

THE EFFECT OF THE PYLE POLLEN AND TEMPERATURE
UPON THE HOMOELOGOUS PAIRING IN TRITICUM AESTIVUM L. X
SECALE CEREALE L. F₁ HYBRIDS

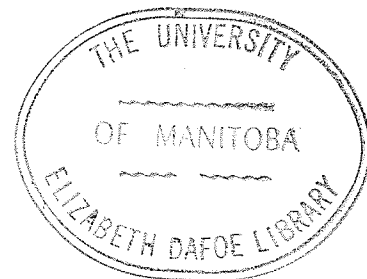
BY

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ABSTRACT

A study of meiotic chromosome behavior as influenced by temperature was conducted on wheat-rye hybrids produced from the cross T. aestivum L. c.v. Chinese Spring x S. Cereale L. c.v. Prolific. Two genotypic classes of hybrids were used, viz., those containing a complete haploid complement from each parent (i.e. $2n = 28$) and those deficient for chromosome 5B of wheat ($2n = 27$).

Three different levels of temperature were employed, viz., 15°C , 21°C and 32°C and hybrid plants of each constitution ($2n = 28$ and $2n = 27$) were allowed to undergo development during meiosis at each temperature level.

It was found that temperature of 32°C affected chromosome behavior by reducing homoeologous synapsis which in turn suppressed chiasma frequency.

A continuous variation of the frequency of homoeologous chromosome pairing was found to exist in both genotypes notwithstanding temperature regime. An hypothesis was advanced that such a distribution frequency was due to the effect of a polygenic system contributed by the heterozygous rye parent and which controlled chromosome behavior. The significance of such a system from both a theoretical and a practical standpoint is discussed.

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INTRODUCTION

Hexaploid wheat Triticum aestivum L. ($2n = 6x = 42$) is made up of three different genomes A, B and D. The three genomes were derived from closely related 14 chromosome diploid species. Each pair of homologous chromosomes has a corresponding homoeologous pair in each of the other two genomes.

In spite of the very close genetic relationships between homoeologous chromosomes in hexaploid wheats, normal meiotic behavior precludes pairing between homoeologues. This lack of pairing was explained by postulating gene mutation which suppressed homoeologous synapsis. Sears and Okamoto, (1958); and Riley and Chapman, (1958), showed that a gene (s) on the long arm of chromosome 5B (5B^L), was responsible for the suppression of homoeologous pairing at meiosis and that in the absence of this arm, homoeologous synapsis occurs as it does in the absence of the complete chromosome.

Since the discovery of the 5B^L gene (s) in wheat, many attempts have been made to elucidate its true method of action in the control of meiotic pairing in wheat and its hybrids.

Early reports in most hybrids between T. aestivum and 14 chromosome diploid species in the genera Secale, Agropyron, and the abandoned genera Aegilops, (now included in Triticum), showed that there is little chromosome pairing at meiosis presumably because homoeologous synapsis is precluded by the unmodified effect of chromosome 5B. Nevertheless, Nakajima, (1952); and Nakajima and Zennyozzi,

(1966), have shown that depending upon the specific combination, wheat-rye F_1 hybrids can exhibit varying degrees of chromosome pairing even though chromosome 5B is present. Furthermore, the findings of Feldman, (1966), clearly illustrated that $5B^L$ activity affects the premeiotic spatial distribution and relative orientation of homologous and homoeologous chromosomes and that chromosomes 5A and 5D have an effect on premeiotic association opposite to that of their homoeologue 5B. His suggestion that every diploid species in the wheat group may have a gene similar to the one present on chromosome 5D, encouraged us to undertake a review on the meiotic behavior of wheat-rye hybrids.

REVIEW OF LITERATURE

The behavior of chromosomes, especially during the first meiotic metaphase in wheat-rye hybrids has been studied in detail for many years. Early reports from Kihara, (1924); Thompson, (1926); Muntzing, (1935); Liljefors, (1936); Nakajima, (1956); and others, have stressed the low frequency of bivalents at first metaphase of meiosis and showed the distant relationship of Secale with members of the wheat group. Some exceptions to this general condition have been reported. For example, Nakajima, (1952), described a wheat-rye hybrid with an unusually high frequency of bivalents. Later Nakajima and Zennyozzi, (1966), showed that in wheat-rye hybrids there is a continuous variation in the mean number of bivalents among plants, ranging from complete asynapsis to 7.9 bivalents per plant and a range from 0 - 11 pairs per cell. They concluded that the variation in the number of bivalents observed was influenced by the genetic background of the wheat used in the cross..

Prior to the discovery of the 5B^L gene effect on the control of homoeologous pairing in hexaploid wheats by Sears and Okamoto, (1958); and Riley and Chapman, (1958); only one class of wheat-rye hybrids was reported, viz, 28-chromosome hybrids. These hybrids showed very little pairing at metaphase I of meiosis. With the knowledge of the 5B^L gene, Riley and Chapman, suggested that the genetic mechanism which restricts pairing between homoeologous chromosomes of

wheat, might also be responsible for the failure of wheat chromosomes to pair with those of certain species in related genera. Riley, Chapman and Kimber, (1959), tested this hypothesis by comparing 28-chromosome (5B present) wheat-rye and wheat-Aegilops longissima hybrids with 27-chromosome (5B deficient) hybrids and found an increased number of bivalents in the 27 chromosome hybrids along with trivalents and quadrivalents. To explain the presence of quadrivalents they suggested that homoeologous chromosomes from each of the three genomes of wheat and a rye chromosome might be associated. Nevertheless, the wheat-rye hybrid deficient for chromosome 5B, showed a lower frequency of bivalents per cell as compared with the level of wheat-Aegilops longissima pairing and they suggested that some interference from the rye chromosomes during meiosis may exist.

