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Genome-specific control of meiotic pairing evidenced in mutant *Aegilops ventricosa-Secale cereale* amphidiploids

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Summary. The *Ae. ventricosa* and *S. cereale* genomes were distinguished at meiosis by the C-banding procedure. Only two plants of the amphiploid *Ae. ventricosa-S. cereale* were found to exhibit the high degree of asynapsis limited to *Aegilops ventricosa* genomes. In addition, these genomes showed higher homoeologous pairing than homologous pairing frequencies. These results can be explained by the existence of separate genome-specific control of meiotic pairing between the chromosomes of both species in these synaptic mutant plants.

Key words: *Ae. ventricosa-S. cereale* amphidiploids – Genome-specific control – Meiotic pairing

Introduction

The genetic control of processes related to meiotic pairing in diploids as well as in allopolyploids can be altered by specific mutations. In general, meiotic mutations show an effect over all chromosomes of the complement although a few cases have been observed in diploid organisms in which irregular meiotic behaviour is limited to a single chromosome pair (Parker 1975; Tease and Jones 1976) or to a chromosome group (Rees 1957; John and Naylor 1961). However, there no case has been reported in the literature about any genetic control on chromosome pairing affecting specific genomes in allopolyploids, probably due to the impossibility of identifying different genomes by conventional staining techniques.

In *Ae. ventricosa-S. cereale* amphiploid plants it is possible to distinguish the genomes of *Ae. ventricosa* from those of *S. cereale* by using the C-banding procedure (Cermeño et al. 1985).

In this work we describe genome-specific synaptic mutant plants in *Ae. ventricosa-S. cereale* amphiploids.

Material and methods

Plants of the amphiploid *Aegilops ventricosa-Secale cereale* formed the material for this study.

The amphiploid seeds were kindly supplied by Dr. F. Dosba, Plant Breeding Station, Research Center of Rennes. INRA (France).

In order to analyze meiotic cells, anthers were fixed in acetic-ethanol 1:3 and stored at 4 °C for several months. The fixed material was squashed and stained following the Giemsa C-banding technique described previously (Giraldez et al. 1979).

Results

The synthetic amphiploid *Ae. ventricosa-S. cereale* was obtained from the cross, and further chromosome doubling occurred between the allotetraploid *Ae. ventricosa* (genome constitution *DDUnUn*) (Kimber et al. 1983) and diploid *S. cereale* (genome constitution *RR*). With conventional staining methods is impossible to distinguish the genomes of the two species, but when the C-banding technique is applied, *Ae. ventricosa* shows twelve chromosomes with centromeric C-bands, and sixteen with clearly centromeric, pericentromeric and interstitial or dispersed C-bands. These two groups could represent, in part, the D and Un genomes respectively, though at least one chromosome pair of the D genome is included in the Un group because it shows the same C-banding pattern as Un chromosomes. Rye chromosomes show prominent heterochromatin blocks located in the telomeres (Fig. 1a). These different C-banding patterns make the identification of all meiotic

