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Genetic Regulation of Diploid-Like Chromosome Pairing in *Avena*

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Summary. The genetic control of diploid-like chromosome pairing in *Avena* is discussed and compared with the diploidizing mechanisms in the hexaploid breadwheat and the hexaploid tall fescue. An examination of the published literature reveals that there is a remarkable similarity in these three regulatory mechanisms (Table 3). It is further concluded that the diploidizing gene system in the polyploid species of *Avena* is as complex as in wheat. A reappraisal of the published information on *Avena* and other polyploids, followed by further studies, might yield more information about the functional aspects of the diploidizing mechanisms.

1. Introduction

Although allopolyploidy has provided the basis for the evolution of our most important grain, forage and fibre crops, the super-imposition of a precise genetic control on chromosome pairing could be vital for conferring meiotic, and hence reproductive, stability in sexually reproducing polyploids. Thus, in the allohexaploid (2n = 6x = 42) bread wheat (AABBDD) (Okamoto 1957; Riley 1960), allohexaploid oats (AACCDD) (Rajhathy and Thomas 1972, 1974) and allohexaploid tall fescue (*Festuca arundinacea* Schreb., AABBCC) (Jauhar 1975a,b) the diploid-like chromosome pairing is under genetic control. It is likely that the diploid-like meiosis in most, if not all, other natural polyploids is also genetically regulated: without such a control precise bivalent pairing in these polyploids, having several sets of related genomes, would not be achieved. And some evidence of this is available in the published literature on several polyploid taxa of grasses and of other families.

In a recent comprehensive monograph on the cytogenetics of oats, Rajhathy and Thomas (1974) have discussed the genetic control of diploid-like pairing in the polyploid species of *Avena*. I feel, however, that there is considerably more evidence of the presence of a diploidizing gene system in *Avena* in the published literature than these authors have considered, and some of this evidence is discussed in this report. A reappraisal of the published literature on *Avena*, and indeed on several other polyploid taxa, may also yield some useful information on the genetic regulation of chromosome pairing.

2. Effectiveness of genetic control of chromosome pairing in polyploid species

Pairing in eu-, aneu- and nulli-haploids

The amount of chiasmate pairing in the polyhaploids (eu-, aneu- and nulli-haploids) of a species, or in the haploid complements of its hybrids with related species, could provide a critical test of the effectiveness of the genetic control of pairing. Thus in a polyhaploid (2n = 3x = 21) of tall fescue (*Festuca arundinacea* Schreb.), upto 7_{II} (mean = 4.01_{II} per cell), among them several ring bivalents, were observed by Malik and Tripathi (1970), presumably as a result of the hemizygous ineffectiveness of the genetic control in this species (Jauhar 1975 a,b). In wheat (Riley and Chapman 1958) and oats, *Avena byzantina* C. Koch. (Nishiyama and Tabata 1964), however, the polyhaploids (2n = 3x = 21) show very little chiasmate pairing because the regulatory mechanism is effective in the hemizygous state. In the wheat euhaploids, rod bivalents are occasionally formed (mean of 12 euhaploids = 0.97 per cell, Riley 1960), whereas in the oat euhaploids even rod bivalents are much

Table 1. Dosage effect of the diploidizing gene(s) in *Avena*

Ploidy level and hybrids	Chromosome number	Genomic constitution	Supposed* number of regulators	Multivalents V	IV	III
Avena sativa L. Nullihaploid	2n = 20	A C D-1	Nil		-	0.50**
A. sativa L. Nulli-tetra haploid	2n = 21	A C D-1+1	1		-	-
A. byzantina Euhaploid	2n = 21	A C D	1		-	0.003***
A. sativa	2n = 42	AA CC DD	2		-	-
A. byzantina	2n = 42	AA CC DD	2		-	-
A. abyssinica	2n = 28	AA BB	2		-	-
A. abyssinica × *A. sativa*	2n = 35	AA BCD	2		0.08	1.07
A. abyssinica × *A. byzantina*	2n = 35	AA BCD	2		0.04	0.71
A. hirtula × *A. sativa*	2n = 35	AAA CD	3		-	0.95
A. abyssinica × *A. sativa* Decaploids	2n = 70	AAAA BBCCDD	4		0.29	
A. longiglumis CW 57 × *A. sativa* var. Pendek	2n = 28	A ACD	Nil (whole regulatory apparatus presumably switched off)	0.11	0.41	3.11

* These values are based on the assumption that A genome has the principal regulator like the
** The authors observed a mean of 3.5 associations per cell. The values for trivalents and bivalents
*** Only two trivalents observed in the 714 cells scored

rarer (Table 1) and a "ring-shaped bivalent was never observed" in the 714 cells analysed (Nishiyama and Tabata, loc. cit).