In a further examination of hybrids displaying homoeologous pairing, Muramatsu, (1959); Riley, (1960-1963); Cauderon, (1963); Upadhyaya and Swaminathan, (1963); and Lacadena, (1967) reported hybrids involving hexaploid wheat and most of the diploid species of Aegilops, Secale and Agropyron. In all but a few hybrids examined to date, the suppression of homoeologous pairing was effective in the presence of 5B, but not in its absence. Where exceptions occurred, they included hybrids between T. aestivum and the diploid species Triticum speltoides (= Aegilops speltoides) or T. tripsacoides (= Ae. mutica), in which considerable meiotic pairing occurred and which Riley, (1960), proposed to be due to the suppression of the 5B^L gene by the genotype of those species. Riley (1963); also pointed out the anomalous behavior of rye which when crossed with wheat, gave rise to hybrids in

which the absence of $5B^L$ cause only a relatively small increase in pairing. This finding led him to propose that the rye genotype inhibits pairing in a way very similar to that of chromosome 5B. However, Melnyk and Unrau, (1959); contrary to the established opinion, demonstrated that the chromosomes of rye are capable of intergeneric pairing at least with those of T. tauschii (Ae. squarrosa), donor of the D genome in T. aestivum. They found that up to 25% of the bivalents observed were formed by Secale-Aegilops conjugations.

Okamoto, (1962, 1963); and Riley, Chapman and Belfield, (1966); studied the effect of mutagens on the action of the 5B chromosome in wheat-rye hybrids. A mutated 5B might possibly be detected by an increased incidence of homoeologous chromosome pairing (i.e. suppression of diploidization). These investigations led to the finding that in at least some hybrids an unusually high frequency of homoeologous conjugations occurred. Nevertheless, it was not possible to recover or fix the "mutated" material in later generations, possibly because the high frequency of homoeologous pairing as exhibited by the few hybrids was due solely to the effect of the rye pollen per se as distinct from a mutational effect involving the $5B^L$ "locus".

One of the most important studies in the understanding of the effect of the 5B gene (s) was provided by Feldman, (1966), using plants of T. aestivum with different dosages of the long arm of 5B as an isochromosome. Feldman concluded that the $5B^L$ gene (s) operates by regulating the premeiotic spatial distribution of both homologous and homoeologous chromosomes. He also reported that to a lesser

extent, chromosomes 5D and 5A have an effect on premeiotic association which is opposite to that of their homoeologue 5B^L, and that high temperature relaxes somatic association in plants with extra dosages of 5B^L, presumably by affecting the action of the promoters.

In a later report, Feldman, Mello-Sampayo and Sears, (1966), concluded that the phenomenon of premeiotic association of homologous, and to a lesser extent homoeologous chromosomes (personal communication) in T. aestivum, is not exclusive of the meiotic cells, but rather a common situation in all cells throughout the life of the plant. These workers also presented a list of references which supported their concept that somatic association occurs normally in many animal and plant genera.

Very recently Feldman and Mello-Sampayo, (1967), presented evidence to show that the phenomenon of somatic association in T. aestivum is a very complex one. In addition to promoters 5D and 5A, the short arm of 5B (5B^S) also may act in the same manner as suggested by Riley, Chapman, Young and Belfield, (1966). Feldman (personal communication); also has evidence which suggest that the short arm of 5A and 5D are implicated in the same phenomenon. These data show clearly that all the homoeologous chromosomes of the group 5 in T. aestivum are implicated in the same phenomena and renders plausible Feldman's assumption that the 5B^L gene (s) initially promoted premeiotic association but subsequently mutated to a form with the opposite effect.

Feldman and Mello-Sampayo, (1967); studied the meiotic behavior of wheat-T. speltoides hybrids and the effect of temperature upon them. Their results led them to suggest that the T. speltoides genotype, has

a gene (s) which, in combination with those present in 5A, 5B^S and 5D^L can induce homoeologous pairing notwithstanding the presence of 5B^L in the same genotype.

In a very recent report by Driscoll, Darvey and Barber, (1967), on the effect of colchicine on meiosis of T. aestivum, evidence was found to support early findings that premeiotic association in hexaploid wheat does in fact exist. Furthermore, when the drug was applied before the onset of meiosis it acts in a way very similar to 5B^L, possibly enhancing its effect in the suppression of homologous pairing.

MATERIAL AND METHODS

All wheat-rye hybrids used in the present study were derivatives of T. aestivum L. c.v. Chinese Spring which genotypically were either euploid, $2n = 6x = 42$ or monosomic for the 5B chromosome, $2n = 6x-1 = 41$. The rye parental genotype was a strain of Secale cereale L. c.v. Prolific, $2n = 14$. Both species were maintained by the Department of Plant Science; University of Manitoba.

Synthesis of Hybrids

The parental species were grown in a greenhouse in six-inch pots and crosses were made during late spring of 1967. With the aid of embryo culture method in the way described by Melnyk, (1957), 52, 28-chromosome hybrids (21 chromosome from wheat and 7 from rye), and 18, 27-chromosome hybrids (deficient for 5B), were established.

The hybrids were first grown in a growth chamber in which day and night temperatures averaged approximately 18°C and 10°C (± 1) respectively with a 16-hour photoperiod. These growing conditions were effective in initiating good tiller development during early growth of the hybrid plants.

