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Analysis of metaphase I chromosome association in species of the genus *Aegilops*

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Summary. Metaphase-I chromosome associations in every diploid and polyploid species of the genus *Aegilops* were studied using C-banding in order to analyse the cytogenetic behaviour of the whole complement as well as of specific genomes in different polyploid species. Differences were observed in the frequency of associations per cell among different species of the same ploidic level and even between species sharing the same genomic constitution. Differences were also found between different genomes within the same polyploid species and between the same genome when present in several diploid and polyploid species. Several factors proposed as having an influence on the frequency of metaphase-I associations, such as chromosome morphology, C-heterochromatin content, genetic control and genome interactions, are discussed. Most of the polyploid *Aegilops* species showed a diploid-like behaviour at metaphase I although multivalents involving homoeologous associations were occasionally observed in *Ae. biuncialis, Ae. juvenalis* and *Ae. crassa*(6x); therefore, the *Aegilops* diploidising genetic system is not equally effective in all polyploid species.

Key words: *Aegilops* species – Genome – Chromosome association at metaphase I–C-banding

Introduction

Wild species of the genus *Aegilops* are potentially very valuable for cultivated wheat breeding, and for this reason many studies have been carried out to elucidate their evolutionary relationships. The most common and most fruitful method in this type of studies has been the cytogenetic analysis of intergeneric and interspecific hybrids, where the frequencies of chromosome associations at metaphase I are taken as an estimation of the phylogenetic closeness between the parental species (see Kimber and Feldman 1987). However, it should be taken into account that there are some factors that can modify these frequencies, such as the existence of parental genetic controls regulating pairing and crossing-over (Riley 1966; Baker et al. 1976; Sears 1976).

On the other hand, polyploid species of *Aegilops* form only bivalents at metaphase I in spite of the presence of several structurally and genetically similar chromosome sets that could pair both homologously and homoeologously (Chennaveeraiah 1960; Cermeño et al. 1985). Some studies on *Aegilops*-wheat hybrids have indicated the existence of diploidising genetic systems in *Aegilops* polyploids though a meiotic regulator comparable to the *Ph* gene has not been found (Riley 1966; Sears 1976; AbuBakar and Kimber 1982; McGuire and Dvorak 1982).

Most of the above-mentioned cytogenetic studies employ traditional staining techniques that do not enable the characterization of individual genomes. Differential staining techniques like C-banding have been shown to be very useful in identifying rye and wheat chromosomes (Gill and Kimber 1974; Jouve et al. 1980; Seal and Bennett 1982), but these have barely been utilised in *Aegilops* species (Gill 1981; Teoh and Hutchinson 1983; Cermeño et al. 1985; Cuñado et al. 1986). The aim of the work presented here was to analyse in detail the metaphase-I chromosome associations in every diploid and polyploid species of *Aegilops* using a C-banding procedure in order to determine the cytogenetic behaviour of complex as well as specific genomes in different species.

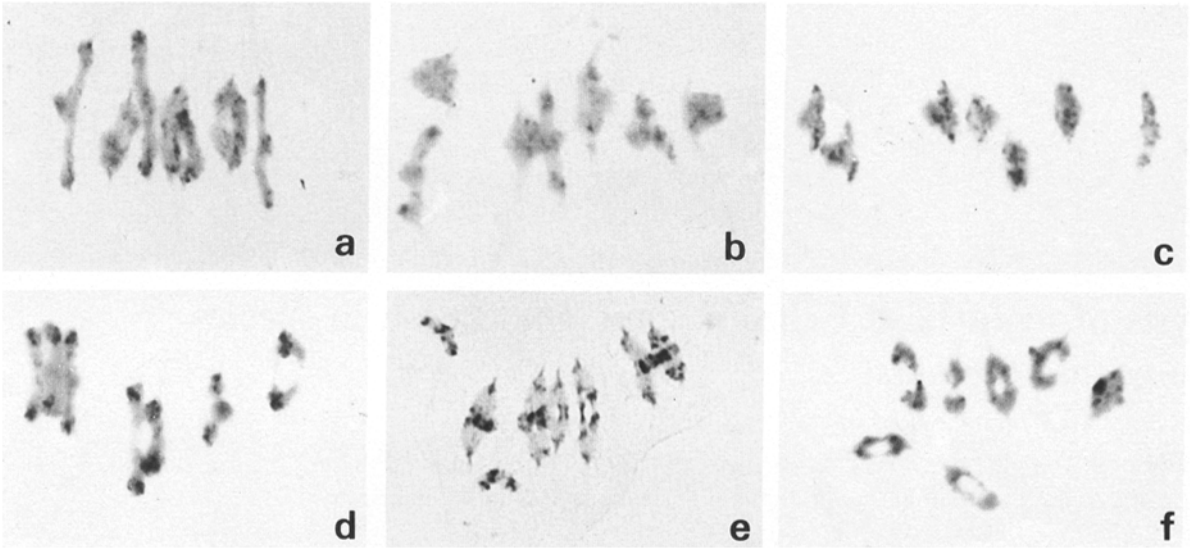

Fig. 1 a–f. C-banded metaphase-I cells of diploid *Aegilops* species: **a** *Ae. umbellulata* (UU), **b** *Ae. caudata* (CC), **c** *Ae. comosa* (MM), **d** *Ae. uniaristata* (NN), **e** *Ae. speltoides* (SS), **f** *Ae. squarrosa* (DD)

