.
    Meiotic pairing in hybrids of the two tetraploids indicates one common genome (maximum of 8II) and multivalents are attributed to structural differences (SADANAGA et al. 1968).

    The prediction of a quasi-autoploid origin of the AB tetraploids from the karyotypic similarities between the A and B genome chromosomes was fully substantiated by the pairing pattern in the AsAB triploids (Figure 5). The chromosomes form up to 6 trivalents, clearly expressing the success of the B genome chromosomes in competition for pairing. Even when the competition for chiasmata is increased as in the AsAsAB situation, the AB chromosomes are so successful that only an average of 4 bivalents are formed, while the rest of the chromosomes associate in trivalents and quadrivalents. This behavior poses the problem of diploidization, since the AABB tetraploids are bivalent formers. The diploidizing system operating in these tetraploids has yet to be uncovered (HOLDEN 1967, SADASIVAIAH and RAJHATHY 1968).

↑Figure 6. Chromosome pairing in A_s X $\underline{A}$. $\underline{magna}$ (A) and in A_1 X $\underline{A}$. $\underline{magna}$ (B) triploid (2n=3x=21) hybrids; A. 13^I 1^{II} 2^{III}, B. 8^I 5^{II} 1^{III}.

←Figure 5. Chromosome pairing in A_sAB (A and B) and in A_sA_sAB (C) hybrids; A. 1^I 1^{II} 6^{III}, B. 3^I 9^{II}, C. 2^I 3^{II} 3^{III} 1^V 1^{VI} Adapted from SADASIVAIAH and RAJHATHY (1968).

Although one genome is indicated to be common to the AB tetraploids and A. magna, pairing is much lower in hybrids between the As genome diploids and A. magna than would be expected (RAJHATHY and SADASIVAIAH 1969, LADIZINSKY 1969). However, pairing is about as high as expected when Al instead of As is used in the hybrids (Table 2, Figure 6). The proportion of the complement paired in the As combination is only .29, while in the Al combination it is .56. Thus, the Al genome appears to be the more probable donor of the A genome of A. magna. I shall return to A. magna and discuss the identity of its second genome and chromosome behaviour in pentaploid hybrids in the next section.

Table 2. Chromosome pairing in A. magna triploid hybrids derived from As and Al genome diploids.

Combination	Genomes	I	II	III	Proportion of complement paired
A. hirtula x A. magna	As AC	14.8	2.5	.4	.29
A. longiglumis x A. magna	Al AC	9.1	4.5	.9	.56

THE HEXAPLOIDS

The four hexaploid oat species share the same karyotype, designated ACD (Figure 7). The striking feature of the hexaploid karyotype is its asymmetry due to the wide range in size and centromere location of the chromosomes. The designation tells us about three substantial features. Firstly, the B genome is not one of the building blocks of the hexaploids; secondly, the A and C genomes are; and thirdly, the identity of the D genome donor is not yet known. As would be expected from the common genomes, the hexaploid species form an interfertile, morphologically and ecologically diverse complex.

The first evidence for a single common genome in the AB tetraploids and the hexaploids was presented by NISHIYAMA (1929) and later by EMME (1932) from chromosome pairing in pentaploid hybrids. This was confirmed by RAJHATHY and MORRISON (1960). Thus, the AB tetraploids did not participate in the formation of the hexaploids.

The presence of the A genome in the hexaploids was first suggested by KIHARA and NISHIYAMA (1932) on the basis of chromosome pairing in A genome diploid X hexaploid hybrids and was later confirmed by MARSHALL and MYERS (1961). The presence of the A and absence of the B genome was also indicated by comparisons of the AB and the hexaploid karyotypes (RAJHATHY and MORRISON 1959). Now we have reason to believe, as we shall see later, that the Al rather than the As diploid was the donor of the A genome of the hexaploids.