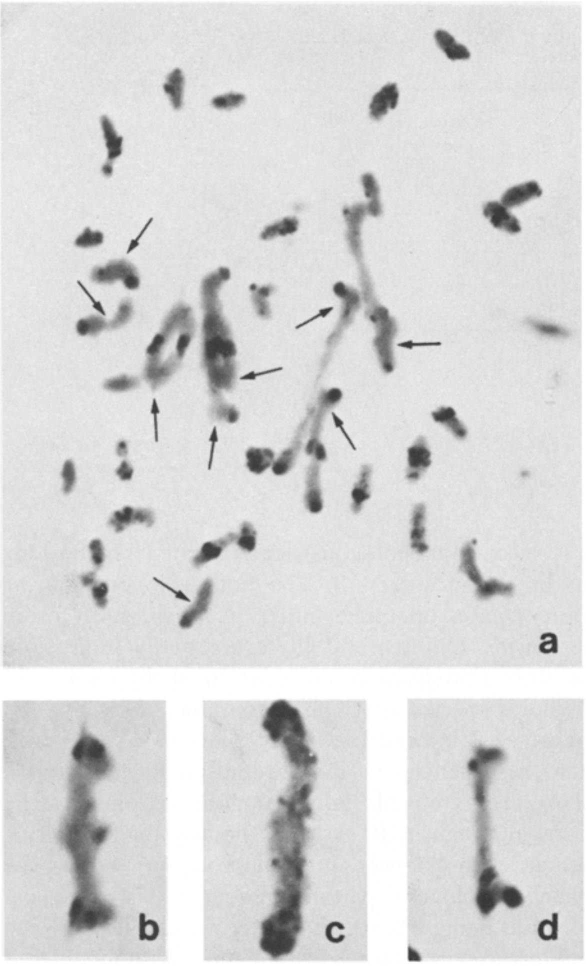

Fig. 1a–d. C-banded metaphase I cell of a meiotic mutant plant of the amphiploid *Ae. ventricosa-S. cereale*. *Arrows* indicate rye bivalents or univalents. (**a, b**) Open bivalents of *Ae. ventricosa* with homologous pairing between D chromosomes and (**c**) between Un chromosomes, and with homoeologous pairing between D and Un chromosomes (**d**)

Table 1. Mean number of bound arms per cell observed at mataphase I for *S. cereale* and *Ae. ventricosa* chromosomes in amphiploid *Ae. ventricosa-S. cereale* normal and mutant plants

Plant	Genome R	Genomes Un + D	
		(Homologous)	(Homoeologous)
AvSc1	8.54	23.74	–
AvSc2	8.04	23.22	–
AvSc3	7.54	22.66	–
AvSc4	7.22	22.76	–
AvSc5	7.42	22.60	–
AvSc6	5.58	0.13	0.36
AvSc7	6.30	0.07	0.31

configurations formed by the chromosomes of the two species possible. In addition, differences among *Ae. ventricosa* chromosomes indicates whether *Ae. ventricosa* bivalents are formed by chromosomes with the same (Fig. 1b–c) or different (Fig. 1d) C-banding patterns, the last possibility being taken as a proof of the existence of homoeologous pairing. Therefore, the different C-banding patterns of chromosomes in a bivalent is an accurate way to estimate the minimum number of homoeologous pairings. The appearance of heteromorphic bivalents due to the existence of hypothetical polymorphisms for C-bands in *Ae. ventricosa* chromosomes could be excluded due to the autogamous habit of this species.

Table 1 shows the mean number of bound arms per cell formed between homologous and homoeologous chromosomes in all plants studied. As can be observed, two of the seven plants analyzed show an anomalous meiotic behaviour.

Five *Ae. ventricosa-S. cereale* amphiploid plants (AvSc1-AvSc5) show a normal meiotic behaviour with low frequencies of the meiotic irregularities, such as univalents and failures of meiotic pairing, which mainly affect rye chromosomes. No case of homoeologous pairing, either within *Ae. ventricosa* or between *Ae. ventricosa* and *S. cereale* chromosomes, was found. These irregularities are very common in synthetic allopolyploid plants in which rye genomes are involved, and they have been exhaustively studied in triticale (see Gupta and Priyadarshan 1982). For this reason these plants have been taken as the normal situation and are consequently considered as control plants.

The meiotic behaviour of the other two plants analyzed (AvSc6 and AvSc7) was most anomalous because practically all partners of the *Ae. ventricosa* complement could form univalents and the low pairing observed at metaphase I was almost exclusively between chromosomes having a different C-banding pattern (heteromorphic pairing). The excess of such heteromorphic pairing could not be explained by the existence of a structural interchange between D and Un genomes in plants AvSc6 and AvSc7, since more than two heteromorphic bivalents were observed in some cells. This is confirmed by the total absence of quadrivalents (Table 2). Therefore, the heteromorphic pairing seems to be actual homoeologous pairing. Rye chromosomes paired as usual (Cermeño et al. 1985), although meiotic pairing frequencies were lower than those of the control plants ($t = 4.08$; d.f. $= 5$; $0.01 > P > 0.001$) (Table 1).

