Further Evidence for the Suppression of Meiotic Chromosome Pairing by *Hordeum californicum*

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During meiosis, the diploid-like behaviour of the common wheat (*Triticum aestivum* L.), an allohexaploid with three homoeologous genomes (ABD), is genetically controlled (Riley 1960, Sears 1976). Some of the diploid species of the genus *Aegilops*, such as *Ae. speltoides*, *Ae. mutica* (Riley 1966, Dover and Riley 1972) and *Ae. longissima* (Avivi 1976, Dvorak 1977), *Secale cereale* (for details see Gupta and Fedak 1985a) and *Hordeum vulgare* (Fedak 1977) have been shown to suppress the activity of the meiotic pairing control system of hexaploid wheat and thus permit the pairing of homoeologous chromosomes.

In contrast, Rajhathy (1967) reported that the *H. vulgare* genome in the hybrids (*H. stenostachys* × *H. cordobense*) × *H. vulgare* drastically reduced meiotic pairing. Similarly, an asynaptic influence of *H. vulgare* (Bothmer *et al.* 1983) and desynaptic influence of *H. violaceum* (Wang 1984) in interspecific hybrids has been reported. Recently, we demonstrated that accession number 1843 of *H. californicum* ($2n=2x=14$, HH) has the ability to suppress the pairing between homoeologous chromosomes of A and B genomes of $4x$ and $6x$ wheats (Balyan and Fedak 1988). In the present communication we present and discuss the results of the suppression by *H. californicum* of meiotic chromosome pairing in a hybrid ($2n=7x=49$, AABDGH) involving (*T. timopheevii* × *H. bogdanii*) × (*H. californicum* × *T. aestivum*).

Materials and methods

The maternal parent used to develop the hybrid for the present study was the amphiploid (*Triticum timopheevii* × *Hordeum bogdanii*)² obtained from Dr. Gordon Kimber, University of Missouri, Columbia (Kimber and Sallee 1976). The paternal parent used in the hybrid combination was another amphiploid (*Hordeum californicum* × *Triticum aestivum*)² (Fedak unpublished). The strain of *H. californicum*, Covas and Stebbins used to produce the hybrid with *Triticum aestivum* cv. Chinese Spring (Gupta and Fedak 1985b) to develop the latter amphiploid was strain number CHC 1843 collected in the Carmel Valley of California (Baum *et al.* 1984). The seeds of both the above amphiploids were germinated on moistened filter paper in petri dishes. The seedlings were transplanted to a soil-proroot mixture in pots and grown in a growth room maintained at day/night temperature of 20°/15°C and light intensity of 300 $\mu\text{E m}^{-2} \text{sec}^{-1}$.

Spikes of the (*T. timopheevii* × *H. bogdanii*)² amphiploid were emasculated and covered with dialysis tubing prior to pollination by the paternal amphiploid (*H. californicum* × *T. aestivum*)². At 24 and 48 h after pollination, gibberellic acid (GA_3) at concentrations of 75 ppm was applied to individual florets by means of a hypodermic syringe. At 15 days after pollination, the hybrid embryos were excised and plated on a B5 medium modified by the exclusion of 2, 4-dichlorophenoxyacetic acid (2, 4-D). For meiotic study, the spikes were fixed in Carnoy's solution (6 parts ethanol: 3 parts chloroform: 1 part glacial acetic acid) for at

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least 24 h and squashed in 1% acetocarmine. For better staining the anthers were immersed in Snow's solution (Snow 1963) overnight before squashing.

Results

Synthesis of hybrid

A total of 84 florets of the amphiploid (*T. timopheevii* × *H. bodganii*)² were pollinated by pollen collected from the amphiploid (*H. californicum* × *T. aestivum*)². A total of four seeds were obtained which yielded four embryos.

Meiosis in the hybrid

The genomic constitution of the hybrids examined during the present study is expected to be AABDGHH with $2n=7x=49$. The chiasmata frequency per PMC in the four hybrid plants varied from 7.61 to 8.61 (Table 1). Chromosome configurations were predominantly bivalent types, although up to three trivalents were observed in 30% of the PMCs and a single

Table 1. Chromosome associations per pollen mother cell (PMC) at metaphase I in the F_1 hybrids ($2n=7x=49$) involving two amphiploids (*Triticum timopheevii* × *Hordeum bodganii*)² and (*H. californicum* × *T. aestivum* cv. Chinese Spring)²