When, for the first time in 1965, we saw the karyotype of A. ventricosa, later designated Cv, immediately it became a suspect as a donor of the subterminal chromosomes of the hexaploids. The same idea occurred also to LADIZINSKY and ZOHARY (1967). The notion gained support first from meiotic and later from biochemical studies (RAJHATHY 1966, THOMAS and RAJHATHY 1967, THOMAS and JONES 1968). The cytological results are summed up in Table 3. From these it is clear that the hexaploids have genomes in common with both A and C genome diploids and that the hexaploid-diploid homology is greater than that of A to C. This estimate is further strengthened if the action of a
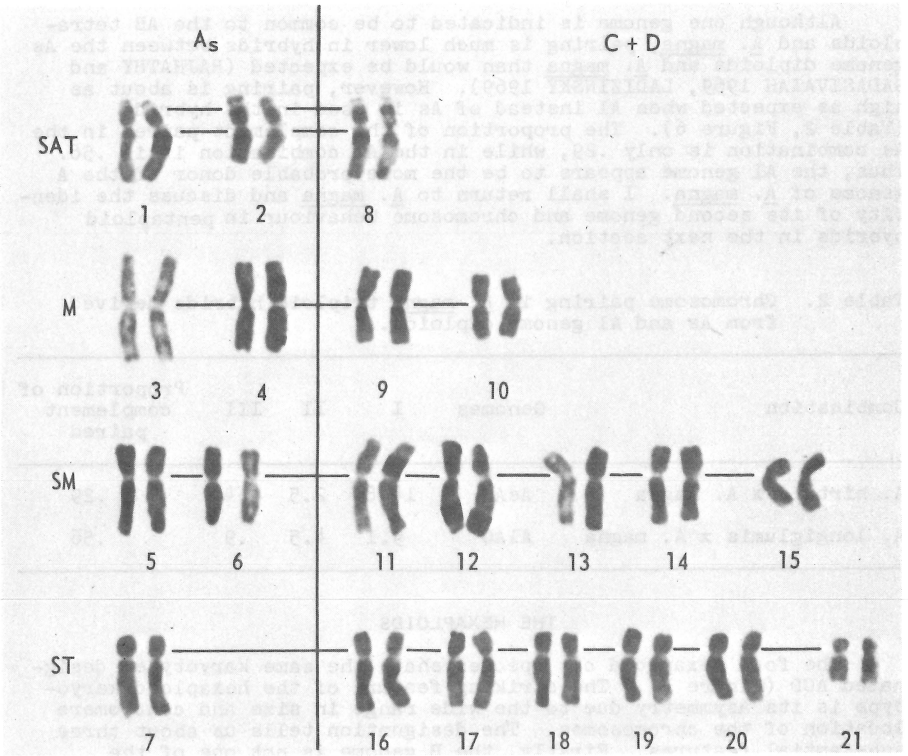
Figure 7. The standard karyotype of hexaploid Avena. If As is
           substituted for Al, then chromosomes 1-4, 9-10 and 11 or
           12 are putative members of A . Chromosomes 8, 7 and 16-20
           are putative members of C. From RAJHATHY (1963).

Table 3. Chromosome pairing in hybrids of A and C genome diploids
          and the hexaploid, and between their synthetic alloploids.
          Adapted from THOMAS and RAJHATHY (1967).

Combination	Genomes	I	II	III
A. hirtula x A. sativa	AsACD	13.9	5.9	.7
A. pilosa x A. sativa	CpACD	17.9	4.9	.1
(A. hirtula x A. sativa)^2 X (A. pilosa x A. sativa)^2	AsCpAACCDD	11.5	20.8	1.0

diploidizing gene, discriminating between homology and homoeology, is assumed, because it did not prevent pairing between the genomes of the diploid donors and their equivalent genomes in the hexaploids but it did between the diploid genomes. This suggests that the threshold of pairing affinities is above homoeology between the equivalent 2x and 6x genomes, but it does not exceed the level of homoeology between the two 2x genomes (THOMAS and RAJHATHY 1967).