Upon the development of the third tiller, 10 of the 52, 28-chromosome hybrids and 6, of the 18, 27-chromosome hybrids were cloned in such a way that three clonal units were sectioned from each parent plant. Both populations were then allowed to develop uniformly at 10°C for approximately 4 weeks. Prior to the onset of meiosis, each of the three clonal units derived from each parent plant were transferred to one of three different temperature regimes maintained during

meiotic development, viz., 15°C, 21°C and 32°C (± 1). The remainder of the population of uncloned hybrids were distributed equally among the three treatments resulting in a total of 24, 28-chromosome hybrids and 10, 27-chromosome hybrids tested under each temperature regime. A photoperiod of 16-hour duration was maintained throughout the study.

Cytological Studies

At meiosis, spikes from hybrids in each of the three temperature regimes were fixed in Carnoy's solution and after 48 hours were transferred to 70% alcohol until examination. Preparations of pollen mother cells at first meiotic metaphase were made using the aceto-carmin method.

In the analysis of F_1 hybrids, records were kept of the number of univalents, open and closed bivalents, trivalents and higher multivalents that occurred per pollen mother cell at metaphase I in individual plants in each treatment. In scoring the number of chiasmata per cell, open bivalents were scored as one chiasma, closed bivalents as well as trivalents as two chiasmata, and quadrivalents as three chiasmata. In order to facilitate comparisons of results between the different hybrids and to make possible a clearer evaluation of the pairing frequencies of individual hybrids, the complexities of pairing were reduced to a common denominator of a unit termed a "bivalent association" as suggested by Kihara, (1929). Thus, either a closed or open bivalent as well as a trivalent configuration was interpreted as one bivalent association, while a quadrivalent was considered equivalent to two bivalent associations. Approximately

100 pollen mother cells were examined and scored for each hybrid.

Cytological examination was conducted at a magnification of 1250 diameters, while photomicrographs were recorded at 1000 magnifications.

RESULTS

The variety Chinese Spring was chosen for this study as the wheat parent because it is known to possess the primitive genomic structure of the early wheats, also because of the relative ease with which it can be hybridized with rye. On the other hand, Secale cereale c.v. Prolific is of annual spring growth and used extensively in the Triticale breeding program in the Plant Science Department.

Cytological data of the F_1 hybrids at the three different temperature treatment are summarized in Tables I to VI inclusive. In Plates I and II, typical metaphase I figures of some of the hybrids are presented.

Meiosis of 28-chromosome F_1 Hybrids at 15°C, 21°C and 32°C

Seventeen 28-chromosome wheat-rye hybrids which were grown at the 15°C treatment were analysed at first meiotic metaphase. The average bivalent association per cell showed continuous variation among plants from 0.05 to 5.63 (Table I). Most of the bivalents were rod-shaped; trivalents and or more complex associations were not observed in the more asynaptic hybrids (Plate I. Fig. A). However, as the degree of homoeologous pairing increased, as for example, in hybrids H-36 and H-15 (Table I), rod and ring shaped bivalents were observed as well as trivalents and quadrivalents (Plate I. Figs. B and C). In general a wide variation in the pairing relationship occurred at the 15°C temperature, ranging from cells exhibiting complete asynapsis to some which included up to eighteen chromosomes

Table I. - Mean pairing frequency per cell in 28-chromosome (5B present) wheat-rye hybrids grown at 15°C

Hybrid	Cells Scored	Univ. (Range)	Bivalents		Triv. (Range)	Quad. (Range)	Aver. Chias-mata	
			Open (Range)	Closed (Range)			Biv. Ass.	(Range)
H-25	100	27.90 (26-28)	0.05 (0-1)				0.05	0.05 (0-1)
H-8	100	27.42 (22-28)	0.29 (0-3)				0.29	0.29 (0-3)
H-51	100	27.34 (24-28)	0.32 (0-2)	0.01 (0-1)			0.33	0.34 (0-3)
H-63	100	26.52 (20-28)	0.74 (0-4)				0.74	0.74 (0-4)
H-11	100	26.52 (16-28)	0.72 (0-6)	0.02 (0-1)			0.74	0.76 (0-6)
H-62	100	25.92 (22-28)	1.02 (0-3)	0.02 (0-1)			1.04	1.06 (0-3)
H-14	100	25.52 (18-28)	1.22 (0-5)	0.02 (0-1)			1.24	1.26 (0-5)
H-68	200	24.33 (18-28)	1.77 (0-5)	0.05 (0-1)	0.01 (0-1)		1.83	1.89 (0-5)
H-66	100	24.28 (20-28)	1.79 (0-4)	0.04 (0-4)	0.02 (0-1)		1.85	1.91 (0-4)
H-104	100	23.84 (16-28)	2.00 (0-5)	0.08 (0-1)			2.08	2.16 (0-7)
H-9	100	23.50 (18-28)	2.16 (0-5)	0.06 (0-1)	0.02 (0-1)		2.24	2.32 (0-5)
H-5	100	23.34 (20-28)	2.10 (0-4)	0.20 (0-2)	0.02 (0-1)		2.32	2.54 (0-6)
H-61	100	22.64 (17-28)	2.58 (0-5)	0.04 (0-1)	0.06 (0-1)		2.68	2.78 (0-5)
H-64	100	22.25 (16-28)	2.68 (0-6)	0.18 (0-2)	0.01 (0-1)		2.87	3.06 (0-6)
H-67	100	21.88 (18-28)	2.63 (0-5)	0.16 (0-2)	0.18 (0-1)		2.97	3.31 (0-5)
H-36	100	17.77 (13-28)	3.81 (0-6)	0.54 (0-3)	0.15 (0-2)	0.02 (0-1)	4.54	5.27 (0-10)
H-15	100	15.91 (9-28)	3.31 (0-7)	1.37 (0-3)	0.83 (0-3)	0.06 (0-1)	5.63	7.89 (0-13)

Plate I - First meiotic metaphase in hybrids of Triticum aestivum

L. var. Chinese Spring x Secale cereale L. var. Prolific.

Fig. A - An asynaptic 28-chromosome hybrid grown at 15°C showing one bivalent and 26 univalents.