Table 1. Species and varieties of the genus *Aegilops* used in this work. Symbols in italic indicate modified genomes according to the nomenclature proposed by Kimber and Tsunewaki (1998)

Species	Ploidy level	Genomic constitution	Source[a]	Origin
Ae. umbellulata var typica	2x	UU	J 8-5	Syria
Ae. caudata var typica	2x	CC	J 6-2	Syria
Ae. comosa var typica	2x	MM	J 17-1	Greece
Ae. heldriechii var subventricosa	2x	MM	J 18-1	Turkey
Ae. uniaristata var typica	2x	NN	J 19-1	Turkey
Ae. mutica var typica	2x	TT	J 5641	Turkey
Ae. speltoides var typica	2x	SS	J 7712	Iraq
Ae. longissima var typica	2x	S^lS^l	J 4-1	Israel
Ae. sharonensis var typica	2x	S^lS^l	J 5-3	Israel
Ae. searsii	2x	S^sS^s	J 4-7	Syria
Ae. bicornis var typica	2x	S^bS^b	J 3-2	Israel
Ae. squarrosa var typica	2x	DD	J 20-1	C.I.S.
Ae. triuncialis var typica	4x	UU*CC*	J 4801	Iran
Ae. variabilis var typica	4x	UU*SS*	J 13-2	Israel
Ae. kotschyi var leptostachya	4x	UU*SS*	J 13-6	Jordan
Ae. biuncialis var typica	4x	UU*MM*	J 6457	Turkey
Ae. ovata var hirsuta	4x	UU*MM*	J 9-3	Turkey
Ae. columnaris	4x	UU*MM*	A. D.	–
Ae. triaristata(4x)	4x	UU*MM*	A. D.	–
Ae. cylindrica var typica	4x	DDCC	J 4653	Turkey
Ae. ventricosa var vulgaris	4x	DDNN	J 22-6	Egypt
Ae. crassa(4x) var macrathera	4x	DD*MM*	J 21-2	Iraq
Ae. triaristata(6x) var vulgaris	6x	*UUMMNN*	J 10-8	Italy
Ae. juvenalis var typica	6x	*DDMMUU*	J 23-6	Iran
Ae. crassa(6x) var typica	6x	*DDDDMM*	J 21-1	C.I.S.
Ae. vavilovii var palaestina	6x	*DDMMSS*	J 21-7	Jordan

[a] J, Plant Germ Plasm Institute, Faculty of Agriculture, Kyoto University, Japan; A. D., Aula Dei, Estación Experimental, C.S.I.C. Zaragoza, Spain