At this point the question is: what is the source of the A and C genomes of the hexaploids? Rather compelling cytological, morphological and biochemical results point to A. magna, the recently discovered tetraploid. The strongest cytological evidence comes from chromosome pairing in hybrids of A. magna X hexaploid, and is clearly illustrated by the difference in pairing patterns between pentaploid hybrids derived from AB tetraploids and from A. magna (Table 4, Figure 8). In the ABACD pentaploid hybrid only a single common
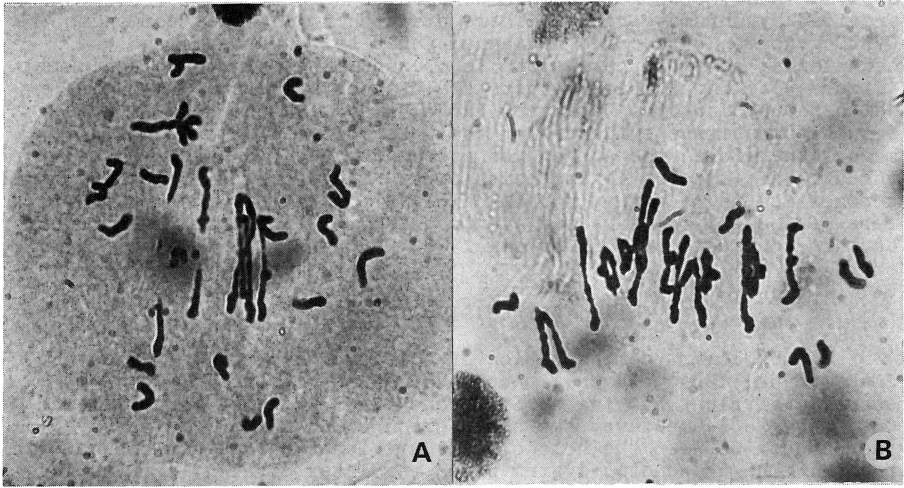

Figure 8. Chromosome pairing in ABACD (A) and in A. magna X AACCDD (B) pentaploid (2n=5x=35) hybrids; A. $23^I \ 6^{II}$, B. $7^I \ 9^{II} \ 2^{III} \ 1^{IV}$. Adapted from RAJHATHY and SADASIVAIAH (1969).

genome is indicated. Incidentally, the AB genome chromosomes failed to express their homoeology to A in this combination which again implies some sort of effect suppressing homoeologous pairing in a hexaploid background. In contrast, both genomes of A. magna participated in pairing in its hybrids with the hexaploids. The same results were obtained independently by RAJHATHY and SADASIVAIAH (1969) and LADIZINSKY (1969). Thus, A. magna is the putative ancestral tetraploid of the hexaploids.

Table 4.   Chromosome pairing in pentaploid hybrids derived from AB
           and AC genome tetraploids. Adapted from RAJHATHY and
           SADASIVAIAH (1969).

Combination	Genomes	I	II	III	IV	Proportion of complement paired
A. barbata x A. sterilis	AABCD	22.8 (15-30)	4.6 (2-7)	1.0 (0-2)	--	.34
A. magna x A. sterilis	AACCD	8.0 (5-13)	10.1 (5-13)	1.8 (0-3)	.3 (0-2)	.76

As I stated before, one of the genomes of A. magna is A and
because of its better pairing with Al than As, the former is consid-
ered the donor. What do we know about the identity of its second
genome? Is it C or D? Since a hybrid of A. magna X C genome
diploids has yet to be examined we turn to another line of evidence
provided by chromatography. There are 6 phenolic spots common to the
C-ACD genomes, 2 to C and A. magna, and 8 to C, A. magna and the
hexaploids; none of these spots is present in the A genome diploids
(Figure 9). In addition 7 spots are diagnostic to the hexaploids,
which should mark the D genome (RAJHATHY et al., in press). These
results constitute evidence for the C as the second genome of A.
magna, therefore, the AC genomes appear to have been transmitted
through this species to the hexaploids. The presence of 5 subterminal
chromosomes in A. magna, morphological similarities, the ultrastruc-
ture of the chloroplasts and electrophoretic results all lend support
to this conclusion (STEER et al. 1970, MURRAY et al. 1970).