Figs. B and C - Hybrids with higher homoeologous pairing grown at 15°C.

B. two trivalents, two bivalents and 18 univalents.

C. One quadrivalent, four bivalents and 16 univalents.

Fig. D - Asynaptic hybrid grown at 21°C showing one bivalent and 26 univalents.

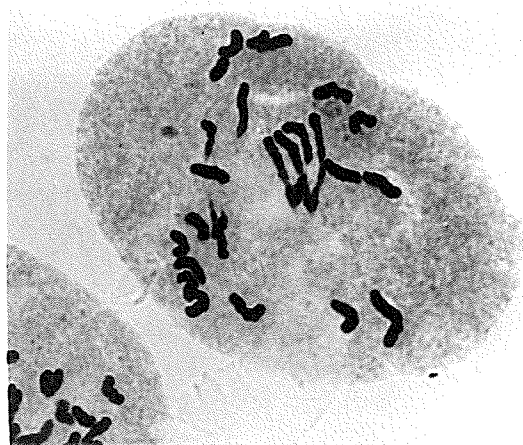
Figs. E and F - Hybrids with higher homoeologous pairing grown at 21°C.

E. three closed and one open bivalents and 20 univalents

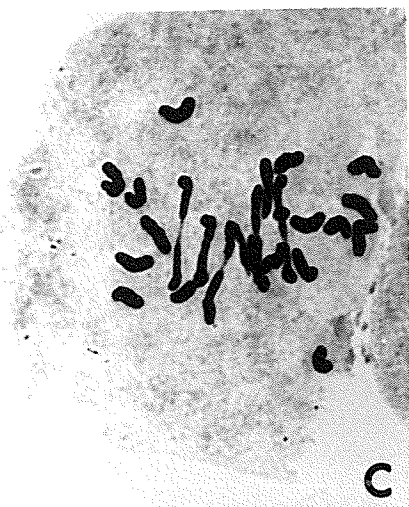
F. one trivalent, five bivalents and 15 univalents.



A



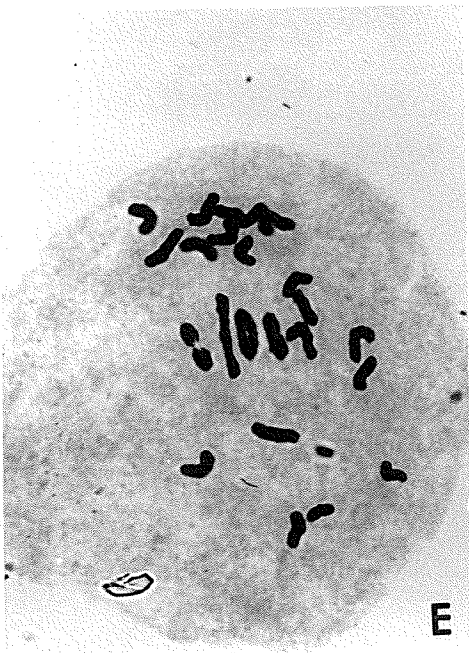
B



C



D



E



F

involved in paired configurations. Average chiasma frequency per cell ranged from 0.05 in the most asynaptic plant, to 7.89 in those hybrids with a high level of homoeologous synapsis.

At 21°C 28-chromosome F_1 hybrids of T. aestivum x S. cereale behaved similarly to those studied at 15°C. Average bivalent association per cell ranged from 0.47 to 3.09, while the mean chiasma frequency varied from 0.50 to 3.39 (Table II). Most bivalents were rod-shaped but occasionally ring bivalents as well as trivalents and quadrivalents were observed (Plate I, Figs. D, E and F).

Ten of the 28-chromosome hybrids grown at 32°C were analysed at first meiotic metaphase. The average bivalent association per cell ranged from 0.12 to 1.12 and average chiasma frequency per cell was very low, ranging from 0.12 to 1.13 (Table III). Almost all the bivalents scored were rod-shaped and no trivalents or higher associations were seen. Marked asynapsis was observed in all hybrids grown at this temperature (Plate II, Figs. 1 and 2).

