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Genomic analysis in the genus *Aegilops*.

3. Intergeneric hybrids between different species of *Aegilops* and *Secale cereale*

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Summary. Hybrids between different *Aegilops* species and *Secale cereale* were studied at metaphase I by means of a C-banding technique. On the basis of differences in the C-banding patterns of some of the chromosomes of these hybrids it was possible to carry out an accurate analysis of several types of *Aegilops-Aegilops* and *Aegilops-Secale* chromosome associations and, consequently, to establish intraspecific and intergeneric genome relationships. Genomes present in the majority of polyploid *Aegilops* species are shown to maintain similar patterns of evolutionary affinity to those reported for their proposed diploid parents although in some species there are differences indicating either that differentiations occurred during the evolution of the polyploid species or, on the contrary, that the diploid donors proposed are not the correct ones. On the other hand, differences in the relationships not only between the R genome and different *Aegilops* genomes but also among different homoeologous groups have been found.

Key words: *Aegilops* × *S. cereale* hybrids – Genomic analysis – Metaphase-I chromosome association – C-banding

Introduction

Genus *Aegilops* is known to have evolved stepwise through processes involving diploid divergence and polyploid convergence (Kihara 1954). An affinity for meiotic associations between chromosomes of different genomes still exists although it is not manifested at metaphase I in the polyploid species (Cuñado 1992), and on this basis the existence of a genetic system which restricts meiotic chromosome associations to strictly homologous chromosomes and prevents the associations of homoeologous ones has been proposed (AbuBakar and Kimber 1982; McGuire and Dvorák 1982).

In wheat × rye hybrids, the *Secale cereale* genome interferes with the diploidizing system of wheat and thus promotes homoeologous chromosome associations (see Gupta and Fedak 1986). In intergeneric hybrids with several species of *Hordeum* (Gupta and Fedak 1985a) and *Aegilops* (Gupta and Fedak 1985b; Cuñado et al. 1986) the rye genome also induces homoeologous associations at metaphase I.

Although several hybrids between *Aegilops* species and rye have been obtained, few attempts have been made to study the meiotic behaviour of the different genomes involved (Hutchinson et al. 1980). C-banding techniques enable chromosomes of rye to be distinguished from those of *Aegilops* and therefore can be used to analyse more accurately chromosome associations at metaphase I in these hybrids (Cermeño et al. 1985; Cuñado et al. 1986; Orellana et al. 1989). In the paper presented here the nature of the different chromosome associations observed in several *Aegilops*-rye intergeneric hybrids are studied in order to elucidate the relationships among genomes of different polyploid species of *Aegilops*, and between them and the *Secale cereale* genome.

Materials and methods

Hybrids were obtained by crossing different species of *Aegilops* as females and *Secale cereale* cv 'JNK' as male. *Aegilops* species showed three different ploidy levels: (1) diploid: *Ae. uniaristata* (NN); (2) tetraploid: *Ae. triuncialis* (UUCC), *Ae. variabilis*

(UU*SS*), *Ae. biuncialis* (UU*MM*), *Ae. ovata* (UU*MM*), *Ae. triaristata* (UU*MM*), *Ae. cylindrica* (DDCC) and *Ae. ventricosa* (DDNN); (3) hexaploid: *Ae. triaristata* (*UUMMNN*), *Ae. crassa* (*DDDDMM*) and *Ae. juvenalis* (*DDMMUU*). Genomes of the different *Aegilops* species are designated according to the nomenclature proposed by Kimber and Tsunewaki (1988). Modified genomes in most of the polyploid species are in italics.

Hybrid embryos were germinated on mineral salts of Murashige and Skoog medium (1962) supplemented with the B5 vitamins of Gamborg (Gamborg et al. 1968). Hybrid seedlings were transplanted to pots of soil and grown in a greenhouse.

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

The mean number of chromosome associations per metaphase-I cell was calculated as the minimum number of chiasmata required for each meiotic configuration. In those cases in which several hybrid plants were obtained, data were pooled since no significant differences among them were obtained.