                         DIPLOIDIZATION

The brilliant demonstration of homoeologous groups in wheat by
SEARS (1952, 1954) and the function of a gene on chromosome 5B
ensuring bivalent pairing by SEARS and OKAMOTO (1958) and RILEY and
CHAPMAN (1958) blew away the smokescreen of bivalency and resolved
the paradox between the homoeologous architecture and diploid meiotic
regime. The 5B genetic system which regulates bivalent pairing is
well known and needs no discussion here (RILEY and LAW 1965, SEARS
1969). It is tempting to generalize and predict a diploidizing
mechanism in many bivalent forming polyploids, because of its effi-
ciency in converting a multivalent forming regime into a bivalent
forming one by a single mutational step. However, a similar system
has yet to be demonstrated in another alloploid. Although KIMBER
(1961) reported evidence for genetic control of bivalent pairing in
tetraploid cotton and tobacco, this may or may not be similar to the
5B system, since no evidence could be obtained as to the mechanism.
I shall present evidence for a 5B-like system in hexaploid Avena.

Hexaploid oats are bivalent forming, many of the loci are
triplicated and they tolerate chromosome deficiency so well that a
monosomic series is now nearing completion. These features indicate
basically similar architectures in both wheat and oats.

The first evidence for a genetic regulation of bivalency in
hexaploid oats came from the absence of pairing in the only 21
chromosome euhaploid ever reported in Avena by NISHIYAMA and TABATA
(1964). Only 1.4% of the chromosomes paired which ruled out differ-
ential affinities as the sole reason for bivalency in the normal
euploid. In contrast, 36% of the 20 chromosomes paired in one of the
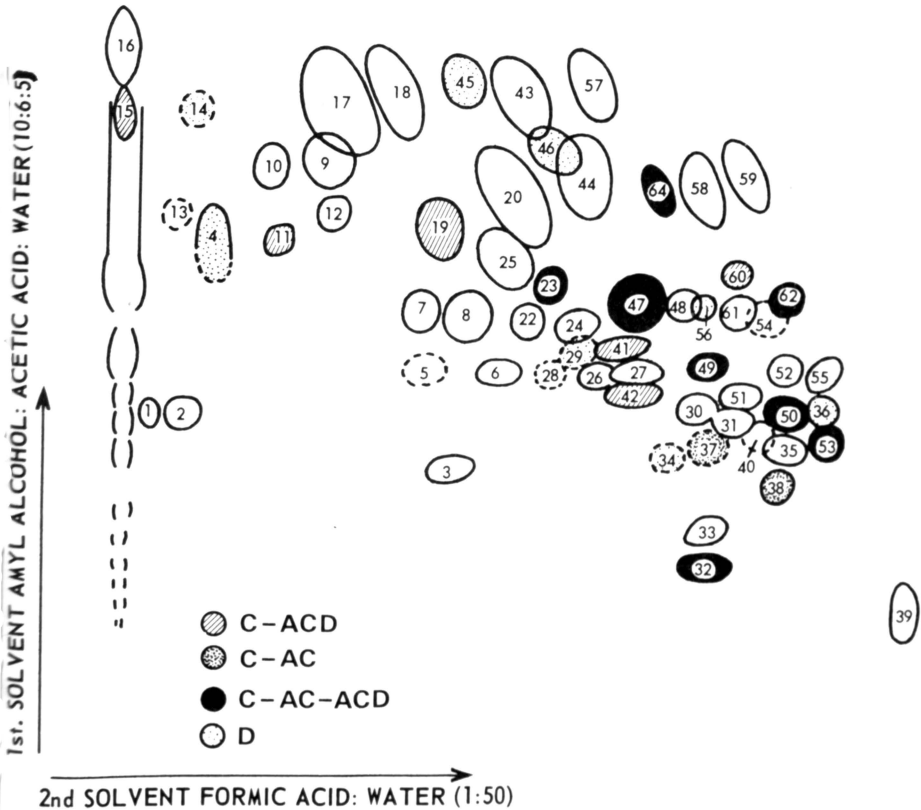
Figure 9.   The master chromatogram of Avena. The white spots are
            common to most or all of the species, marking the A
            genome. Adapted from RAJHATHY et al. (in manuscript).