It would, therefore, appear that the genetic control suppressing homoeologous pairing is much more effective in the hemizygous state in *A. byzantina*, and indeed in *A. sativa* (Bhatti 1972; Thomas and Bhatti 1975), than in *Triticum aestivum*. It seems that there are different degrees of effectiveness of genetic control in these three hexaploid species, being very strong in *A. sativa* and *A. byzantina* and least effective in the tall fescue polyhaploids. An alternative possibility is that the diploidizing gene(s) in the hemizygous state show amplified activity in oats and wheat, but not in tall fescue which is an incipient species. More polyhaploids derived by anther culture (Craig 1974; Niizeki and Kita 1974) should be studied in all these species before drawing any more conclusions as to the functional aspects of these three diploidizing mechanisms. A comparison of the three regulatory mechanisms is given in Table 3.

In a nulli-tetrahaploid (2n - 1 + 1 = 21) of *A. sativa*, which was nullisomic for one chromosome but had an extra dose of another (Bhatti 1972), very little chiasmate homoeologous pairing occurred and a mean of only 0.05_{II} per cell (in addition to one homologous bivalent) was observed; this is even less than one-third the figure obtained in the *A. byzantina* polyhaploid (Table 1) and only about one-twentieth of that realized in the wheat euhaploids (Riley 1960). Furthermore, in this nulli-tetrahaploid side-to-side associations of univalents at diakinesis and metaphase I, which are presumably a reflection of residual homology in the haploids of bread wheat (Person 1955)

II	I	Chiasmata per cell	Chiasmata per paired chromosome	Number of cells scored	Reference
2.90	12.80			237	Gauthier and McGinnis, 1968
(1+)0.05	18.89			93	Calculated from Bhatti, 1972
0.17	20.65			714	Calculated from Nishiyama and Tabata, 1964
21	-	39.70	0.945	20	
21	-				
14	-	26.65	0.952	20	
5.63	20.15	8.10	0.546	200 cells (10 hybrids)	
6.59	19.53	8.33	0.532	100 cells (5 hybrids)	
6.85	18.45	14.30	0.864	40 (2 hybrids)	
33.44 (35_{II} in several cells)	2.31	58.40	0.857	100 (5 hybrids)	Calculated from Thomas and Jones, 1964
4.83	6.83				Rajhathy and Thomas, 1972

5B of wheat
are given in Rajhathy and Thomas (1974, p. 63)

and of *Pennisetum typhoides* (Jauhar 1970), were less frequent than in wheat (Person, loc. cit). These somewhat contrasting results in the polyhaploids of oats and wheat have been interpreted as indicating greater structural divergence of the constituent genomes and a stronger suppression of homoeologous pairing in *A. sativa* than in *T. aestivum* (Thomas and Bhatti 1975).

It may, well, be that genetic information for bivalent pairing is present in more than one genome (possibly A and C) of *A. sativa*, so that if one chromosome carrying the 'regulator' is lost, e.g. in the nulli-haploid (Gauthier and McGinnis 1968), the amount of homoeologous pairing observed is still far less than in the nulli-5B haploids of wheat (Riley 1960; Noronha-Wagner and Mello-Sampayo 1972). The nullisomic-tetrasomic compensation pattern in *A. sativa* (Bhatti 1972; Thomas and Bhatti 1975) conforms largely to that in wheat (Sears 1966), also suggesting that inter-genomal differentiation in *A. sativa* is not much different from that in *T. aestivum*.

It seems that the genetic control in *A. sativa* is also as complex as that being revealed in *T. aestivum*. This point is discussed later in this paper.

3. Is genetic control of pairing hemizygous ineffective in tetraploid species of *Avena*?

The type of hemizygous ineffective genetic control discussed in polyploid species of *Festuca* (Jauhar 1975b) was also inferred for some tetraploid species of *Avena*, e.g. *A. barbata*. However, the inference of a hemizygous ineffective diploidizing mechanism in *A. barbata*

(2n = 28) by Sadasivaiah and Rajhathy (1968) and by Rajhathy and Thomas (1974, p.56) deserves reconsideration. Although the genomic constitution of *barbata* is not established, one view is that it is an autotetraploid (Ladizinsky 1973), yet these workers based their conclusion on trivalent formation in its triploid hybrids (A^S AA) with *A. strigosa* (A^S A^S).