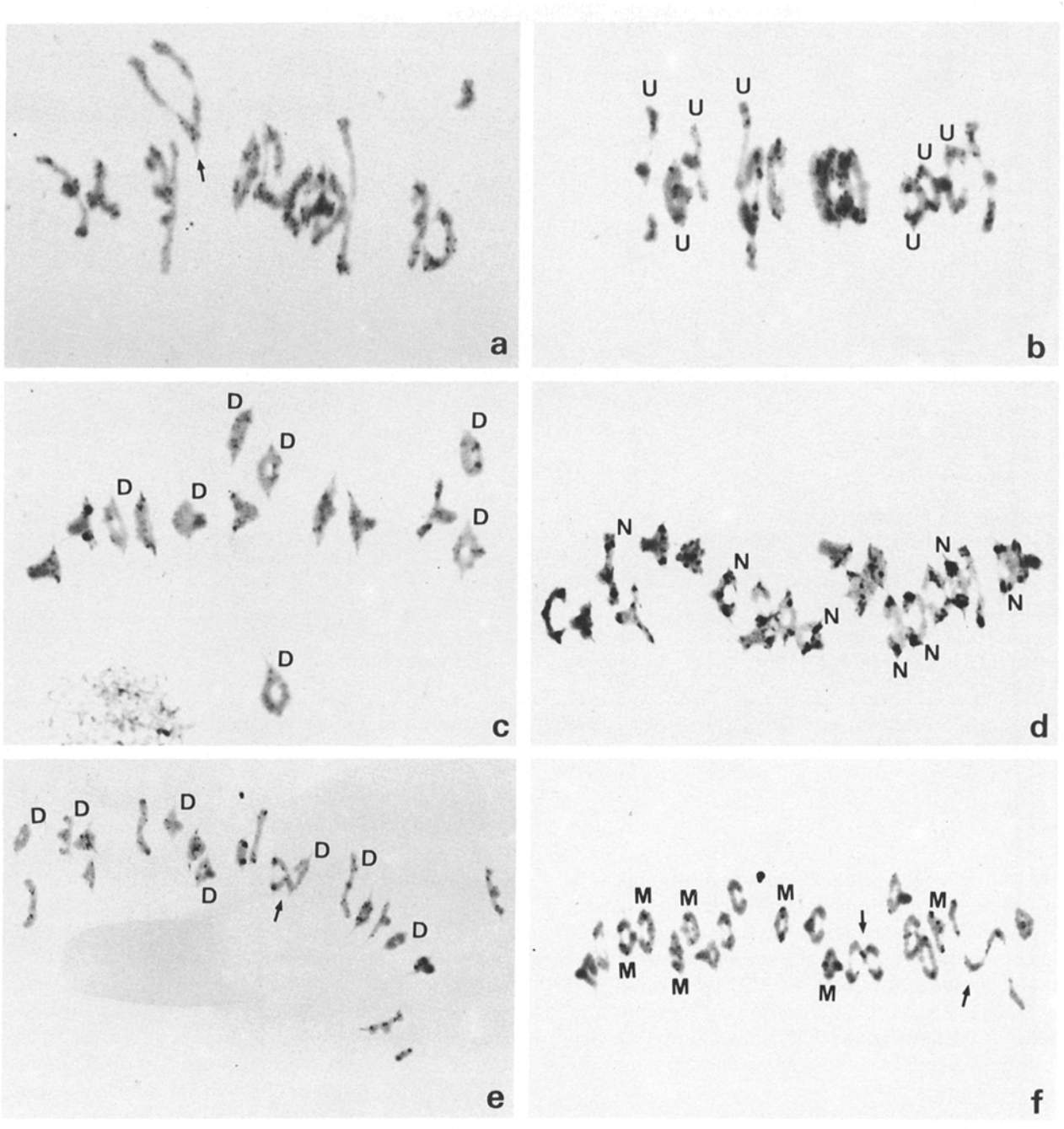

Fig. 2a–f. C-banded metaphase-I cells of polyploid *Aegilops* species: **a** *Ae. biuncialis* (UU*MM*), **b** *Ae. variabilis* (UU*SS*), **c** *Ae. cylindrica* (DDCC), **d** *Ae. triaristata*(6x) (*UUMMNN*), **e** *Ae. juvenalis* (*DDMMUU*), **f** *Ae. crassa*(6x) (*DDDDMM*). In most of the species, bivalents of one genome are indicated by its *symbol* while the remaining genomes (one or two) are *unmarked. Arrows* indicate multivalents associations

Materials and methods

The different diploid, tetraploid and hexaploid species of the genus *Aegilops* employed in this work are listed in Table 1. To designate the genomes of the different *Aegilops* species, nomenclature proposed by Kimber and Tsunewaki (1988) was followed. Some of the genomes present in most of the polyploid species are in italics in order to indicate that they are modified forms from those genomes found in their diploid ancestors.

To analyse meiotic cells, anthers were fixed in ethanol-acetic acid (3:1) and stored in the fixative liquid for 1–3 months at 3°–4°C. Fixed material was squashed in a drop of 45% acetic acid and stained following a Giemsa C-banding technique described previously by Giráldez et al. (1979).

The chromosome association frequency per metaphase-I cell (CAF) was calculated as the minimum number of chiasmata required for each meiotic configuration (rod and ring bivalents, trivalents and quadrivalents). In those cases in which several plants were analysed, data were pooled since no significant differences between them were obtained.

Table 2. Mean values of the different meiotic configurations and chromosome associations per metaphase I cell in all *Aegilops* species

