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Author(s): T E Miller and S M Reader
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Variation in the meiotic chromosome pairing of hybrids between hexaploid and diploid wheats

T E Miller and S M Reader

Plant Breeding Institute, Cambridge

Summary

A range of diploid wheats was crossed to the hexaploid wheat Chinese Spring. Some hybrids of some combinations had sterile anthers. This pattern is compared with that of the semi-lethal effect found in crosses between diploid and tetraploid wheats. Meiotic pairing studies revealed slight differences in the level of chromosome pairing. There was no significant difference in the pairing level within accessions of any species, but there were differences between accessions. These differences, however, were not confined to any particular species. It is concluded that there may be genes in diploid wheat which affect homoeologous chromosome pairing in hybrids, but they are of low potency.

Introduction

In recent years there have been reports of variation in the level of meiotic chromosome pairing in hybrids between *Triticum aestivum* (2n = 6x = 42) and diploids of other genera of the *Triticinae*. Kimber and Athwal (1972) and Dvorak (1972) found differing levels of chromosome pairing in hybrids of *T. aestivum* with different genotypes of *Aegilops speltoides*. Dover and Riley (1972) recognised four levels of pairing in hybrids between *T. aestivum* and *Ae. mutica*. Variation has also been detected in hybrids between *T. aestivum* and *Secale cereale* which had either an increased dosage of chromosome 3R (Lelley, 1976) or of chromosome 3B (Chapman, Miller and Riley, 1977). Variation in the frequency of trivalents was found in a comparison of the chromosome pairing in hybrids of *T. aestivum* with *T. thaoudar* and *T. urartu* (Chapman, Miller and Riley, 1976).

The purpose of this investigation was to test diploid wheats for allelic variation affecting meiotic chromosome pairing by studying the meiosis of hybrids between *T. aestivum* and a range of diploid wheats.

Materials and Methods

The diploid wheats (2n = 2x = 14) used were all from the collection of the Plant Breeding Institute, Cambridge. Accessions of *T. aegilopoides*, *T. monococcum*, *T. thaoudar* and *T. urartu* were used as male parents in crosses to *T. aestivum* var. Chinese Spring. Previous experience had shown that some of these crosses did not produce viable grains. Therefore, the embryo culture technique was used on all the hybrid grains. The embryos were excised approximately 21 days after pollination and cultured on nutrient agar medium at 20°C with continuous illumination. Plants which grew from the embryos were transplanted into potting compost and thereafter grown in a controlled environment chamber at 20°C with continuous illumination.

Anthers containing pollen mother cells at first metaphase of meiosis were fixed in three parts of absolute alcohol: one part of glacial acetic acid and subsequently stained by the Feulgen procedure. Permanent slides were prepared for the meiotic studies.

Results

At least one hybrid plant was obtained from each of 31 different crosses and a total of 165 plants were available for meiotic study (Table 1). There was an unexpectedly high level of anther sterility in some of the hybrids. In some plants all the anthers were sterile, while in others a few normal pollen mother cells were found in some anthers. Consequently meiotic analysis was possible in only 119 plants. The distribution of the anther sterility amongst the crosses is shown in Table 1.

The meiotic chromosome pairing behaviour of the hybrids is summarised in Table 2.

The ABD genomes of hexaploid wheat are believed to have originated in the A genome of diploid wheat and the B and D genomes of two diploid *Aegilops*. Therefore, in hybrids (AABD) between hexaploid wheat (AABBDD) and diploid wheat (AA) pairing between the chromosomes of the two A genomes could be expected. On the simplest interpretation of this pairing a maximum of seven bivalents per cell would be expected. Previous reports have shown and this experiment confirms that the observed pairing is less. However, in the hybrids of *aegilopoides* 8, *monococcum* 3, 29, 30 and *thaoudar* 3 cells were observed with fewer than 14 univalents (Table 3). In these cells the pairing was higher than that which would result from the maximum pairing of the two A genomes. One or more chromosomes of the B or D genomes must also have participated in the pairing.

An analysis of the pairing (Table 4) shows that there was no significant difference in the number of chromosomes paired or in the frequency of bivalents or trivalents within each accession. However, there was a significant difference in the total number of chromosomes paired (as shown by univalent frequency) between accessions within a species, although the difference between species was not significant. Similarly the frequencies of bivalents and trivalents were significantly different between accessions but not between species.