Table II. -- Mean pairing frequency per cell in 28-chromosome (5B present) wheat-rye hybrids grown at 21°C

Hybrid	Cells Scored	Univ. (Range)	Bivalents		Triv. (Range)	Quad. (Range)	Aver. Biv. Ass.	Chias- mata (Range)
			Open (Range)	Closed (Range)				
H-34	100	27.06 (24-28)	0.44 (0-2)	0.03 (0-1)			0.47	0.50 (0-2)
H-71	100	26.64 (22-28)	0.68 (0-3)				0.68	0.68 (0-3)
H-70	50	25.72 (22-28)	1.14 (0-3)				1.14	1.14 (0-3)
H-61	100	25.62 (16-28)	1.18 (0-5)	0.01 (0-1)			1.19	1.20 (0-5)
H-41	180	25.39 (20-28)	1.27 (0-4)	0.02 (0-1)	0.01 (0-1)		1.30	1.33 (0-4)
H-62	100	25.28 (22-28)	1.27 (0-3)	0.09 (0-1)			1.36	1.45 (0-3)
H-64	200	24.90 (18-28)	1.52 (0-5)	0.05 (0-1)			1.57	1.62 (0-5)
H-68	150	24.43 (20-28)	1.71 (0-4)	0.07 (0-1)			1.78	1.88 (0-4)
H-66	100	24.30 (18-28)	1.85 (0-5)				1.85	1.85 (0-5)
H-38	150	23.93 (16-28)	1.92 (0-6)	0.10 (0-3)	0.01 (0-1)		2.03	2.14 (0-3)
H-18	100	23.14 (16-28)	2.20 (0-6)	0.15 (0-3)	0.04 (0-1)	0.01 (0-1)	2.41	2.61 (0-8)
H-47	150	23.17 (18-28)	2.28 (0-5)	0.12 (0-1)	0.01 (0-1)		2.41	2.54 (0-6)
H-50	120	21.78 (16-28)	2.79 (0-6)	0.26 (0-2)	0.04 (0-1)		3.09	3.39 (0-8)

Table III. - Mean pairing frequency per cell in 28-chromosome (5B present) wheat-rye hybrids grown at 32°C

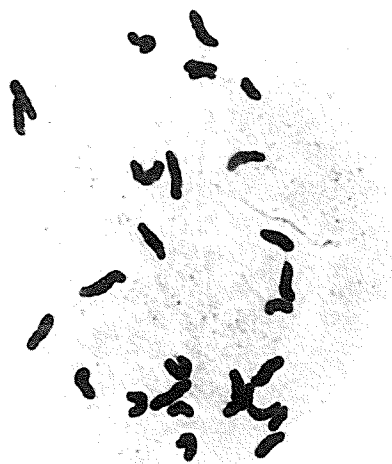
Hybrid	Cells Scored	Univ. (Range)	<u>Bivalents</u>		Triv. (Range)	Quad. (Range)	Aver. Biv. Ass.	Chias- mata (Range)
			Open (Range)	Closed (Range)				
H-40	100	27.76 (24-28)	0.12 (0-2)				0.12	0.12 (0-2)
H-64	100	27.74 (24-28)	0.13 (0-2)				0.13	0.13 (0-2)
H-68	100	27.70 (24-28)	0.15 (0-2)				0.15	0.15 (0-2)
H-7	100	27.68 (24-28)	0.16 (0-2)				0.16	0.16 (0-2)
H-61	200	27.66 (24-28)	0.17 (0-2)				0.17	0.17 (0-2)
H-49	100	27.32 (22-28)	0.34 (0-3)				0.34	0.34 (0-3)
H-37	100	26.88 (22-28)	0.55 (0-3)	0.01 (0-1)			0.56	0.57 (0-4)
H-62	50	26.80 (24-28)	0.60 (0-2)				0.60	0.60 (0-2)
H-27	100	26.66 (24-28)	0.67 (0-2)				0.67	0.67 (0-2)
H-26	200	25.76 (18-28)	1.11 (0-5)	0.01 (0-1)			1.12	1.13 (0-5)

Plate II - First meiotic metaphase in hybrids of Triticum aestivum
var. Chinese Spring x Secale cereale var. Prolific.

Figs. 1 and 2 - A 28-chromosome hybrids grown at high temperature
(32°C) showing asynapsis (28 univalents, and one
bivalent and 26 univalents respectively).

Figs. 3, 4, 5 and 6 - 27-chromosome (5B deficient) hybrids.

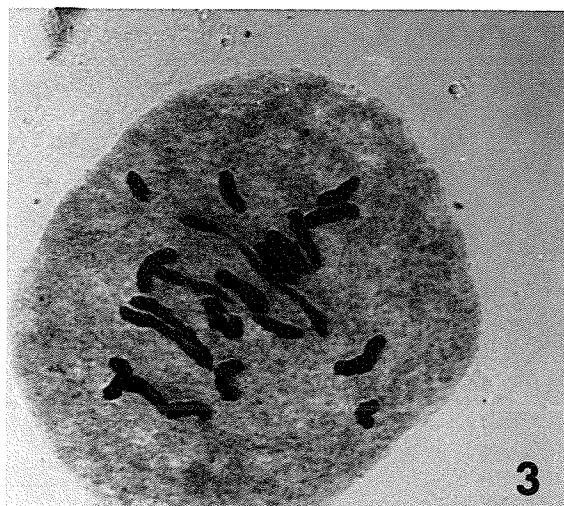
3. A hybrid grown at 15°C showing one trivalent, four
closed and two open bivalents and 12 univalents.
4. A hybrid grown at 15°C showing three trivalents,
one closed and five open bivalents and 6 univalents.
5. A hybrid grown at 21°C showing five trivalents,
one bivalent and 10 univalents.
6. A hybrid grown at 32°C showing two trivalents,
three closed and two open bivalents and 11 uni-
valents.