Species	Number of plant	Number of cells	IIro	IIri	U	Mult	$\bar{X}$
Ae. umbellulata (UU)	3	90	3.07	3.93	–	–	10.94
Ae. caudata (CC)	3	90	2.87	4.13	–	–	11.13
Ae. comosa (MM)	3	90	0.89	6.11	–	–	13.11
Ae. heldriechii (MM)	3	90	1.19	5.79	0.02	–	12.77
Ae. uniaristata (NN)	6	180	4.07	2.90	0.03	–	9.88
Ae. mutica (TT)	3	90	0.64	6.36	–	–	13.35
Ae. speltoides (SS)	6	180	1.42	5.41	0.17	–	12.23
Ae. longissima (S^lS^l)	3	90	0.55	6.45	–	–	13.45
Ae. sharonensis (S^lS^l)	3	90	0.73	6.27	–	–	13.27
Ae. searsii (S^sS^s)	3	90	0.69	6.31	–	–	13.31
Ae. bicornis (S^bS^b)	3	90	1.06	5.90	0.04	–	12.86
Ae. squarrosa (DD)	6	180	0.54	6.46	–	–	13.45
Ae. triuncialis (UU*CC*)	6	180	5.45	8.46	0.09	–	22.36
Ae. variabilis (UU*SS*)	3	90	2.61	11.34	0.04	–	25.30
Ae. biuncialis (UU*MM*)	6	180	4.26	9.69	0.03	0.01	23.67
Ae. columnaris (UU*MM*)	3	90	2.23	11.73	0.03	–	25.70
Ae. ovata (UU*MM*)	3	90	3.01	10.99	–	–	24.99
Ae. triaristata(4x) (UU*MM*)	3	90	3.65	10.30	0.04	–	24.26
Ae. cylindrica (DDCC)	6	180	3.61	10.30	0.09	–	24.21
Ae. crassa(4x) (DD*MM*)	3	90	3.02	10.88	0.01	–	24.78
Ae. ventricosa (DDNN)	5	150	1.55	12.41	0.04	–	26.53
Ae. triaristata(6x) (*UUMMNN*)	6	180	5.31	15.57	0.12	–	36.45
Ae. juvenalis (*DDMMUU*)	3	90	2.50	18.33	0.03	0.06	39.37
Ae. crassa(6x) (*DDDDMM*)	3	90	4.27	15.78	0.17	0.39	36.98
Ae. vavilovii (*DDMMSS*)	6	180	1.72	19.11	0.17	–	39.94

Abbreviations: IIro, rod bivalents; IIri ring bivalents; U, univalent pairs; Mult, multivalents (trivalents and quadrivalents); $\bar{X}$, mean of chromosome associations per metaphase I cell

Results

In *Aegilops* species C-heterochromatin usually appears in centromeric, pericentromeric and interstitial regions, however there are qualitative as well as quantitative differences among certain species and/or genomes (Teoh and Hutchinson 1983; Cermeño et al. 1985) (Figs. 1, 2). This fact, together with differences in chromosome morphology (Chennaveeraiah (1960), have allowed the identification of a certain number of genomes in most polyploid *Aegilops* species.

With respect to the tetraploid species, in *Ae. variabilis* (UU*SS*) (Fig. 2b) and *Ae. columnaris* (UU*MM*) the U genome could be differentiated from genomes *S* and *M*, respectively, by the lower C-heterochromatin content of the former. In the three tetraploid species sharing the D genome, identification was based on the almost total absence of C-bands in the D genome, and whereas the chromosomes of genome C of *Ae. cylindrica* (DDCC) are smaller and show thin interstitial bands (Fig. 2c), the N chromosomes of *Ae. ventricosa* (DDNN) show more C-heterochromatin mainly in centromeric and pericentromeric regions, and the *M* chromosomes of *Ae. crassa*(4x) (DD*MM*) show several bands throughout their length.

In each of the hexaploid species, one single genome could be identified. In *Ae. triaristata* (*UUMMNN*), *N* chromosomes were differentiated by their high content in C-heterochromatin, whereas in *Ae. juvenalis* (*DDMMUU*), *D* chromosomes were differentiated by the absence of C-bands. In none of these species could the *U* and *M* genomes be distinguished (Figs. 2d–e). In *Ae. crassa*(6x) (*DDDDMM*), the *M* chromosomes were identified by the presence of small dispersed C-bands, whereas there were not differences between the two *D* genomes (Fig. 2f). In *Ae. vavilovii* (*DDMMSS*), *M* chromosomes could also be distinguished from genomes *D* and *S*.

So, in all of the *Aegilops* species it was possible to analyse not only the chromosome association frequencies at metaphase I (CAF) of the whole complement (Table 2) but also to analyse those of some specific genomes in most of them (Table 3).

Diploid species

Diploid species show generally seven bivalents at metaphase I though occasionally a pair of univalents appears in some cells of *Ae. heldriechii* (MM), *Ae. uniaristata* (NN), *Ae. bicornis* (S^bS^b) and, more often, in *Ae. speltoides* (SS) (Fig. 1e; Table 2). However, differences in

Table 3. Mean values of the different meiotic configurations and chromosome associations[a] per metaphase-I cell in the genomes identified in *Aegilops* polyploid species

Species	U Genome				*S* Genome				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. variabilis	1.41	5.54	0.04	12.50	1.20	5.80	–	12.80	
	U Genome				*M* Genome				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. columnaris	1.58	5.39	0.03	12.36	0.65	6.34	–	13.34	
	D Genome				C Genome				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. cylindrica	1.01	5.99	–	12.99	2.71	4.30	0.09	11.21	
	D Genome				*M* Genome				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. crassa(4x)	0.97	6.02	–	13.02	2.04	4.86	0.10	11.76	
	D Genome				N Genome				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. ventricosa	0.32	6.68	–	13.68	1.22	5.74	0.04	12.70	
	N Genome				U*M* Genomes				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. triaristata(6x)	2.13	4.81	0.05	11.75	3.16	10.78	0.06	24.69	
	D Genome				U*M* Genomes				*DD-UM*
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	Mult.
Ae. juvenalis	0.56	6.37	–	13.37	1.93	11.97	0.03	25.93	0.06
	M Genome				*DD* Genomes				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	Mult	$\bar{X}$
Ae. crassa(6x)	1.58	5.39	0.03	12.35	2.69	10.38	0.14	0.38	24.62
	M Genome				*DS* Genomes				
	IIro	IIri	U	$\bar{X}$	IIro	IIri	U	$\bar{X}$	
Ae. vavilovii	0.39	6.63	–	13.63	1.33	12.49	0.17	26.32	

[a] For abbreviations, see footnote to Table 1

the total CAF among species are mainly due to differences in the frequencies of rod and ring bivalents (Table 2) (Figs. 1a–f).