Discussion

The failure of pollen mother cell development before the start of meiosis has not been previously reported in interspecific hybrids of *Triticum*. In a range of hybrids and amphiploids between tetraploid and diploid wheat Bell, Lupton and Riley (1955) found that a semi-lethal gene caused the early death of some plants and retarded the growth of others. In these crosses the semi-lethal effect was never found in hybrids involving *T. thaoudar*, but it did affect all the plants in some crosses with *T. monococcum* or *T. aegilopoides* and only some plants in other crosses. A similar pattern for the anther sterility was found in the present experiment, where the *T. thaoudar* hybrids were again unaffected. The anther failure in some of the hybrids between *T. aestivum* var. Chinese Spring and *T. monococcum* or *T. aegilopoides* may be a different expression of the same system that produced semi-lethality in similar hybrids between tetraploid and diploid wheats.

Table 1. The occurrence of anther sterility in hybrids between *T. aestivum* Chinese Spring and diploid wheats

		No. of plants	No. examined meiotically	Anthers		
				Fertile	Partially sterile	Sterile
Chinese Spring	1	6	1	1	1	4
x	3	3				3
T. aegilopoides	4	3				3
	8	9	8	7	1	
	10	8				8
	11	1	1	1		
	12	2				2
	15	4	1		1	3
	18	3				1
	19	4				4
	20	3				3
Chinese Spring	3	31	31	31		
x	6	5	2	2		1
T. monococcum	7	3				2
	9	1	1	1		
	11	1	1	1		
	13A	6	5	5		1
	14	3	2	2		
	18	1				1
	25	1	1		1	
	26	1				1
	29	13	5	5	2	6
	31	7	1	1	1	5
	31A	7	7	7		
Chinese Spring	1	5	5	5		
x	2	8	8	8		
T. thaoudar	3	10	9	9		
	4	4	3	3		
	9	1	1	1		
Chinese Spring	A	10	10	10		
x	C	1	1	1		
T. urartu						

Table 2. Mean chromosome pairing at first metaphase of meiosis in hybrids between T. aestivum Chinese Spring and diploid wheats. 30 cells per plant. Ranges in parenthesis.

		No. of plants	Univ.	Biv. rod	Biv. ring	Biv. total	Triv.	Quad.	Xta.
Chinese Spring x T. aegilopoides	1	1	23.09 (17-28)	2.18 (0-5)	0.26 (0-2)	2.44 (0-5)	0.01 (0-1)		2.91 (0-7)
	8	8	19.03 (10-26)	3.10 (0-7)	1.17 (0-4)	4.27 (1-7)	0.13 (0-3)	0101 (0-1)	6.08 (1-12)
	15	1	19.18 (15-24)	3.33 (2-5)	0.93 (0-2)	4.26 (2-5)	0.10 (0-1)		5.93 (2-9)
Chinese Spring x T. monococcum	3	31	20.00 (11-28)	2.86 (0-6)	0.99 (0-5)	3.85 (0-8)	0.10 (0-2)	* (0-1)	5.30 (1-12)
	6	2	19.35 (14-26)	2.77 (1-6)	1.15 (0-4)	3.92 (3-7)	0.27 (0-2)		5.80 (2-11)
	9	1	18.83 (14-24)	3.33 (1-5)	1.00 (0-3)	4.33 (2-7)	0.17 (0-1)		5.97 (2-10)
	11	1	19.85 (16-26)	2.67 (0-5)	1.30 (0-3)	3.97 (1-6)	0.07 (0-1)		5.73 (1-9)
	13A	5	20.45 (15-27)	2.78 (0-5)	0.87 (0-4)	3.65 (1-7)	0.07 (0-1)	0.01 (0-1)	5.26 (1-13)
	14	2	19.62 (16-24)	3.10 (1-6)	1.15 (0-3)	4.25 (2-6)	0.05 (0-1)		4.69 (1-10)
	25	1	21.29 (16-26)	2.80 (1-5)	0.60 (0-2)	3.40 (1-6)			4.00 (1-7)
	29	5	19.30 (11-26)	3.07 (1-5)	1.12 (0-4)	4.19 (1-7)	0.11 (0-2)		5.93 (1-13)
	30	1	17.08 (13.22)	3.33 (1-5)	1.47 (0-4)	4.80 (3-7)	0.40 (0-2)	0.03 (0-1)	8.27 (4-13)
	31A	7	19.21 (14.26)	3.09 (0-7)	1.17 (0-4)	4.26 (1-7)	0.09 (0-1)	* (0-1)	5.97 (1-12)
Chinese Spring x T. thaoudar	1	5	19.58 (14.26)	3.08 (1-6)	0.98 (0-4)	4.06 (1-7)	0.10 (0-1)		5.32 (1-11)
	2	8	20.21 (14-28)	2.86 (0-6)	0.91 (0-4)	3.77 (1-7)	0.07 (0-1)	0.01 (0-1)	4.64 (0-11)
	3	9	17.31 (13-26)	3.23 (0-6)	1.65 (0-4)	4.88 (1-7)	0.31 (0-2)		7.89 (3-14)
	4	3	19.70 (16-28)	3.06 (0-6)	0.91 (0-3)	3.97 (0-6)	0.12 (0-1)		5.57 (3-10)
	9	1	17.23 (14-23)	3.30 (0-5)	1.83 (0-3)	5.13 (2-7)	0.17 (0-2)		8.23 (4-13)
Chinese Spring x T. urartu	A	10	18.69 (14-28)	2.99 (0-5)	1.95 (0-5)	4.94 (0-7)	0.01 (0-1)		7.60 (0-12)
	C	1	22.06 (16-28)	2.60 (0-5)	0.37 (0-1)	2.97 (0-5)			3.37 (0-6)