On the basis of the published data (Thomas and Jones 1964) on chromosome pairing in autoallodecaploids (AAAA BB CC DD) between *A. abyssinica* (AA BB) and *A. sativa* (AA CC DD), Jauhar (1975c) suggested that A is the "hot genome" carrying the principal regulator of bivalent pairing, like the 5B of wheat. If this is indeed true, as discussed later in section 4 d, then the diploid-like pairing in *A. barbata* (AAAA) could perhaps be due to the dosage effect of the diploidizing gene which in four doses brings about 2 × 2 pairing of the homologous sets. This, then, would well explain the results of Ladizinsky (1973) that a single gene in the quadriplex condition could control bivalent pairing in *barbata*. A similar dosage effect of the regulatory mechanism was observed in dodecaploid (2n = 12x = 84) tall fescue (Jauhar 1975c).

When the diploidizing mechanism is fully effective in the hemizygous condition in hexaploid oats, it should perhaps be effective in tetraploid oats too, unless a totally different regulatory mechanism is working in the tetraploids. It seems unlikely that the genetic control of bivalent pairing should be hemizygous effective in some tetraploid species of *Avena* (Rajhathy and Thomas 1974, p. 57), but ineffective in some other tetraploid species of the same genus (Rajhathy and Thomas 1974, p.56).

It is not unlikely that the hemizygous ineffective genetic control of bivalent pairing observed in polyploid species of *Festuca* (Jauhar 1975b) may be of wide occurrence in the grass family, and that such a regulatory mechanism may be working in some polyploid taxa of other families also. The data of Khoshoo and Arora (1969) on chromosome pairing in the hexaploid *Verbena aubleita* (2n = 6x = 30) and its hybrids with the diploid *V. tenuisecta* (2n = 10) can be meaningfully explained on the basis of the existence of a regulatory mechanism in the hexaploid *aubleita*, which exercises its regulatory control on bivalent pairing when it is present in the disomic condition but is hemizygous ineffective: thus, is had no influence upon pairing in the haploid complements of the hybrids. Essentially similar data obtained in *Physaria vitulifera* (Mulligan 1967), and in *Rhynchosinapis* and *Hutera* (Harberd and McArthur 1972) can also be satisfactorily explained on the basis of this regulation hypothesis.

4. Chromosome pairing in some hybrids and amphiploids

No attempt will be made here to review the entire literature on chromosome pairing in hybrids and amphiploids of *Avena*. However, some examples which clearly demonstrate the genetic regulation of pairing will be discussed.

a) *A. abyssinica* (AABB, 2n = 28) × *A. strigosa* (A^SA^2, 2n = 14) amphiploids

The data on chromosome pairing in some euploid (2n = 42) and aneuploid (2n = 41, 40, 39, 38, 37, 25) amphiploids calculated from Thomas and Peregrine (1964) are given in Table 2. The A^S A^S genome of *strigosa* is homologous enough to the AA genome of *abyssinica* to form some quadrivalents and trivalents even in the euploid amphiploids and it would be difficult to assess precisely the extent of homoeologous pairing. But if more homoeologous pairing occurs in the aneuploids it should be reflected in higher multivalent frequency. Thus, while 31.83 percent of the chromosomes paired as multivalents in the 42-chromosome amphiploids and most aneuploids also showed similar multivalent frequencies, the 40-, 38-, and 25-chromosome amphiploids had 38.55, 43.47 and 48.00 percent, respectively, of their chromosomes paired as multivalents (Table 2).

Based on chromosome homologies alone, the mere loss of four chromosomes in the 38-chromosome amphiploids, for example, should not markedly affect the multivalent frequency which goes up, however, by 11.64 percent of the chromosome complement. This excessive pairing in these aneuploids studied by Thomas and Peregrine can be satisfactorily explained on the basis that some chromosomes carrying the genetic information for diploid-like pairing have been lost. This situation is somewhat analogous to the euploid (2n = 56) and aneuploid (2n = 52, 53, 54) amphiploids between *Triticum aestivum* and *Aegilops longissima*, with and with-

Table 2. Chromosome pairing in some euploid (2n = 42) and aneuploid amphiploids between *Avena abyssinica* (AA BB, 2n = 28) and *A. strigosa* (A^sA^s)