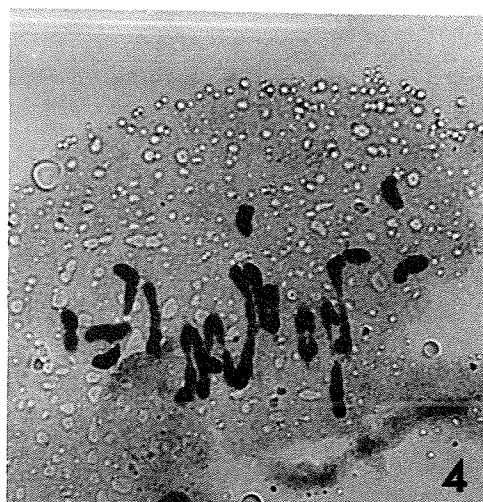
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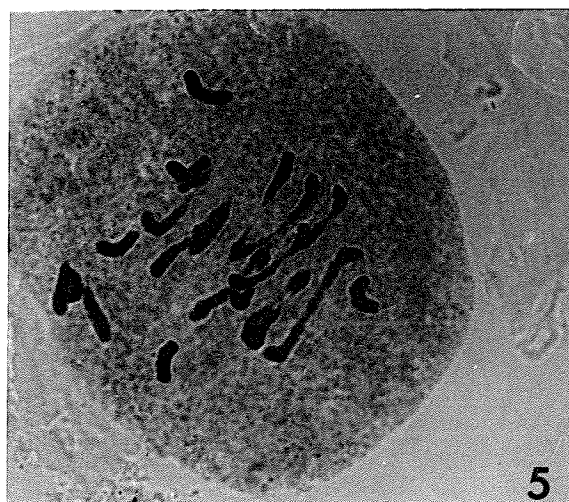
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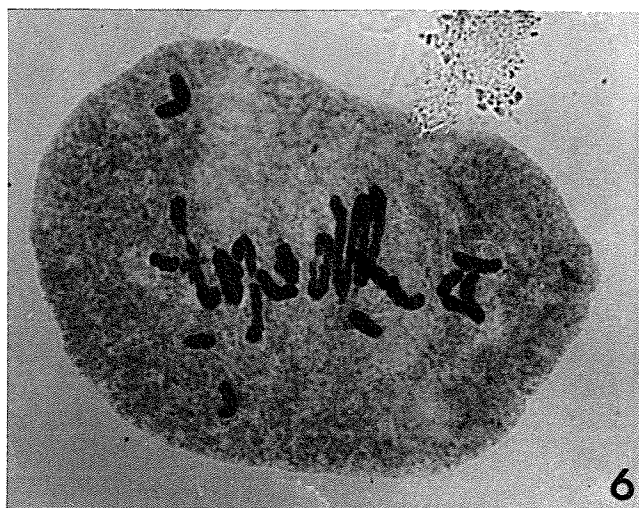
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4



5



6

Meiosis of 27-chromosome F_1 hybrids at 15°C, 21°C and 32°C

Six hybrids grown at 15°C and lacking the 5B chromosome were studied at first meiotic metaphase. The average bivalent association per cell varied among plants from 4.09 to 6.26 with a chiasma frequency ranging from 4.78 to 10.00 per cell (Table IV). The majority of the bivalents observed in plants exhibiting low pairing frequency were rod-shaped, however, an exceptionally high occurrence of ring bivalents also existed, ranging as high as 5 per cell in those hybrids exhibiting a high level of homoeologous pairing (Plate II, Fig. 3.). Trivalents were also common as would be expected in the absence of the 5B gene (s), under which conditions homoeologous affinity was expressed more or less freely. Nevertheless, trivalents frequency showed a marked variation from plant to plant ranging from a low of 0.34 in hybrids with relatively little pairing to a previously unreported high of 2.01 per cell in hybrids with a high level of homoeologous synapsis. Quadrivalents were occasionally seen in hybrids grown at this temperature, their presence ranging from 0.05 to 0.13 per cell. The presence of quadrivalents is perhaps one indication that three homoeologous wheat chromosomes and the corresponding rye homoeologue had associated. Furthermore, in some cells more than seven different associations were scored (Plate II, Fig. 4), which would indicate that sometimes the rye chromosome were allosyndesically (or, perhaps autosyndesically) paired in simple associations such as heteromorphic rod-shaped bivalents. The frequency of quadrivalents was lower than one might expect with the occurrence of

Table IV - Mean pairing frequency per cell in 27-chromosome (5B absent) wheat-rye hybrids grown at 15°C

Hybrid	Cells Scored	Univ. (Range)	Bivalents		Triv. (Range)	Quad. (Range)	Aver. Chias-	
			Open (Range)	Closed (Range)			Biv. Ass.	mata (Range)
H-035	100	18.38 (14-22)	3.33 (1-6)	0.20 (0-3)	0.34 (0-2)	0.11 (0-1)	4.09	4.78 (3-7)
H-033	100	18.19 (13-23)	3.24 (2-6)	0.26 (0-2)	0.43 (0-2)	0.13 (0-1)	4.19	5.55 (3-9)
H-023	100	17.35 (13-21)	3.45 (3-7)	0.47 (0-3)	0.41 (0-2)	0.10 (0-1)	4.53	5.41 (3-8)
H-021	100	16.60 (12-23)	3.94 (2-7)	0.44 (0-3)	0.48 (0-2)	0.05 (0-1)	4.96	5.93 (3-10)
H-01	80	12.83 (8-20)	2.75 (0-9)	1.20 (0-5)	2.01 (0-4)	0.06 (0-1)	6.08	9.35 (3-12)
H-03	100	12.47 (6-18)	2.43 (0-9)	1.64 (0-5)	2.01 (0-6)	0.09 (0-1)	6.26	10.00 (7-13)

homoeologous synapsis, however, only those cells which could be scored without any doubt of the nature of existing configurations were considered in this study. Cells which apparently contained more complex associations but which were not clearly discernable were not included.