It was noticeable that species sharing the same genome, i.e. *Ae. comosa* and *Ae. heldriechii* (both MM) and several species with the S genome, present different CAF (Table 4); an observation which suggests that the genomes shared by these species are different as a result of modifications that occurred during their evolution.

Polyploid species

Polyploid species of the genus *Aegilops* are a clear example of evolution by allopolyploidy, showing, as do most

natural allopolyploids, a diploid-like behaviour at metaphase I (Tables 2 and 3). Nevertheless, multivalents occasionally appeared in some cells of *Ae. biuncialis, Ae. juvenalis* and *Ae. crassa*(6x) (Tables 2, 3; Figs. 2b, e–f). These multivalents are unlikely to be due to translocation heterozygosity since polyploid *Aegilops* species are autogamous and consequently homozygotic. Moreover, in *Ae. juvenalis* (*DDMMUU*), quadrivalents observed at metaphase I involved two homologous chromosomes of the *D* genome and a second pair of homologues belonging to either of the undifferentiated *U* or *M* genomes (Fig. 2e; Table 3), which supports its homoeologous origin.

Nevertheless, multivalents observed in *Ae. crassa* (6x) (*DDDDMM*) only involved chromosomes of the two *D* genomes (Fig. 2f; Table 3), hence they can be attributed to the partial autopolyploidy of this species as suggested by Chapman and Miller (1978). However, the mean of multivalents per cell in *Ae. crassa*(6x) (0.39) is much lower than that found in autotetraploid *Ae. squarrosa* (DDDD): 4.02 multivalents plus 5.94 bivalents per cell; mean of associations per cell: 25.87. This could be due to either differences between both *D* genomes of the

Table 4. Student's *t*-tests of the means of chromosome associations per metaphase-I cell between diploid and tetraploid *Aegilops* species with similar genomic constitutions

Genomes compared	Species compared	*t*	*df*	Significance level
M	*Ae. comosa–Ae. heldriechii*	3.72	4	$P<0.05$
S –S^l	*Ae. speltoides – Ae. longissima*	16.28	7	$P<0.001$
S –S^s	*Ae. speltoides – Ae. searsii*	14.36	7	$P<0.001$
S –S^l	*Ae. speltoides – Ae. sharonensis*	12.31	7	$P<0.001$
S –S^b	*Ae. speltoides – Ae. bicornis*	7.92	7	$P<0.001$
S^l–S^s	*Ae. longissima – Ae. searsii*	2.39	4	$P<0.05$
S^l–S^l	*Ae. longissima – Ae. sharonensis*	2.21	4	$P<0.05$
S^l–S^b	*Ae. longissima – Ae. bicornis*	8.55	4	$P<0.01$
S^s–S^l	*Ae. searsii – Ae. sharonensis*	0.52	4	ns
S^s–S^b	*Ae. searsii – Ae. bicornis*	6.45	4	$P<0.001$
S^l–S^b	*Ae. sharonensis – Ae. bicornis*	4.50	4	$P<0.01$
U*M*	*Ae. biuncialis-Ae. columnaris*	14.21	7	$P<0.001$
	Ae. biuncialis-Ae. ovata	8.53	7	$P<0.001$
	Ae. biuncialis-Ae. triaristata	4.21	7	$P<0.001$
	Ae. columnaris-Ae. ovata	4.72	4	$P<0.01$
	Ae. columnaris-Ae. triaristata	13.16	4	$P<0.001$
	Ae. ovata-Ae. triaristata	5.15	4	$P<0.01$

ns, Non-significant

Table 5. Mean values of chromosomes associations per metaphase-I cell in the genomes identified in polyploid species and in their putative parental diploid species, and Student's *t*-tests comparisons between them