Chromosome number	Genomic constitution	Multivalents VI	V	IV	III	Total	II	I	% of the complement forming multivalents
42	AAA^SA^SBB	0.12 (0-1)	0.18 (0-1)	1.88 (0-3)	1.41 (0-4)	3.59	13.10 (8-19)	2.35 (0-9)	31.83
41	AAA^SA^SBB-1	0.01 (0-1)	0.15 (0-1)	1.85 (0-4)	1.54 (0-3)	3.55	13.15 (9-17)	1.61 (0-4)	31.29
40	AAA^SA^SBB-2	-	0.71 (0-2)	2.00 (0-5)	1.29 (0-2)	4.00	10.71 (7-14)	3.28 (1-8)	38.55
39	AAA^SA^SBB-3	0.33 (0-1)	0.12 (0-1)	1.38 (0-3)	0.92 (0-2)	2.75	11.46 (9-13)	2.08 (0-6)	27.85
38	AAA^SA^SBB-4	0.13 (0-1)	0.13 (0-1)	3.12 (1-5)	0.87 (1-3)	4.25	10.12 (9-12)	1.25 (0-3)	43.47
37	AAA^SA^SBB-5	-	0.20 (0-1)	2.20 (1-4)	0.80 (0-4)	3.20	10.18 (7-12)	2.80 (2-4)	32.97
25	AAA^SA^SBB-17	-	-	3.00 (1-4)	-	3.00	5.00 (3-5)	3.00 (1-3)	48.00

Range of chromosome configurations is given in brackets (Calculated from: Thomas and Peregrine 1964)

out chromosome 5B which has the principal regulator of bivalent pairing (Riley and Chapman 1963). While the amphiploids with 5B showed little homoeologous pairing, the loss of 5B in the aneuploids resulted in considerable homoeologus pairing. Similar results have been reported for euploid and aneuploid amphiploids between *Lolium multiflorum* and *Festuca arundinacea* (Jauhar 1975b,c).

b) *A. abyssinica* × *A. sativa* hybrids (2n = 5x = 35)

Since the diploidizing mechanism must have developed in the hexaploid as well as tetraploid species, it would be more appropriate to consider chromosome pairing in the pentaploid hybrids between them, and in the derived decaploids. The mean chromosome configurations in ten pentaploid (AABCD, 2n = 35) hybrids as calculated from Thomas and Jones (1964) are given in Table 1. While most of the bivalents could have formed between the A genomes of *abyssinica* and *sativa*, the formation of trivalents and quadrivalents is a reflection of inter-genomal pairing. In ten hybrids a mean of $0.08_{IV} + 1.07_{III} + 5.63_{II} + 20.15_{I}$ was observed. The formation of as many as 5.63 bivalents in these pentaploid hybrids would suggest that the A genomes from the parental species are sufficiently homologous to pass the discrimination limits of the diploidizing gene(s).

c) Other pentaploid hybrids

The mean chromosome configurations in the pentaploid hybrids between *A. abyssinica* × *A. byzantina*, its reciprocal *byzantina* × *abyssinica*, *abyssinica* × *sterilis*, and in *hirtula* (AAAA, 2n = 4x = 28) × *sativa* have been calculated from Thomas and Jones (1964) and some of these data are given in Table 1. The formation of as many as 6.59_{II} and 6.03_{II} in the *abyssinica* × *byzantina*, and *abyssinica* × *sterilis* hybrids, respectively, would also indicate that the A genomes of *abyssinica* and of the hexaploid species, *byzantina* and *sterilis*, are highly homologous.

d) *A. abyssinica* × *A. sativa* decaploids (2n = 10x = 70)

Chromosome pairing in the auto-allodecaploids (AAAA BB CC DD) derived by colchicine treatment of the pentaploid *abyssinica* × *sativa* hybrids described in section 4b was remarkably regular (see Thomas and Jones 1964). Whereas 35_{II} were observed in several cells, the mean per cell in five decaploids was 33.44_{II} (Table 1). The frequency of multivalents was much lower than in the parental pentaploid hybrids.

Thomas (1963) and Thomas and Jones (1964) explained the diploid-like synaptic behaviour of these decaploids entirely on the basis that the A genomes

of *abyssinica* and *sativa* had sufficiently differentiated as to show preferential pairing. It appears, however, that Thomas (1963) and Thomas and Jones (1964) have overemphasized the differentiation between the A genomes of *abyssinica* and *sativa*. Their explanation of the diploid-like pairing in the synthetic decaploids, resting entirely on the differentiation hypothesis, is questionable because it has been shown that there is complete homology between the A genomes of the tetraploid and the hexaploid species of *Avena* (Griffiths et al. 1959; Rajhathy and Morrison 1960). Even if the A genomes of *abyssinica* and *hirtulg* have somewhat differentiated from the A genome of *sativa*, as claimed by Thomas (1963) and Thomas and Jones (1964), their similarity would be more towards homology than homoeology. In any case, even some amount of differentiation might make it easier for the diploidizing gene(s) to make them pair as bivalents.

