

# Chromosome and genomic relationships between the diploid species *Avena strigosa*, *A. eriantha* and the tetraploid *A. maroccana*

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Chromosome pairing in the diploid species *Avena strigosa* (genome AsAs), *A. eriantha* (genome CpCp) and the hybrid between them was broadly similar to a previous report. The derived autoallotetraploid (*A. strigosa* × *A. eriantha*)<sup>2</sup> showed greater variation of chromosome pairing than expected, particularly with regard to the frequency of rod bivalents and univalents. The hybrid (*A. strigosa* × *A. eriantha*)<sup>2</sup> × *A. maroccana* (genomes AACCC) would be expected to form 14 bivalents if the AsAs and CpCp genomes of *A. strigosa* and *A. eriantha* were completely homologous, respectively, to the AA and CC genomes of *A. maroccana*. Chromosome pairing in the hybrid was poor, however, indicating that it is unlikely that *A. eriantha* or *A. strigosa* participated in the formation of the tetraploid *A. maroccana*.

**Keywords:** *Avena*, chromosome pairing, interspecific hybrids, phylogeny.

## Introduction

The wild tetraploid oat *Avena maroccana* Gdgr. ( $2n = 4x = 28$ ; genomes AACCC) is thought to be the evolutionary link between the diploids and the cultivated hexaploid oat *A. sativa* L. ( $2n = 6x = 42$ ; genomes AACCCDD). The A and C genomes occur at all three ploidy levels, whereas the D genome is found only in the hexaploid species (Leggett & Markhand, 1995).

This paper describes the meiotic chromosome pairing of *A. strigosa* Schreb. (genome AsAs) and *A. eriantha* Dur. (genome CpCp), the hybrid between them, the derived allotetraploid of this cross (*A. strigosa* × *A. eriantha*)<sup>2</sup> and the hybrid produced by crossing this allotetraploid with *A. maroccana*. The results are discussed in relation to the evolution of *A. maroccana*.

## Materials and methods

In the diploid cross, *A. strigosa* cultivar Saia was the female parent, and the accession Cc7056 of *A. eriantha*, originally collected in Iraq, was the male parent. The autoallotetraploid was derived by treating tillers of the *A. strigosa* × *A. eriantha* hybrid with colchicine.

The contrived allotetraploid was the female parent in the cross with *A. maroccana* accession Cc7071, originally collected in Morocco. Embryo rescue, plant growth and preparation of plant material for microscopic examination was as described by Leggett (1992).

## Results

The meiotic chromosome pairing of *A. eriantha* and *A. strigosa* was regular, with the formation of seven bivalents (Table 1), although the number of ring bivalents was 5 per cent lower in *A. strigosa* than in *A. eriantha*. In the hybrids *A. strigosa* × *A. eriantha* (Av5569/1 and /2) no pollen mother cells (PMCs) were recorded with fewer than four univalents and synapsis completely failed in 17.69 per cent of PMCs. Fewer than four bivalents (and no multivalents) were recorded in 76.18 per cent of PMCs and quadrivalents and trivalents were observed in only 2.12 per cent of PMCs. The maximum chromosome pairing was five bivalents and four univalents per PMC and the minimum, 14 univalents (Table 1).

The colchicine-treated *A. strigosa* × *A. eriantha* plant (Av5569/2)<sup>2</sup> contained only 27 chromosomes. Thirteen bivalents and a univalent (the monosome) were recorded in 45.71 per cent of PMCs, the

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**Table 1** Chromosome pairing at meiotic metaphase I of *Avena eriantha*, *A. strigosa*, the hybrid *A. strigosa* × *A. eriantha*, the derived autoallotetraploid (*A. strigosa* × *A. eriantha*)<sup>2</sup>, and the hybrid (*A. strigosa* × *A. eriantha*)<sup>2</sup> × *A. maroccana*

	Chromosome number	Cells ( <i>n</i> )	Mean chromosome pairing and chiasmata frequency per pollen mother (range in parentheses) cell					
			Chiasmata/PMC	IV	III	II(ring)	II(rod)	I
<i>A. eriantha</i>	14	75	13.32	—	—	5.64 (4–7)	1.36 (0–3)	—
<i>A. strigosa</i>	14	100	12.53	—	—	5.26 (2–7)	1.74 (0–5)	—
Av5569/1*	14	267	1.55	0.0112 (0–1)	0.0075 (0–1)	—	1.5 (0–5)	10.90 (4–14)
Av5569/2*	14	157	1.45	—	0.03 (0–1)	—	1.39 (0–4)	11.13 (6–14)
Av(5569) <sup>2</sup> †	27	35	20.54	—	—	5.74 (2–9)	6.43 (3–11)	2.66 (1–9)
Av5616/2‡	27	50	9.16	0.12 (0–2)	1.14 (0–4)	0.46 (0–1)	5.36 (2–9)	11.46 (6–16)
Av5616/3‡	27	25	10.04	0.20 (0–1)	1.60 (0–4)	0.60 (0–1)	4.88 (2–9)	10.64 (5–18)

\**A. strigosa* × *A. eriantha*.