Polyploid species	Genome	$\bar{X}$	Diploid species	Genome	$\bar{X}$	*t*	*df*	Significance level
variabilis	U	12.50	*umbellulata*	U	10.94	15.99	4	$P<0.001$
	S	12.80	*speltoides*	S	12.93	6.96	7	$P<0.001$
			longissima	S^l	13.45	8.31	4	$P<0.001$
			searsii	S^s	13.31	6.45	4	$P<0.001$
			sharonensis	S^l	13.27	4.75	4	$P<0.01$
			bicornis	S^b	12.86	0.61	4	ns
columnaris	U	12.36	*umbellulata*	U	10.94	13.24	4	$P<0.001$
	M	13.34	*comosa*	M	13.11	3.03	4	$P<0.05$
			heldriechii	M	12.77	8.82	4	$P<0.001$
			uniaristata	N	9.88	33.09	7	$P<0.001$
cylindrica	D	12.99	*squarrosa*	D	13.46	8.09	10	$P<0.001$
	C	11.21	*caudata*	C	11.13	0.84	7	ns
ventricosa	D	13.68	*squarrosa*	D	13.46	4.13	9	$P<0.001$
	N	12.70	*uniaristata*	N	9.88	20.41	9	$P<0.001$
			comosa	M	13.11	2.32	6	$P<0.05$
			heldriechii	M	12.77	0.40	6	ns
crassa(4x)	D	13.02	*squarrosa*	D	13.46	5.60	7	$P<0.05$
	M	11.76	*comosa*	M	13.11	16.28	4	$P<0.001$
			heldriechii	M	12.77	14.04	4	$P<0.001$
			uniaristata	N	9.88	17.58	7	$P<0.001$
triaristata(6x)	*N*	11.75	*uniaristata*	N	9.88	20.83	10	$P<0.001$
			comosa	M	13.11	14.35	7	$P<0.001$
			heldriechii	M	12.77	11.22	7	$P<0.001$
juvenalis	*D*	13.37	*squarrosa*	D	13.46	1.30	7	ns
crassa(6x)	*M*	12.35	*comosa*	M	13.11	4.93	4	$P<0.01$
			heldriechii	M	12.77	2.82	4	$P<0.05$
			uniaristata	N	9.88	18.16	7	$P<0.001$
vavilovii	*M*	13.63	*comosa*	M	13.11	8.84	7	$P<0.001$
			heldriechii	M	12.77	16.52	7	$P<0.001$
			uniaristata	N	9.88	50.42	10	$P<0.001$

ns, Non-significant

Table 6. Student's *t*-tests comparisons of the mean values of associations per metaphase-I cell between the genomes shared by different polyploid *Aegilops* species

Genomes compared	Species compared	*t*	*df*	Significance level
U	*variabilis* – *columnaris*	1.38	4	ns
M	*columnaris* – *crassa*(4 x)	30.11	4	$P<0.001$
	columnaris – *crassa*(6 x)	7.10	4	$P<0.001$
	columnaris – *vavilovii*	6.98	7	$P<0.001$
	crassa(6 x) – *crassa*(4 x)	4.17	4	$P<0.01$
	crassa(6 x) – *ventricosa*	1.77	6	ns
	vavilovii – *crassa*(4 x)	41.09	7	$P<0.001$
	vavilovii – *crassa*(6 x)	13.27	7	$P<0.001$
	vavilovvi – *ventricosa*	7.90	9	$P<0.001$
N	*ventricosa* – *triaristata*(6 x)	7.27	9	$P<0.001$
M–N	*columnaris* – *ventricosa*	3.78	6	$P<0.01$
	columnaris – *triaristata*(6 x)	18.80	7	$P<0.001$
	crassa(4 x) – *ventricosa*	5.50	6	$P<0.001$
	crassa(4 x) – *triaristata*(6 x)	0.02	7	ns
	crassa(6 x) – *triaristata*(6 x)	4.93	7	$P<0.001$
	vavilovii – *triaristata*(6 x)	30.59	10	$P<0.001$
U*M*	*juvenalis* – *biuncialis*	7.11	7	$P<0.001$
	juvenalis – *columnaris*	2.67	4	$P<0.05$
	juvenalis – *ovata*	7.49	4	$P<0.001$
	juvenalis – *triaristata*(4 x)	23.19	4	$P<0.001$
	juvenvalis – *triaristata*(6 x)	12.01	7	$P<0.001$
	triaristata(6 x) – *biuncialis*	8.93	10	$P<0.001$
	triaristata(6 x) – *columnaris*	8.65	7	$P<0.001$
	triaristata(6 x) – *triaristata*(4 x)	3.84	7	$P<0.01$
	triaristata(6 x) – *ovata*	2.30	7	$P<0.05$
D	*cylindrica* – *ventricosa*	10.27	9	$P<0.001$
	cylindrica – *crassa*(4 x)	0.28	7	ns
	cylindrica – *juvenalis*	4.32	7	$P<0.001$
	juvenalis – *crassa*(4 x)	2.81	4	$P<0.05$
	juvenalis – *ventricosa*	3.76	6	$P<0.01$
	ventricosa – *crassa*(4 x)	7.12	6	$P<0.001$
DD	*crassa*(6 x) – *squarrosa*(4 x)	17.48	4	$P<0.001$

hexaploid species or to the existence of a control constraining the formation of bivalents at metaphase I.