At 21°C treatment, hybrids deficient for the 5B chromosome presented a very similar pattern to the ones studied at 15°C. The average bivalent association per cell ranged from 4.18 to 6.34 with a mean chiasma frequency ranging from 5.24 to 10.40 per cell (Table V). On the average there were many more open bivalents than closed ones but in some individual cells, the number of ring bivalents ranged as high as five. Trivalents were quite common ranging from 0.44 to 1.95 per cell (Plate II, Fig. 5); while the presence of quadrivalents was again an indication of homoeologous synapsis between wheat and rye chromosomes. In general there was little difference in the degree of homoeologous pairing between hybrids grown at 21°C and those subjected to a 15°C temperature during meiosis.

Six hybrids deficient for chromosome 5B were studied at the 32°C temperature. The average bivalent association per cell varied from 2.01 to 4.7 among plants, with a mean chiasma frequency ranging from 2.62 to 5.94 (Table VI). The majority of the bivalents observed were rod-shaped with terminal chiasmata. Trivalents were also present in some hybrids, but in general they were not as numerous as observed at either the 15°C or 21°C temperatures (Plate II, Fig. 6). Quadrivalents were observed at a very low frequency (less than 0.1%).

Table V - Mean pairing frequency per cell in 27-chromosome (5B absent)
wheat-rye hybrids grown at 21°C

Hybrid	Cells Scored	Univ. (Range)	<u>Bivalents</u>		Triv. (Range)	Quad. (Range)	Aver. Biv. Ass.	Chias- mata (Range)
			Open (Range)	Closed (Range)				
H-020	100	18.21 (12-21)	2.96 (1-6)	0.37 (0-3)	0.53 (0-3)	0.16 (0-1)	4.18	5.24 (3-10)
H-033	50	17.36 (14-23)	3.30 (1-6)	0.20 (0-3)	0.72 (0-3)	0.12 (0-1)	4.46	5.50 (5-9)
H-060	100	17.44 (13-21)	3.16 (1-6)	0.62 (0-3)	0.44 (0-2)	0.17 (0-1)	4.56	5.79 (3-11)
H-016	100	15.17 (12-21)	3.85 (2-6)	1.04 (0-4)	0.55 (0-2)	0.10 (0-1)	5.64	7.33 (4-11)
H-01	100	12.85 (9-20)	3.01 (1-6)	1.02 (0-5)	1.95 (0-4)	0.08 (0-1)	6.14	9.19 (3-12)
H-03	100	12.64 (9-18)	2.15 (2-6)	2.25 (0-5)	1.68 (0-4)	0.13 (0-1)	6.34	10.40 (7-12)

Table VI - Mean pairing frequency per cell in 27-chromosome (5B absent) wheat-rye hybrids grown at 32°C

Hybrid	Cells Scored	Univ. (Range)	<u>Bivalents</u>		Triv. (Range)	Quad. (Range)	Aver. Chias-	
			Open (Range)	Closed (Range)			Biv. Ass.	mata (Range)
H-055	200	22.66 (17-25)	1.39 (0-5)	0.28 (0-2)	0.32 (0-2)	0.01 (0-1)	2.01	2.62 (1-5)
H-023	100	20.22 (17-25)	2.52 (0-5)	0.25 (0-2)	0.32 (0-2)	0.07 (0-1)	3.23	3.87 (1-5)
H-043	100	19.75 (13-25)	2.33 (1-7)	0.31 (0-2)	0.55 (0-2)	0.08 (0-1)	3.35	4.29 (1-9)
H-021	100	19.40 (15-23)	2.84 (2-6)	0.18 (0-3)	0.48 (0-2)	0.03 (0-1)	3.56	4.18 (2-8)
H-01	100	17.52 (13-21)	2.04 (2-5)	0.51 (0-3)	1.30 (0-3)	0.05 (0-1)	3.95	5.76 (3-8)
H-03	100	17.44 (13-21)	2.14 (2-6)	0.45 (0-3)	1.42 (0-4)	0.03 (0-1)	4.07	5.94 (3-8)

DISCUSSION AND CONCLUSIONS

Genotypic Control on Chromosome Pairing

The occurrence of genotypic control of chromosome pairing and chiasmata formation, has been clearly established in many plants and animals and both continuous and discontinuous variation has been recognised to exist by many authors (Rees, 1961; Riley and Law, 1965). However, no organism has been more thoroughly investigated from this point of view than rye. It is known that significant differences in chiasma frequency exist between individuals of different genotype which in turn is dependent upon a polygenic system of control. It is also known that such genes controlling chromosome behavior exercise their control in a way similar to those that govern the more simply inherited phenotypic characteristics.

Our results concerning the level of homoeologous pairing in the 28-chromosome wheat-rye hybrids, are not in agreement with the early reports of Kihara, (1924); and Thompson, (1926); and more recently those of Upadhyia and Swaminathan, (1963); Riley and Law, (1965); and Lacadena, (1967). These workers reported the occurrence of a low frequency of homoeologous pairing to occur in F_1 wheat-rye hybrids. On the other hand, the work of Nakajima and Zennyozzi, (1966), confirms the present results in that they also demonstrated the possible variation one might find when a sufficiently large number of hybrids is analysed. Nakajima and Zennyozzi assumed that the variation observed in homoeologous pairing among their hybrids was due to the genotype of the wheat

parent. They omitted any mention of the possibility of explaining such variation as possibly being due solely to the effect of the rye pollen, which in specific combinations with wheat could give rise to hybrids exhibiting varying degrees of chromosome pairing, even in the presence of chromosome 5B.