That the A genomes from the two species (*abyssinica* and *sativa*) are sufficiently homologous is borne out by the fact that they pass the discrimination limits of the diploidizing gene(s) in the pentaploid hybrids (AA BCD), in which as many as 5.63_{II} (Thomas and Jones 1964) are formed. A high percentage of pollen stainability (Thomas and Jones, loc. cit.) and complete seed fertility (Lesik 1948) in the decaploids would further discount the differentiation hypothesis of Thomas (1963).

The synaptic behaviour of the synthetic auto-allodecaploids (Table 1) can be satisfactorily explained on the basis of genetic regulation if it is assumed: 1) that A, which is the most important genome in *Avena* common to all the bivalent-forming polyploid species (Rajhathy and Morrison 1959; Rajhathy 1963), is the "hot genome" carrying at least the major information for bivalent pairing (like the 5B of wheat), and 2) that more than two doses of this diploidizing gene system completely suppress homoeologous pairing and also bring about 2 × 2 pairing of the homologous chromosomes of the A genomes. This conclusion is supported by the low frequency of trivalents (only 0.95_{III} per cell instead of the 4.62_{III} expected at coefficient of realization = 0.66) in the pentaploid hybrids (AAACD) between *hirtula* (AAAA) and *sativa* (AACCDD) (Table 1).

This situation is analogous to that in the auto-allododecaploid tall fescue (AAAA BBBB CCCC; 2n = 12x = 84), in which the diploidizing gene(s) in quadruplicate dose not only completely suppress homoeologous pairing, as evidenced by the absence of hexavalents or higher multivalents, but also bring about 2 × 2 pairing of the 21 homologous sets of 4 chromosomes each (Jauhar 1975c). Such a dosage effect seems to be exhibited by the 5B system also. When extra doses of the long arm of the 5B chromosome ($5B^L$) were fed in the form of isochromosomes, suppression of both homoeologous and homologous pairing was observed in wheat (Feldman 1966, 1968).

5. Complexity of the genetic control and possible dosage effect of the diploidizing gene(s)

From Table 1 it is clear that one dose of the diploidizing gene(s) in the hexaploid species *Avena sativa* and *A. byzantina* is very effective in suppressing homoeologous pairing, as evidenced by the almost complete absence of pairing in the haploids of these species. Table 1 lists some haploids, euploid species, interspecific hybrids and amphiploids supposedly having 0 to 4 doses of the A genome. In some interspecific hybrids and the derived amphiploids which have more than two doses of A genome, there is a considerable tendency towards bivalent pairing (Table 1). In such cases, not only is homoeologous pairing suppressed but also apparently homologous chromosomes of a particular genome tend to pair mostly as bivalents.

If it is assumed that the A genome of *Avena* has the principal regulator of chromosome pairing like the 5B of wheat (Jauhar 1975c), then *abyssinica* × *sativa* decaploids (AAAA BB CC DD) will have four doses of this regulatory mechanism, which not only suppress homoeologous pairing but also drastically reduce quadrivalent formation even among homologues of the four A genomes. This type of dosage effect is evident in the *hirtula* × *sativa* pentaploid hybrids (AAACD) which, with three A genomes, show a very low frequency of trivalents (0.95 trivalents per cell as against a theoretical expectation of 7). This seems to be a plausible explanation for the drastic reduction in trivalent frequency in these hybrids.

Based on chromosome pairing in the nullihaploid of *A. sativa*, which was supposedly nullisomic for a critical chromosome, Gauthier and McGinnis (1968) inferred that the missing chromosome carried the genetic information for the regulation of pairing. It is, however, not unlikely that some other chromosome(s) also carry such information so that even if one critical chromosome is missing, gene(s) on some other chromosome(s) carry out some regulatory function. This is indicated by the amount of homoeologous pairing in this nullihaploid, which is far less than in the nulli-5B haploids of wheat (Riley 1960).

Bivalent pairing in the 8x *ventricosa-sativa* amphiploids (AAC^uC^uCCDD) (Thomas 1970) could also be due to genetic enhancement of the differential affinity of the C^u and C genomes or due to dosage effect of the possible diploidizing genes on the A and C genomes, as described earlier in the *abyssinica* × *sativa* decaploids.