As in diploid species, there is a variation in the CAF between different species of the same ploidic level (Table 2). There are also several tetraploid species sharing the same origin and genomic constitution (UU*MM*) (Kimber and Feldman 1987) that nonetheless show significant differences (Table 4). Likewise, those genomes that in polyploids supposedly originate from the same diploid donor could be expected to show similar CAF in the different species possessing it; however, when the CAF of each of these genomes was compared with those of the diploid parentals (Table 5) and among the polyploids (Table 6), there were significant differences in most cases. For instance, U genomes of *Ae. variabilis* (UU*SS*) and *Ae. columnaris* (UU*MM*) show a CAF higher than that of their diploid parent *Ae. umbellulata* (UU) though it is similar between them. In the case of the D genome, *Ae. ventricosa* (DDNN) shows a higher CAF than the diploid donor *Ae. squarrosa* (DD); on the contrary, in *Ae. cylindrica* (DDCC) and *Ae. crassa* (4) (DD*MM*), the CAF are similar between them but lower than in the diploid. Comparable results are obtained with the remainder of the genomes (Tables 5 and 6).

These results could be explained by two alternative, but non-excluding hypotheses: (1) the genomes shared by several diploid and polyploid *Aegilops* species are at this time different due to modifications that occurred during their evolution; (2) there are interactions between the different genomes present in a species that alter the levels of metaphase-I associations in each one of them.

Discussion

The genus *Aegilops* includes species of three ploidic levels: diploid, tetraploid and hexaploid. When the chromosome association frequency at metaphase I (CAF) is compared between species of the same ploidic level considerable variation was found that was mainly due to differences in the frequencies of rod and ring bivalents (Table 2). These differences may be attributable to variation in the relative arm length of the chromosomes of different genomes and/or species, in such a way that in species with markedly heterobrachial chromosomes, these would appear mostly as rod bivalents at metaphase I. On the contrary, species with meta- or submetacentric chromosomes would form mainly ring bivalents, their CAF thus being higher. Likewise, diploid species having subtelocentric chromosomes such as *Ae. umbellulata* (UU), *Ae. caudata* (CC) and *Ae. uniaristata* (NN), would display the lowest CAF, whereas species lacking this type of chromosomes, like *Ae. mutica* (TT), *Ae. squarrosa* (DD) and the species with the S genome, would present the highest CAF (Table 2; Fig. 1) (Chennaveeraiah 1960).

However, significant differences between species with similar karyotypes and genomes have also been found, for instance between the two species with the M genome, *Ae. comosa* and *Ae. heldriechii*, which are considered to be subspecies by Kimber and Feldman (1987) and different species by Tanaka (1985). Similarly, there are differences between the majority of species with the S genome, even between *Ae. sharonensis* and *Ae. longissima* (both S^1S^1), which are considered to be the same species by some authors (Tanaka 1955; Miller 1981) and different species by others (Yen and Kimber 1990) (Table 4).

The relationship between the CAF and karyotype morphology is even less evident when the same genome is analysed in different polyploid and diploid species. The

subtelocentric chromosomes of the U genome are clearly identifiable in the tetraploids *Ae. variablilis* (UU*SS*) (Fig. 2b) and *Ae. columnaris* (UU*MM*) (Kihara 1982), but the CAF for the U genome is significantly higher in these species than in the diploid *Ae. umbellulata* (UU) (Table 5). Thus, the centromere position does not seem to be the only factor involved in the determination of the CAF, as shown by the different genomes and/or species.

The presence of C-heterochromatin has been another factor proposed as having an influence on the frequency of metaphase-I associations, although the results obtained are contradictory. Dvorak and McGuire (1981) and Ferrer et al. (1984) attributed the differences found among the three genomes (A, B and D) of *Triticum aestivum* to differences in DNA and C-heterochromatin content in such a way that the genomes with a higher C-heterochromatin content showed lower CAF. On the contrary, Naranjo and Lacadena (1980) did not found in rye any effect of telomeric C-heterochromatin on the association frequency of the chromosome arms carrying it.

In diploid *Aegilops* species there seems to be an inverse relationship between C-heterochromatin content and CAF since species with highly heterochromatic chromosomes, like *Ae. uniaristata* (NN) and *Ae. speltoides* (SS), show a CAF lower than *Ae. squarrosa* (DD) and *Ae. mutica* (TT) with less heterochromatic chromosomes (Table 2; Fig. 1). Nevertheless, this relationship is not so evident in polyploid species; for instance, the D genome presents a similar C-banding pattern in *Ae. squarrosa* and in the polyploid species but there are in general significant differences between species in the CAF (Tables 5, 6; Figs. 1, 2). Likewise, the N genome has a similar C-banding pattern in *Ae. uniaristata* (NN) and *Ae. ventricosa* (DDNN), but in the latter the CAF is much higher (Table 5). Therefore, differences in C-heterochromatin content cannot account for all of the observed variation in the frequency of chromosome associations.