nullihaploids obtained by GAUTHIER and McGINNIS (1967). They con-
cluded that a gene which effectively suppressed homoeologous pairing
in the hemizygous condition in the euhaploid, was located on the
chromosome missing from the critical nullihaploid. The function of
this gene appears to be very similar to that of 5B in wheat. Rela-
ting this to my research it seems safe to assume that this gene
prevents the B genome chromosomes from pairing in the ABACD penta-
ploid hybrids, because they are homoeologous to those of the A genome
as was clearly reflected by their pairing behaviour in AsAB triploid
hybrids. Similarly, this gene is probably responsible for preventing
pairing between the chromosomes of the A and C genomes in the pre-
sence of the hexaploid complement.

        There is more evidence. We have recently discovered a Moroccan
genotype of A. longiglumis, a wild diploid, which induces homoeolo-
gous pairing in the hexaploid complement. We compared chromosome
pairing behaviour in hybrids between two genotypes of A. longiglumis
(2x) and A. sativa (6x). From the hybrid with longiglumis I, tri-
valents were virtually absent and only 41% of the chromosomes paired;
this originated from the Al and A genomes (Table 5). In the hybrid

with <u>longiglumis</u> II, the Moroccan genotype, 75% of the complement
paired with a maximum of 6 trivalents, many of which were hetero-
morphic (RAJHATHY and McKENZIE, unpublished). Clearly, the <u>longiglu-
mis</u> II genotype suppressed the function of the diploidizing gene in
the hexaploid complement. According to the simplest hypothesis of
allelic relationships, the <u>longiglumis</u> II condition is dominant to
the <u>sativa</u> condition, which, in turn, is dominant to the <u>longiglumis</u>
I condition which has a null effect on pairing. This system is simi-
lar, if not identical, to the <u>speltoides</u> - <u>aestivum</u> - <u>longissima</u>
system described by RILEY (1965) in wheat. Similar systems of gene-
tic diploidization demonstrated in wheat and oats, and implicated in
cotton and tobacco, lend validity to the notion of its general occur-
rence probably in many bivalent-forming alloploids.

Table 5. Chromosome pairing in euploid, euhaploid and a nullihaploid
          of hexaploid <u>Avena</u>, and in tetraploid hybrids derived from
          two different genotypes of <u>A</u>. longiglumis (2x).

Line or combination	2n	I	II	III	Proportion of complement paired
Euploid	42	--	21.0	--	1.00
Euhaploid	21	20.7	.1	<.1	.14
Nullihaploid	20	12.8	2.9	.5	.36
A. longiglumis I x 6x	28	16.4	5.7	.1	.41
A. longiglumis II x 6x	28	6.8	4.8	3.1*	.75

*Maximum of 6III, many heteromorphic.

     An alternative and classical mode of diploidization, often sug-
gested in the literature, is structural diploidization (see STEBBINS
1950). This implies the accumulation of structural differences
leading to differential affinities (DARLINGTON 1937) which disrupt
the random pairing of the originally more or less homologous chromo-
somes. The essential difference between the genetic and structural
concepts is one of time of origin. The 5B effect is a genetic
enhancement of 'preexisting' differential affinities evolved 'before'
hybridization and doubling, while structural differences continue to
accumulate, and thus perfect bivalency in the raw alloploid 'after'
its formation. Experimental evidence for this is lacking for the
latter alternative, therefore it is a speculative concept. It appears
improbable in nature, because it would extend the "bottleneck" of
meiotic irregularities and concomitant reduced fertility over many
generations, rendering the initially small raw alloploid population
at a competitive disadvantage during this time.