†(*A. strigosa* × *A. eriantha*)<sup>2</sup>, i.e. Av 5569 chromosome doubled.

‡(*A. strigosa* × *A. eriantha*)<sup>2</sup> × *A. maroccana*.

remaining PMCs contained from nine to 12 bivalents and three to nine univalents (Table 1). No PMCs containing multivalents were observed.

Chromosome pairing in the hybrids Av5616/2 and Av5616/3 between *A. maroccana* and the chromosome doubled hybrid (Av5569)<sup>2</sup> (Table 1) was highly irregular, all PMCs containing univalents, and 77.34 per cent containing multivalents. The maximum chromosome pairing recorded was 1IV 2III 6II and 5I, and the minimum was 4II and 19I.

## Discussion

Only one other hybrid between AA and CC genome diploid oats has been reported previously (Nishiyama & Yabuno, 1975), which also involved the species *A. eriantha* and *A. strigosa*. Nishiyama & Yabuno (1975) observed just over 50 per cent of PMCs with no chromosomes paired and no multivalents were recorded in any PMC, whereas in the present study complete failure of synapsis was recorded in only 17.7 per cent of PMCs and a low frequency of multivalent formation caused by an intragenomic translocation was noted.

The low mean number of bivalent associations (1.45), all rod configurations, together with the high number of unpaired chromosomes, indicates that there is little homology/homoeology between the AsAs and CpCp genome chromosomes of these two

diploid species. This lack of homology is borne out by the *in situ* hybridization studies of Leggett & Markhand (1995), who demonstrated that the AA and CC genomes are quite distinct at the DNA level.

Chromosome pairing in the synthetic allotetraploid derived from the doubling of the chromosome complement of the *A. strigosa* × *A. eriantha* hybrid (Table 1) would be expected to have complete and regular bivalent pairing, as each chromosome would have its true homologue with which to pair. However, the 'chromosome-doubled' plant (Av5569)<sup>2</sup> contained only 27 chromosomes and one would therefore expect a univalent in every PMC. The mean number of univalents per PMC (2.66) was higher than expected, even taking the monosomic into account. The fact that 34 per cent of PMCs contained three univalents suggests that one pair of chromosomes is frequently failing to pair, in addition to the monosome. However, there is no evidence to suggest that the same chromosome pair is involved in each cell.

Chromosome pairing in the hybrids Av5616/2 and Av5616/3 would be expected to form 14 bivalents, if the AsAs and CpCp genomes of *A. strigosa* and *A. eriantha* were completely homologous to the AA and CC genomes of *A. maroccana*, respectively. Meiotic chromosome pairing of the hybrids (both of which contained only 27 chromosomes), however, was

poor, with a mean of 11 chromosomes remaining as univalents (Table 1).

Multivalents were recorded in 77 per cent of PMCs, a frequency over twice as high as the combined multivalent frequency reported in the triploid hybrids *A. strigosa* × *A. maroccana* (Sadanaga *et al.*, 1968) and *A. eriantha* × *A. maroccana* (Kummer & Miksh, 1977). Interpreting these differences is difficult because the genotypes used to produce the triploid hybrids differed from those used in this study, which could, in part, account for the discrepancies.

Multivalent formation in the Av5616 hybrids could result from homologous/homoeologous chromosome pairing, or from translocations, the latter especially if the diploidizing mechanism as described by Rajhathy & Thomas (1974) is operative in this hybrid. The general lack of homology between the AsAs and CpCp genomes in the diploid hybrids reported here and by Nishiyama & Yabuno (1975), together with the chromosome pairing data of the triploid hybrids involving AA and CC genome diploid species and *A. maroccana* (Sadanaga *et al.*, 1968; Kummer & Miksh, 1977) and the synthetic allotetraploid Av5616, indicate that it is probable that the multivalent formation recorded in the Av5616 hybrids results from translocations between AA and CC genome chromosomes.

*In situ* hybridization studies by Leggett *et al.* (1994) have shown that in *A. maroccana* there are indeed four CC genome segments translocated onto AA genome chromosomes (at least three of which appear to be of a nonreciprocal nature) and a further AA genome segment translocated onto a CC genome chromosome. Nevertheless, chromosome pairing in *A. maroccana* is confined to bivalent formation. This lends further weight to the theory that the multivalent formation in the Av5616 hybrid described above is more likely to be caused by translocations than by homoeologous chromosome pairing.

In conclusion, it is evident from the *in situ* hybridization studies of Leggett *et al.* (1994) that *A. maroccana* contains both AA and CC genomes and the data presented here indicate that the CpCp genome of *A. eriantha*, and the AsAs genome of *A. strigosa*, are only distantly related to the AA and CC genomes of *A. maroccana* at the chromosome level and are, therefore, unlikely to have played any role in the formation of this tetraploid.

### Acknowledgements

Financial support from the BBSRC (UK) during the execution of these studies is gratefully acknowledged by the author.

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