It is likely that the diploidizing mechanism in *A. sativa* is also as complex as that of wheat. Although $5B^L$ has the principal regulator of chromosome pairing in wheat, it is becoming clear that other chromosomes also have some genetic information for bivalent pairing, e.g. 3D (Upadhya and Swaminathan 1967; Mello-Sampayo 1971) and 3A (Driscoll 1972). Regulation of bivalent pairing is such an important character, so vital for the survival of the wheat plant, that it is unlikely that it would be governed just by one gene or a few genes located on one chromosome. Many more chromosomes concerned with the regulation of pairing may subsequently become known but 5B is unquestionably the "chief constable" which "disciplines" the chromosomes. Perhaps it may never be possible to determine precisely the number of chromosomes involved in the regulation of pairing by the technique of nullisomic analysis, for the simple reason that in a nullisomic for one critical chromosome the functionally similar genes on the other chromosomes might show amplified activity. Perhaps this phenomenon of gene amplification will need to be considered when deriving conclusion based on the study of nullisomics or even monosomics.

An alternative explanation for the almost complete absence of chiasmate homoeologous pairing in the mono-5B of wheat could be that the diploidizing gene(s) on the 5B monosome or on other chromosomes show amplified activity. This seems an imaginative hypothesis apparently difficult to put to experimental verification. But perhaps one way in which the complexity of this control could be tested is to cross wheat with different genotypes of *Aegilops speltoides* and other related species which interfere with the regulatory mechanism. *Ae. speltoides* or other related genotypes could presumably "switch off" or repress the entire regulatory apparatus in its hybrids with wheat. The quantum of chromosome pairing in such hybrids should therefore be compared with that in different aneuploids of wheat and its hybrids deficient for different chromosomes. Such a comparison might give a further clue as to how many chromosomes exercise a regulatory effect on pairing. The same or similar genotypes should be used in order to avoid genotypic background effect.

Some very interesting observations have been made in *Avena sativa* (Table 1). When this species is crossed with a genotype (CW 57) of *A. longiglumis*, the regulatory mechanism controlling bivalent pairing is seriously interfered with in the hybrids. Although in this cross (AACD) about seven bivalents and 14 univalents would be expected, a large number of trivalents and quadrivalents are formed in addition to bivalents. These multivalents would be formed only through extensive homoeologous pairing which is even more than in the nullihaploid of *sativa* supposedly deficient for a critical chromosome.

It would appear that this particular genotype of *longiglumis* somehow "switches off" the whole regulatory apparatus in *sativa*, so that the multivalent frequency in the hybrid increases to nearly seven times that in the multihaploid of *sativa* (Table 1). In the microbial systems there are some instances known where several functionally similar genes are controlled through the action of the same repressor. In *Escherichia coli*, for example, the biosynthesis of arginine is under the control of eight structural genes which, although not closely linked, are coordinately controlled through the action of one repressor (Jacoby and Gorini 1969).

It seems that the regulatory mechanism in the hexaploid oat is quite complex-perhaps even more than in wheat - and that many chromosomes may be concerned with the balanced regulation of chromosome pairing. The data in Table 1 strongly suggest the com-

Table 3. Similarities and differences of the three regulators of chromosome pairing discovered so far in the grass family

Features	Genetic regulatory systems and references					
	5B control	Reference	C control	Reference	A control	Reference
Species in which chromosome pairing is regulated	Tetraploid and hexaploid wheats	Okamoto, 1957; Sears and Okamoto, 1958; Riley and Chapman, 1958	*Festuca arundinacea*, *F. rubra* and other polyploid fescues	Jauhar, 1975a,b	Tetraploid and hexaploid species of *Avena*	Rajhathy and Thomas, 1972
Probable location	$5B^L$	Sears and Okamoto, 1958; Riley, 1960	C genome?	Jauhar,	A genome?	Jauhar, 1975c
Effectiveness	Hemizygous effective	Riley and Chapman, 1958; Riley, 1960	Hemizygous ineffective	Jauhar, 1975a,b	Hemizygous effective	Nishiyama and Tabata, 1964; Bhatti, 1972; Rajhathy and Thomas, 1972
Dosage effect	+	Feldman, 1966, 1968	+	Jauhar, 1975c	+	Jauhar, 1975c Ladizinsky, 1973
Genetically repressible	+	Riley, 1960; Dvořák, 1972	+	Jauhar, 1975b,c	+	Rajhathy and Thomas, 1972, 1974

Note: The regulatory mechanisms in the hexaploid tall fescues and in the hexaploid oats are tentatively referred to as C-control and A-control, respectively, because it is felt that the major genetic information for the regulation of bivalent pairing is located in the C and A genomes of these species

plexity of this control and the need for a further study by analysing also the degree of suppression of homoeologous pairing in hybrids of hexaploid species of *Avena* with different genotypes of *A. longiglumis* and other species which could interfere with the regulatory mechanism.