* one quadrivalent

Table 3. Cells with more than the expected maximum level of chromosome pairing.

Accession		Univ.	Biv.			Triv.
			rod	ring	total	
T. aegilopoides	8	10	4	1	5	2
		13	4	1	5	1
		13	3	3	6	1
T. monococcum	3	12	5	3	8	
		11	5	2	7	1
		13	5	1	6	1
	29	11	6	1	7	1
		13	5	1	6	1
	30	13	3	3	6	1
T. thaoudar	3	13	3	6	1	1
		13	5	1	6	1
		13	5	1	6	1
		13	2	4	6	1
		12	4	1	5	2
		12	3	2	5	2
		13	5	1	6	1
		13	4	2	6	1
		13	3	3	6	1
		13	5	1	6	1
		13	5	1	6	1

Table 4. Analysis of variance of meiotic chromosome pairing data of hybrids between *T. aestivum* Chinese Spring and diploid wheats.

Item	Chinese Spring x *T. aegilopoides* df	MS	Chinese Spring x *T. monococcum* df	MS	Chinese Spring x *T. thaoudar* df	MS	Chinese Spring x *T. urartu* df	MS	Overall df	MS
Univalent frequency										
Between species	-	-	-	-	-	-	-	-	3	4.7704
Between accessions	2	7.1210	10	1.9097	4	11.7569 ***	1	12.0517 *	17	5.4364 ***
Between plants	7	1.7605	45	1.5443	21	1.5952	9	1.5879	82	1.5805
Bivalent frequency										
Between species	-	-	-	-	-	-	-	-	3	2.2798
Between accessions	2	1.7218 *	10	0.3063	4	1.5718 **	1	3.5532 ***	17	0.9616 **
Between plants	7	0.2503	45	0.3026	21	0.2937	9	0.2014	82	0.2883
Trivalent frequency										
Between species	-	-	-	-	-	-	-	-	3	64.7315
Between accessions	-	-	10	15.7637 *	3	89.6253 ***	-	-	13	32.8086 ***
Between plants	-	-	45	7.1410	21	6.1792	-	-	82	6.6535

In hybrids of Chinese Spring with Ae. mutica Dover and Riley (1972) reported mean chiasmata frequencies per cell as high as 14.76 and as low as 0.87. In this investigation the differences in mean pairing levels were small. The higher pairing levels with increased trivalent frequency in some hybrids with T. aegilopoides compared with hybrids with T. urartu has been discussed previously be Chapman, Miller and Riley (1976) and Dvorak (1976). It was thought that in the aegilopoides hybrids there was homoeologous pairing in addition to the homologous pairing between the two A genomes. The evidence from this experiment suggests that although there are differences in pairing levels, the higher pairing is not confined to the hybrids of any one diploid species. Consequently if there are genes in diploid wheat which can alter the threshold of homoeologous pairing in hybrids they are not a characteristic of any one species, and do not produce effects of the magnitude reported in hybrids with other diploid genera of the Triticinae.

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