On the other hand, the differences in the CAF between diploid and polyploid species with the same genomic constitution could be attributed to the action of genetic controls on pairing and crossing-over determining a different CAF in each species. In most of the synaptic mutants described in the literature, the whole chromosome complement seemed to be affected; however there are some cases revealing the parallel existence of specific genetic controls (Koduru and Rao 1981; Jones 1984). In particular, in an *Aegilops ventricosa-Secale cereale* amphiploid (DDNNRR), Orellana et al. (1985) found some mutant plants that showed almost total asynapsis in *Ae. ventricosa* chromosomes but normal meiotic behaviour for the rye chromosomes. The authors concluded that in addition to a global control there could be genome-specific controls. The existence of such controls could explain the differences in the CAF both between different genomes in the same polyploid species and between the same genome when present in several diploid and polyploid species (Tables 3, 6).

Finally, another factor that could also be taken account in explaining the variation found is the existence of genome interactions like those described in several wheat-rye combinations where the presence of wheat and rye chromosomes together produces reciprocal decreases in homologous chromosome association frequencies (Lelley 1976; Orellana et al. 1984).

Diploidising mechanism in polyploid Aegilops species

As mentioned above, polyploid *Aegilops* species usually form only bivalents at metaphase I due to exclusively homologous associations (Tables 2, 3; Fig. 2) (Chennaveeraiah 1960; Cermeño et al. 1985). From analyses of different interspecific *Aegilops* hybrids many authors have suggested the existence of reciprocal translocations between chromosomes of different genomes and/or homoeology groups (Kimber and Zhao 1983). This would support the hypothesis that the lack of homoeologous associations in the parental species was due to structural and/or molecular modifications of the genomes that occurred during evolution. However, the high levels of association found in hybrids between polyploids and their parental diploid species led some authors to propose the existence of diploidising genetic systems (Riley 1966; McGuire and Dvorak 1982). Additional evidence has emerged from studies of hybrids between polyploid *Aegilops* species and *Triticum aestivum* with or without chromosome 5B and with or without chromosome 3D. In the absence of 5B there is always an increase in homoeologous associations, indicating that there is no compensating mechanism in the *Aegilops* chromosomes. However, the extent of this increase is variable, depending on the *Aegilops* species involved in the hybrids, which indicates a certain degree of control. Conversely, in the absence of 3D, the polyploid *Aegilops* species carrying the D genome compensate for the absence of this chromosome, which suggests the existence in this genome of a similar meiotic regulator (AbuBakar and Kimber 1982; McGuire and Dvorak 1982).

However, the *Aegilops* diploidising genetic system is not equally effective in all polyploid species since in *Ae. biuncialis* (UU*MM*) and *Ae. juvenalis* (*DDMMUU*) multivalents involving homoeologous associations have occasionally been observed (Tables 2, 3; Figs. 2a, e). Gupta and Fedak (1985a) reasoned that the lower effectivity of the diploidising mechanism in hexaploid *Hordeum* species compared to that of the tetraploid species was due to the more recent evolutionary origin of the former. A similar inference would indicate a recent origin for *Ae. biuncialis* and *Ae. juvenalis* since their diploidising systems are not so efficient as those in other species.

A special case is the high frequency of multivalents involving only the *D* chromosomes found in *Ae. crassa*(6x) (*DDDDMM*) (Table 3; Fig. 2f), which would be due to the partial autopolyploid character of this species (Gupta and Fedak 1985b). The frequency we found was higher than that reported by Chapman and Miller (1978), perhaps due to the use of another variety or to environmental differences. Even though the effectivity of the diploidising system in this species is not total, it is remarkably efficient since the frequency of multivalents found in it is much lower than that of autotetraploid *Ae. squarrosa* (DDDD) (4.02). Nevertheless, a recent origin of this species could also account for the existence of homoeologous associations.

Considerable differences in the levels of chromosome associations have been found among *Aegilops* polyhaploids. In *Ae. ventricosa* (DDNN) (Fedak 1983) and *Ae. ovata* (UU*MM*) (Matsumura 1940) haploids the frequencies of associations were extremely low (0.46 and 0.43, respectively), whereas in *Ae. triuncialis* (UU*CC*) (Chapman and Miller 1977) and *Ae. crassa*(6x) (*DDDDMM*) (Shigenobu and Sakamoto 1977) they were much higher (2.53 and 6.44, respectively). It therefore appears that the diploidising system in *Aegilops* seems to be totally effective in all species when in the homozygous condition – except for *Ae. biuncialis*, *Ae. juvenalis* and *Ae. crassa*(6x) – but its effectivity in the hemizygous condition is much lower and varies among species.

Nevertheless, more studies are needed to understand the meiotic genetic controls present in the genus *Aegilops* and their modes of action. In this respect, essential information would be obtained from detailed analyses of the early stages of meiotic prophase I since it is in these stages that pairing and crossing-over actually occur.

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