6. Comparison of the regulatory mechanisms in wheat, oats and tall fescue

An overall comparison of the regulatory mechanisms in the breadwheat, oats and the hexaploid tall fescue is given in Table 3. While the mechanism in wheat is designated as 5B because the principal regulator is located in this chromosome, the mechanisms in tall fescue and in oats are referred to as C-control and A-control, respectively, because it is felt that the major information for the regulation of pairing could be located in the C and A genomes of these species (Jauhar 1975c).

It is evident from Table 3 that there is a remarkable similarity in the three regulatory systems in these hexaploid species of the grass family. All three show dosage effect and are genetically repressible. The regulators in wheat and oats are hemizygous effective while the one in tall fescue seems ineffective. Further studies on these lines might give more clues as to the functional aspects of these three diploidizing mechanisms.

Literature

Bhatti, I.M.: Cytogenetic studies of the genomic structure in *Avena*. Ph. D. thesis, University of Wales (1972) (unpublished)

Craig, I.L.: Haploid plants (2n = 21) from *in vitro* anther culture of *Triticum aestivum*. Can. J. Genet. Cytol. 16, 697-700 (1974)

Driscoll, C.J.: Genetic suppression of homoeologous chromosome pairing in hexaploid wheat. Can. J. Genet. Cytol. 14, 39-42 (1972)

Dvořák, J.: Genetic variability in *Aegilops speltoides* affecting homoeologous pairing in wheat. Can. J. Genet. Cytol. 14, 371-380 (1972)

Feldman, M.: The effect of chromosomes 5B, 5D and 5A on chromosome pairing in *Triticum aestivum*. Proc. Natn. Acad. Sci. USA 55, 1447-1453 (1966)

Feldman, M.: Regulation of somatic association and meiotic pairing in common wheat. Proc. 3rd Int. Wheat Genet. Symp. (Eds. K.W. Finlay and K.