Plant no.	No. of PMCs	Chromosome associations						
		I	II			III	IV	Xta
			Rod	Ring	Total			
1	54	35.20	4.91 (2-9)	1.57 (0-5)	6.48 (2-11)	0.28 (0-3)	—	8.61
2	57	34.92	4.37 (1-6)	1.56 (0-3)	5.93 (2-9)	0.37 (0-2)	—	8.23
3	74	35.54	5.12 (1-8)	1.11 (0-4)	6.23 (3-9)	0.34 (0-2)	0.027 (0-1)	8.10
4	45	36.33	4.73 (1-7)	1.11 (0-4)	5.84 (3-10)	0.33 (0-2)	—	7.61
Mean	—	35.50	4.78	1.34	6.12	0.33	0.007	8.14

quadrivalent in two PMCs. The mean bivalent number in the four plants varied from 5.84 to 6.48 with a high proportion (70-80%) of rod bivalents. The modal class of bivalents in the four plants was represented by five to seven bivalents per PMC, although a bivalent frequency as low as two to as high as 11 per PMC was observed in small proportions of the total PMCs examined.

Discussion

During the present study a septaploid hybrid ($2n=7x=49$) was developed through hybridization of an amphiploid of (*T. timopheevii* × *H. bodganii*)² ($2n=6x=42$, AAGGHH) as maternal parent with another amphiploid involving (*H. californicum* × *T. aestivum* cv. Chinese Spring)² ($2n=8x=56$, AABDDHH) as the paternal parent. The genomic constitution of the hybrid was AABDGHH.

At MI in the present hybrid a high bivalent frequency would be expected from associations between homologous chromosomes of the A and H genomes. The two *Hordeum* species, *H. bodganii* and *H. californicum* share a common H genome (Dewey 1984). In addition it

has been shown that the B and G genomes of *Triticum* species are of common origin and differ from each other by a few non-structural differences (Feldman 1966). Similarly in meiotic studies of the *T. timopheevii* × *H. bogdanii* hybrid, up to four bivalents were observed in some cells (Kimber and Sallee 1976). The latter two factors would be expected to produce additional paired configurations. However the total bivalent frequency did not exceed 11 in any one cell of the present hybrids and the mean bivalent frequency for four plants was only 6.11. The pairing between homologous chromosomes of the A and H genomes and homoeologous chromosomes of the B, G and H is therefore markedly suppressed; presumably by the H genome. The chromosome pairing suppression observed in the present hybrid is even more pronounced than the suppression of A and B genome pairing attributed to *H. californicum* in a previous study (Balyan and Fedak 1988). Similarly a lower frequency of paired configurations was observed in a hybrid of *H. californicum* strain 1843 with *Agropyron caninum* than with the latter crossed to *H. brevisubulatum*, indicative of the meiotic suppression by *H. californicum* strain 1843 (Gupta and Fedak 1985b).

It has previously been shown that markedly different chromosome pairing frequencies are observed in interspecific hybrids with *H. californicum* (syn. *H. brachyantherum*) when different accessions of that species are used (Bothmer *et al.* 1986). For example, in hybrids between *H. californicum* and *H. brevisubulatum* chiasmata frequencies ranged from 1.88 to 7.92 with different accessions of *H. californicum* (Bothmer *et al.* 1986). Clearly the genomes of different accessions of *H. californicum* have a marked effect on meiotic chromosome pairing in hybrids. The accession used in the present study, CHC 1843 has now in several experiments demonstrated a suppression effect on meiotic pairing of homologous and homoeologous chromosomes.

This phenomenon of the effect of meiotic chromosome pairing which may ultimately be resolved to specific pairing regulatory genes may be similar to that reported for certain species of *Aegilops*, e. g. *Ae. speltoides*, *Ae. mutica*, *Ae. longissimum*, etc. although in the latter the specific effects have been opposite in effect. The homoeology between the chromosomes of *H. californicum* and *T. aestivum* has not been demonstrated as yet, but probably exists in the same way that *H. vulgare* (Islam and Shepherd 1981) and *H. chilense* (Jouve, p. c.) share homoeology with *T. aestivum*.

The mechanism involved in the suppression of meiotic chromosome pairing by *H. californicum* is not known but may be related to the complex of asynaptic or desynaptic genes reported in *H. vulgare* (Bothmer *et al.* 1983) or *H. violaceum* (Wang 1984).

Summary

By crossing an amphiploid (*T. timopheevii* × *H. bogdanii*)² as maternal parent with another amphiploid (*H. californicum* × *T. aestivum*) four hybrid plants were recovered at a frequency of 2.4% of the pollinated florets. The meiotic analysis of the data revealed a mean chiasmata frequency per cell in four hybrid combinations ranging from 7.61 to 8.63. Average chromosome associations of 6.12 bivalents, 0.33 trivalents and 0.007 quadrivalents per cell were observed at metaphase I. The lower than expected bivalent frequency in the septavalent hybrid (2n=7x=49, AABDGHH) was attributed to the suppression of meiotic chromosome pairing by *H. californicum*.

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