                        THE ORIGIN OF HOMOEOLOGY

     Homoeology is an essential preadaptation for the diploidizing
gene to function. According to the concept of monophyletic descent,
which in fact is reflected by the homoeology of the ancestral
genomes, these were initially homologous. The process of divergence,
which reduced homology to the level of homoeology is still poorly
understood.

The set of wheat homoeologues are thought to have been derived from the chromosomes of a diploid prototype and the members of each set are thought to have become different from each other as the separate ancestral diploids evolved (cf. RILEY and LAW 1965). The isolation of the homoeologues was further maintained in the polyploid by the 5B mutation. The level of homoeology was attained by the accumulation and selection of differential adaptive gene complexes, while structural changes were of minor importance. Evidence for this was provided by the fact that the amount of pairing in nullisomic-5B haploids equalled the summation of pairing in hybrids between the contemporary diploid progenitors (MOCHIZUKI and OKAMOTO 1961, KIMBER and RILEY 1963). The accumulation of interchange differences between the diploid genomes would seem to be incompatible with the integrity of the homoeologous groups which has been demonstrated by nullisomic-tetrasomic tests (SEARS 1966). These tests, however, did not rule out inversions and deletions. In fact, some differences between the chromosomes within homoeologous groups are noticeable, although the informative value of wheat karyotypes is limited because of the relative uniformity of the chromosomes (MORRISON 1953).

Nullisomic-tetrasomic tests are not available in _Avena_ as yet, but tentative conclusions may be drawn from the karyotypes and pairing behaviours. It is evident from the asymmetry of the hexaploid karyotype that homoeologous triplets must consist of morphologically distinct chromosomes. This was indicated by the hetermorphy of trivalents when the function of the diploidizing gene was suppressed. This and the distinctly different karyotypes of the ancestral diploids point to structural differentiation as a major factor in their divergence. Size differences may have evolved by deletions, arm ratios by pericentric inversions. An example of a pericentric inversion noticeably changing the karyotype was obtained in the putative C genone progenitor, _A. ventricosa_ (CvCv). This population is polymorphic in having two karyotypes, one of which (CvlCvl) has exclusively subterminal chromosomes, whereas in the other (Cv2Cv2), one pair was converted into a pair of submedians. The absence of multivalents and the presence of an asymmetrical bivalent in the heterozygote clearly indicate a single pericentric inversion for the origin of the submedian pair (RAJHATHY, unpublished).

We can make some assumptions if structural differentiation is accepted as a major factor in reducing homology to the level of homoeology in the ancestral diploids and if bivalency in hexaploid oats is under genetic control. The diploidizing mutation should have been redundant and without selective premium if differential affinities 'per se' would have ensured bivalent pairing. As this was clearly not the case, the mutation was essential to reinforce differential affinities regardless of whether they originated primarily through genetic divergence as in wheat or structural divergence as in oats. On this basis, it is even more difficult to accept the concept of structural diploidization in a multivalent forming alloploid.

THE ALLOPLOID MODELS: WHEAT AND OATS

The fundamental elements of the cytogenetic architectures, namely homoeology of the genomes and genic diploidization, appear to be similar in both polyploid wheat and oats. There are differences, however, within the confines of this evolutionary blueprint.

The evolution of the oat species was apparently confined to the genus. Even the taxonomically closest genera in the Tribe _Aveneae_ are cytogenetically remote from _Avena_. In contrast, wheat species 'in sensu stricto' are enmeshed into a large group of species, which were, until recently, classified into several genera. They are

directly or indirectly connected to all genera in the Tribe
Triticeae.