The different behaviour of Un and D genomes with respect to R genomes found indicate that at least in these two mutant plants the *Ae. ventricosa* genomes are under a different meiotic control than *S. cereale* genomes.

Table 2. Distribution of the number of homomorphic and heteromorphic bivalents and trivalents per cell observed at metaphase I for *Ae. ventricosa* chromosomes in the synaptic mutant plants AvSc6 and AvSc7

Plant	Type of pairing								1III	No. cells
	Homomorphic bivalents			Heteromorphic bivalents						
	2	1	0	4	3	2	1	0		
AvSc6	2	12	134	1	1	6	33	105	2[a]	148
AvSc7	–	11	144	1	2	2	34	116	–	155
Total	2	23	278	2	3	8	67	221	2	303

[a] Y-shaped trivalents

Discussion

Meiotic pairing and chiasma formation seem to be under the control of both major genes and polygenic systems (Gale and Rees 1970; Baker et al. 1976). Mutation of major genes could be expressed phenotypically as asynapsis. These mutants are included in two classes (Riley and Law 1965): asynaptic (as) in which no synapsis occurs and desynaptic (ds) in which synapsis is apparently normal but chiasma formation fails. The two mutant plants found here could be classified as asynaptic because in all pachytene or diplotene cells a high number of univalents were observed. We cannot discern if the aberrant meiotic behaviour observed is due to a single gene or several genes because no breeding experiment has been performed due to the absolute infertility of these plants.

The possibility of environmental factors causing these results can be excluded because the data from several anthers of different spikes were very constant in both mutant plants.

In general, meiotic genetic controls are operative over the whole complement, but there are a few exceptions to this, such as the results reported in desynaptic mutants of *Hypochoeris radicata* (Parker 1975) and *Crepis capillaris* (Tease and Jones 1976) in which irregular meiotic behaviour was only limited to a single chromosome pair whereas the remaining chromosomes showed normal behaviour. Similar results have been obtained in asynaptic individuals of *Locusta migratoria* (Rees 1957) and *Schistocerca gregaria* (John and Naylor 1961). In these cases the meiotic irregularities were not limited to a single chromosome but to a chromosome group, the longest or the shortest chromosomes, respectively, and these disturbances in such groups were accompanied by a general reduction in chiasma frequency in all chromosome pairs.

Meiotic pairing between homologous chromosomes in allopolyploids is assured by the existence of gene(s) which suppress homoeologous pairing (see Riley and Law 1965; Sears 1976). This system is well known in wheat, and seems to be mainly due to the activity of the *Ph* (pairing homoeologous) locus located on the long arm of chromosome 5B. The homoeologous pairing suppression is operative either in wheat itself or in interspecific hybrids, and there are many indications that similar systems could exist in such other allopolyploids species as *Avena, Gossypium, Nicotiana* and others (see Riley and Law 1965; Sears 1976). However, when these gene(s) or the chromosome(s) carrying it (them) are removed, homoeologous pairing usually occurs, although in all cases the homoeologous pairing frequencies are lower than homologous ones. The higher homologous pairing frequency has been explained as being due to the greater similarities between homologous chromosomes than between homoeologous ones. However, the higher homoeologous pairing frequencies than homologous ones observed for *Ae. ventricosa* chromosomes in the two synaptic mutants (Table 1) indicate that meiotic pairing does not exclusively depend on the similarities between the chromosomes, at least in extreme conditions such as those of these plants.

The synaptic mutants of *Ae. ventricosa-S. cereale* have a regular pattern of univalence involving two specific genomes of *Ae. ventricosa* suggesting that the genomes of this species are subjected to some degree of autonomous control in addition to general control. These results are of special interest because they indicate that in the allopolyploids, the genomes of different species could maintain a certain degree of independence and therefore meiotic pairing could be regulate at different levels, namely, chromosome, genome and general control.

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