W. Shepherd), pp. 169-178, Austral. Acad. Sci., Canberra (1968)
Gauthier, F.M.; McGinnis, R.C.: The meiotic behaviour of a nulli-haploid plant in *Avena sativa* L. Can. J. Genet. Cytol. 10, 186-189 (1968)
Griffiths, D.J.; Rowlands, D.G.; Peregrin, W.T.H.: Cytogenetic relationships of certain artificial and natural species of *Avena*. J. Agric. Sci. (Camb.) 52, 189-199 (1959)
Harberd, D.J.; McArthur, E.D.: Cyto-taxonomy of *Rhynchosinapis* and *Hutera* (Cruciferae-Brassiceae). Heredity 28, 254-257 (1972)
Jacoby, G.A.; Gorini, L.: A unitary account of the repression mechanism of arginine biosynthesis in *Escherichia coli*. I. The genetic evidence. J. Mol. Biol. 39, 73-87 (1969)
Jauhar, P.P.: Haploid meiosis and its bearing on the phylogeny of pearl millet, *Pennisetum typhoides* Stapf et Hubb. Genetica 41, 532-540 (1970)
Jauhar, P.P.: Genetic control of diploid-like meiosis in hexaploid tall fescue. Nature (Lond.) 254, 595-597 (1975a)
Jauhar, P.P.: Genetic regulation of diploid-like chromosome pairing in the hexaploid species, *Festuca arundinacea* Schreb. and *F. rubra* L. (Gramineae). Chromosoma (Berl.) 52, 363-382 (1975b)
Jauhar, P.P.: Genetic control of chromosome pairing in polyploid fescues: its phylogenetic and breeding implications. Rep. Welsh. Pl. Breed. Stn for 1974, pp. 114-127 (1975c)
Khoshoo, T.N.; Arora, O.P.: Genesis of bivalent pairing in hexaploid clump *Verbena*. Chromosoma (Berl.) 26, 259-269 (1969)
Ladizinsky, G.: Genetic control of bivalent pairing in the *Avena strigosa* polyploid complex. Chromosoma (Berl.) 42, 105-110 (1973)
Lesik, F.L.: Eine experimentelle synthese der Hafer-amphidiploiden. Doklady Akad. Nauk SSSR n.s. 60, Nr. 2, 299-300 (1948)
Malik, C.P.; Tripathi, R.C.: Mode of chromosome pairing in the polyhaploid tall fescue (*Festuca arundinacea* Schreb., 2n = 42). Zeits. Biol. 116, 332-339 (1970)
Mello-Sampayo, T.: Genetic regulation of meiotic chromosome pairing by chromosome 3D of *Triticum aestivum*. Nature new Biol. (Lond.) 230, 22-23 (1971)
Mulligan, G.A.: Diploid and autotetraploid *Physaria vitulifera* (*Cruciferae*). Can. J. Bot. 45, 183-188 (1967)
Niizeki, M.; Kita, F.: Studies on plant cell and tissue culture. III. In vitro induction of callus from anther culture of forage crops. Jour. Fac. Agric. d'Hokkaido 57, 293-300 (1974)
Nishiyama, I.; Tabata, M.: Cytogenetic studies in *Avena*-XII. Meiotic chromosome behaviour in a haploid cultivated oat. Jap. J. Genet. 38, 311-316 (1964)
Noronha-Wagner, M.: Mello-Sampayo, T.: Haploids nulli 5B of *Triticum aestivum*. Agronomia lusita. 33, 315-322 (1972)
Okamoto, M.: Asynaptic effect of chromosome V. Wheat Inform. Serv. 5, 6 (1957)
Person, C.: An analytical study of chromosome behaviour in a wheat haploid. Can. J. Bot. 33, 11-30 (1955)
Rajhathy, T.: A standard karyotype for *Avena sativa*. Can. J. Genet. Cytol. 5, 127-132 (1963)
Rajhathy, T.; Morrison, J.W.: Chromosome morphology of the genus *Avena*. Can. J. Bot. 37, 331-337 (1959)
Rajhathy, T.; Morrison, J.W.: Genome homology in the genus *Avena*. Can. J. Genet. Cytol. 2, 278-285 (1960)
Rajhathy, T.; Thomas, H.: Genetic control of chromosome pairing in hexaploid oats. Nature new Biol. (Lond.) 239, 217-219 (1972)
Rajhathy, T.; Thomas, H.: Cytogenetics of oats (*Avena* L.). Misc. Publ. Genet. Soc. Canada No.2. pp. 90 (1974)
Riley, R.: The diploidisation of polyploid wheat. Heredity 15, 407-429 (1960)
Riley, R.; Chapman, V.: Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature (Lond.) 182, 713-715 (1958)
Riley, R.; Chapman, V.: The effects of the deficiency of chromosome V (5B) of *Triticum aestivum* on the meiosis of synthetic amphiploids. Heredity 18, 473-484 (1963)
Sadasivaiah, R.S.; Rajhathy, T.: Genome relationships in tetraploid *Avena*. Can. J. Genet. Cytol. 10, 655-669 (1968)
Sears, E.R.: Nullisomic-tetrasomic combinations in hexaploid wheat. In: Chromosome manipulations and plant genetics, pp. 29-45. Oliver & Boyd, Edinburgh 1966
Sears, E.R.; Okamoto, M.: Intergenomic chromosome relationships in hexaploid wheat. Proc. X Intern. Cong. Genet. 2, 258-259 (1958)
Thomas, H.: Diploid-like pairing in a synthetic decaploid *Avena*. Nature (Lond.) 199, 1209-1210 (1963)
Thomas, H.: Chromosome relationships between the cultivated oat *Avena sativa* (6x) and *A. ventricosa* (2x). Can. J. Genet. Cytol. 12, 36-43 (1970)
Thomas, H.; Bhatti, I.M.: Notes on the cytogenetic structure of the cultivated oat, *Avena sativa* (2n = 6x = 42). Euphytica 24, 149-157 (1975)
Thomas, H.; Jones, M.L.: Cytological studies of pentaploid hybrids and a decaploid in *Avena*. Chromosoma (Berl.) 15, 132-139 (1964)
Thomas, H.; Peregrine, W.T.H.: Chromosome mosaics in synthetic amphiploids in the Avenae. Chromosoma (Berl.) 15, 123-131 (1964)
Upadhya, M.D.; Swaminathan, M.S.: Mechanisms regulating chromosome pairing in *Triticum*. Biol. Zb. 86 (suppl.), 239-255 (1967)

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