The chromosome phenotype is much more informative in oats than
in wheat, which 'per se' implies that structural differentiation in
the divergence of the ancestral diploids and in acquiring homoeology
was more important in oats. The evolution of the A, C and presumably
the D genomes reflects a phase of major repatterning, followed by a
phase of relatively minor changes which gave 3 subgroups in both A
and C (Figure 10). Polyploid convergence reduced the number of
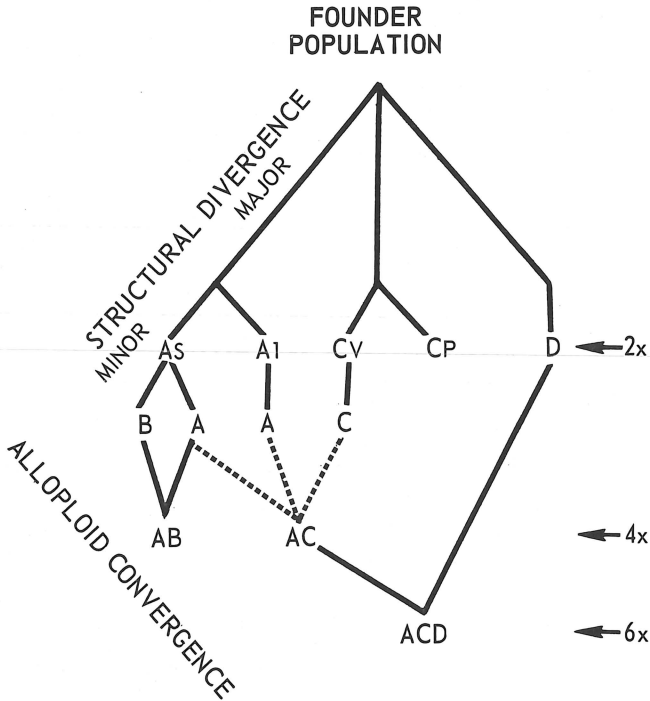karyotypes to two in the tetraploids and one in the hexaploids.

Figure 10. Outline of genome differentiation in Avena.

The diversity in the diploid karyotypes may indicate a trend in
karyotype evolution. An increasing asymmetry from A? to Cv2 is
apparent (Figure 1). Since the symmetrical A karyotype occurs in
every polyploid species this is probably the oldest one and may
reflect on the karyotype of the founder population. This is also
supported by the symmetrical karyotypes of closely related genera
such as Arrhenatherum, Helictotrichon, etc. The generally accepted
concept of general progression toward asymmetry is based on the
metacentric chromosomes of the algae, bryophytes and primitive vascu-
lar plants and on trends in families such as the Cichorieae (STEBBINS
1958) and Dipsacaceae (EHRENDORFER 1965). The general validity of
this concept was recently challenged by JONES (1970) who referred to
the Cycads and Podocarpaceae in which acro- and telocentrics repre-
sent the more primitive state and metacentrics in the latter family
originated by fusions (HAIR and BEUZENBERG 1958). The Avenae pro-
vide another example supporting the original concept. However, JONES
(1970) is probably correct in that chromosome complements may have
evolved in different ways in different organisms.

The AB and AC groups of tetraploids in <u>Avena</u> represent two different avenues of evolution; the former through auto- or nearly autoploidy, the latter from more diverged diploids. While the AB group remained outside of the mainstream of evolution, the AC tetraploid transmitted these diploid genomes to the hexaploids. Although, the <u>araraticum</u> - <u>timopheevi</u> group of tetraploids is isolated from the other species in wheat, this is genic rather than genomic (cf. WAGENAAR 1961).

From this brief summary it is clear that the oat model is still poorly understood and a great deal more information is needed to fill the information gap between oats and wheats. The identification of the D genome carrier and the completion of an aneuploid series should enable us to identify the homoeologous groups and to test the genetic equivalence of the triplets. It should also facilitate studies of gene evolution taking advantage of biochemical markers evolving under different levels of selection pressure. Homoeologous loci present an unique opportunity to study the origin of new gene functions, since they allow experimentation with new mutations while the original function is not impaired. Electrophoretic and chromatographic studies of appropriate aneuploid combinations should make this facet of the alloploid condition accessible.

A thorough understanding of the few alloploid models should also enable us to inquire into and eventually repair the flaws of synthetic alloploids. This may lead to the production of new crop species to meet increasing demands of our ever increasing population.

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