In our studies, continuous variation was clearly apparent at 15°C in which seventeen 28-chromosome hybrids were analysed and the average bivalent association per cell was found to range from 0.05 to 5.63 (Table I). At the 21°C treatment, only thirteen hybrids could be analysed and although the extremes were not as marked as in the 15°C treatment, the same trend for a continuous type of variation of homoeologous pairing was evident (Table II).

Continuous variation in the pairing relationship between wheat and rye chromosomes strongly support the contention that a polygenic system is operative and that the size of sample is obviously an important factor if a complete range of variation in chromosome pairing potentially existing in a hybrid population is to be obtained. This relationship was also shown by Nakajima and Zennyozzi who obtained a broad range of variation in a large population. Unfortunately, most of the previous reports on homoeologous pairing in wheat-rye hybrids were based on the study of a very few plants which could obviously result in an erroneous conclusion regarding the amount of homoeologous synapsis that occurs in such hybrids. Nakajima, (1952) should be credited as the first therefore, to show that chromosome pairing in wheat-rye

hybrids can occur at a very high frequency, even though his assumptions to explain such level of pairing are not in agreement with our own. We suggest that a polygenic system as contributed by the rye pollen governs homoeologous chromosome pairing which can only be detected by a study of a large population.

Feldman and Mello-Sampayo, (1967), showed that the genus Triticum speltoides (Ae. speltoides) carries a gene (s) which in combination with those present on chromosomes 5A, 5B^S and 5D of wheat, can induce homoeologous pairing in wheat-T. speltoides hybrids notwithstanding the presence of 5B^L in the same genotype. A similar mechanism could be postulated to operate in the case of wheat-rye hybrids reported herein. It is not inconceivable that air borne rye pollen carries two genic systems affecting homoeologous chromosome pairing; one inducing asynapsis which is very well known to exist (Rees, 1961); and another which promotes pairing and which may be operative either during premeiosis or early at first meiotic prophase. Depending upon the number and nature of such genes as well as their interaction, chromosome pairing relationships as observed in F₁ wheat-rye hybrids could be extremely variable from plant to plant.

In comparison with 28-chromosome hybrids (5B present), homoeologous pairing in 27-chromosome hybrids (5B deficient) was enhanced as expected, however, a continuous variability in pairing frequency similar to that found in the 28-chromosome hybrids, was again evident. The more asynaptic 27-chromosome hybrids confirm

the reports of Riley, (1963), who suggested that rye chromosomes appear to reduce homoeologous pairing when crossed with wheat. We propose that this phenomenon may be due to specific genes causing asynapsis (or desynapsis) as introduced by the heterozygous rye parent.

Concerning the effect of temperature upon chromosome pairing: in general we can say that for a given chromosome level, there was little difference in the degree of homoeologous synapsis between hybrids grown at the 15°C as compared with those subjected to 21°C (Tables I, II, IV and V). However, at 32°C, the average bivalent association per cell, was the lowest value of the three treatments used (Tables III and VI). It is thus clear that temperatures above optimum, affect chromosome pairing and chiasma frequency per cell which, in our experiments, ranged from 0.12 to 1.13 in the 28-chromosome hybrids, and from 2.62 to 5.94 in the 27-chromosome hybrids respectively. Nevertheless, those hybrids which exhibited the highest chiasma frequency per cell at the lower temperature, again exhibited relatively high values at the 32°C treatment. This supports our assumption that chromosome synapsis in wheat-rye hybrids is primarily under genic control which in turn is modified by temperature prevailing during meiosis.

The variation in chromosome behavior due to environmental factors has long been recognized (Rees, 1961; Riley, 1966). Most attention however, has been directed to the effect of temperature on chromosome synapsis. In general, it has been found that chiasma

formation is progressively reduced as temperature is increased or decreased below the optimal range for the species. Our observations concerning the effect of high temperature confirm this expectation since almost complete asynapsis was recorded in most of the plants analysed at the 32°C temperature level.

The fact that some genes carried by the rye pollen in Triticum x Secale hybrids can influence the degree of homoeologous synapsis during meiosis, is of extraordinary importance from both a theoretical and a practical standpoint. It is now clear that genes affecting meiotic chromosome behavior in the rye parent, are able to interact in a foreign cytoplasm thus either enhance or reverse the action of genes affecting meiotic behavior when transferred to a wheat background. The final meiotic picture depends upon the nature and number of genes involved, and their degree of expressivity in the hybrid genotype. Their "allelism" may be presumed to stem from their common evolutionary origin. It is well known that all the diploid species of the Triticinae arose from a common progenitor. The fact that many of the genetic functions of the present chromosome complex were retained from the original chromosome from which they arose is best exemplified by the Nullisomic-Tetrasomic series as produced by Sears, (1966), in hexaploid wheat. From the practical point of view it is interesting to speculate that most of the anomalies observed in the meiotic and reproductive systems of the amphiploid Triticale may be due to the asynaptic effect of certain

genes of rye, rather than to the interaction of two opposite breeding systems superimposed upon one another in this one species. It is clear that much more information is needed in order to completely evaluate this phenomenon including extensive studies of the genetic linkage relationships within the genus Secale itself. In addition, it is imperative that in the search for a Triticale with improved fertility a wide range of genetic combinations be exploited, not only between the parental species of wheat and rye, but also between Triticale amphiploids already established.

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