Results

Aegilops genomes show intercalary and dispersed C-heterochromatin whereas rye chromosomes have prominent C-bands at one or both telomers (Fig. 1 a–f). On the basis of these differential C-banding patterns it was possible to make an overall estimation of meitoic association frequencies at metaphase I in all of the hybrids analysed, namely: (1) among *Secale* chromosomes, (2) among *Aegilops* chromosomes and (3) among chromosomes of both parental species (Table 1).

Furthermore, in some of these hybrids it was also possible to distinguish either one or all of the genomes of the *Aegilops* species because of quantitative and qualitative differences in their C-banding patterns. Thus, in *Ae. variabilis* × *S. cereale* (U*S*R) hybrid chromosomes from the *S* genome show intercalary and dispersed C-heterochromatin, whereas U chromosomes are smaller and show scattered and dispersed thin C-bands (Fig. 1 a). However, in the cross between rye and the two forms of *Ae. triaristata* (U*M*R and *UMN*R, respectively) only two chromosome groups could be accurately distinguished, i.e. 6 chromosomes with thin C-bands, probably belonging to the U (or *U*) genome, and the remaining 8 or 15 chromosomes displaying prominent C-bands at centromeric and pericentromeric regions (Fig. 1 d).

Similarly, in the *Ae. cylindrica* × *S. cereale* (DCR) hybrid only 5 chromosomes of the C genome were identified on the basis of their smaller size and intercalary thin C-bands while in the remaining 9 chromosomes (2 belong to the C genome and 7 to the D genome) prominent C-bands are absent (Fig. 1 b). In *Ae. ventricosa* × rye (DNR) 6 chromosomes from the D genome are almost entirely euchromatic, whereas in the remaining 8 chromosomes prominent C-bands located at the centromeric and pericentromeric regions are visualized (Fig. 1 c) (Cuñado et al. 1986). Finally, in the hybrids in which *Ae. juvenalis* and *Ae. crassa* (6x) are involved (*DMU*R and *DDM*R, respectively) *D* chromosomes could be distinguished from the remaining ones due to their lack of prominent C-bands (Fig. 1 e–f).

In all of these cases, different types of *Aegilops-Aegilops* and *Aegilops-Secale* associations have been ac-

Table 1. Mean frequencies of meiotic configurations per metaphase-I cell involving intraspecific and interspecific associations in *Aegilops* × *Secale cereale* hybrids

Female parent	Number of plants	Number of cells	*Aegilops-Aegilops*[b]						*Aegilops-rye*	Rye-rye
			IIro	IIri	III	IV	V	$\bar{X}$	$\bar{X}$	$\bar{X}$
Ae. uniaristata (NN)	1	100	0.11	–	–	–	–	0.11	0.23	0.04
Ae. triuncialis (UU*CC*)	1	50	3.14	0.04	0.62	0.18	–	5.04	0.30	0.10
Ae. variabilis (UU*SS*)	4	180	1.67	–	0.29	–	–	2.89	0.20	0.02
Ae. biuncialis (UU*MM*)	5	200	2.19	0.13	1.21	0.08	0.06	5.39	0.16	0.03
Ae. ovata (UU*MM*)	2	100	1.83	–	0.09	–	–	2.01	0.06	–
Ae. triaristata (4×) (UU*MM*)	1	70	2.40	0.10	0.73	0.06	–	4.24	0.24	0.03
Ae. cylindrica (DDCC)	5	200	2.35	0.42	1.57	0.05	0.02	6.59	0.30	0.02
Ae. ventricosa (DDNN)	2	100	2.70	0.04	0.14	–	–	3.11	0.10	0.01
Ae. ventricosa-S. cereale[a] (amphiploid) (DDNNRR)	5	314	2.55	0.06	0.04	–	–	2.78	0.04	6.70
Ae. triaristata (6×) (*UUMMNN*)	1	50	3.90	0.04	1.00	–	–	5.98	0.08	0.02
Ae. juvenalis (*DDMMUU*)	2	110	2.32	0.04	0.95	0.03	–	4.41	0.14	–
Ae. crassa (6×) (*DDDDMM*)	2	80	2.70	1.86	0.87	0.02	–	8.77	0.06	0.01

[a] Data from Cuñado et al. (1986)

[b] IIro, Rod bivalents; IIri, ring bivalents; III, trivalents; IV, quadrivalents; V, pentavalents; $\bar{X}$, mean number of chromosome associations per cell

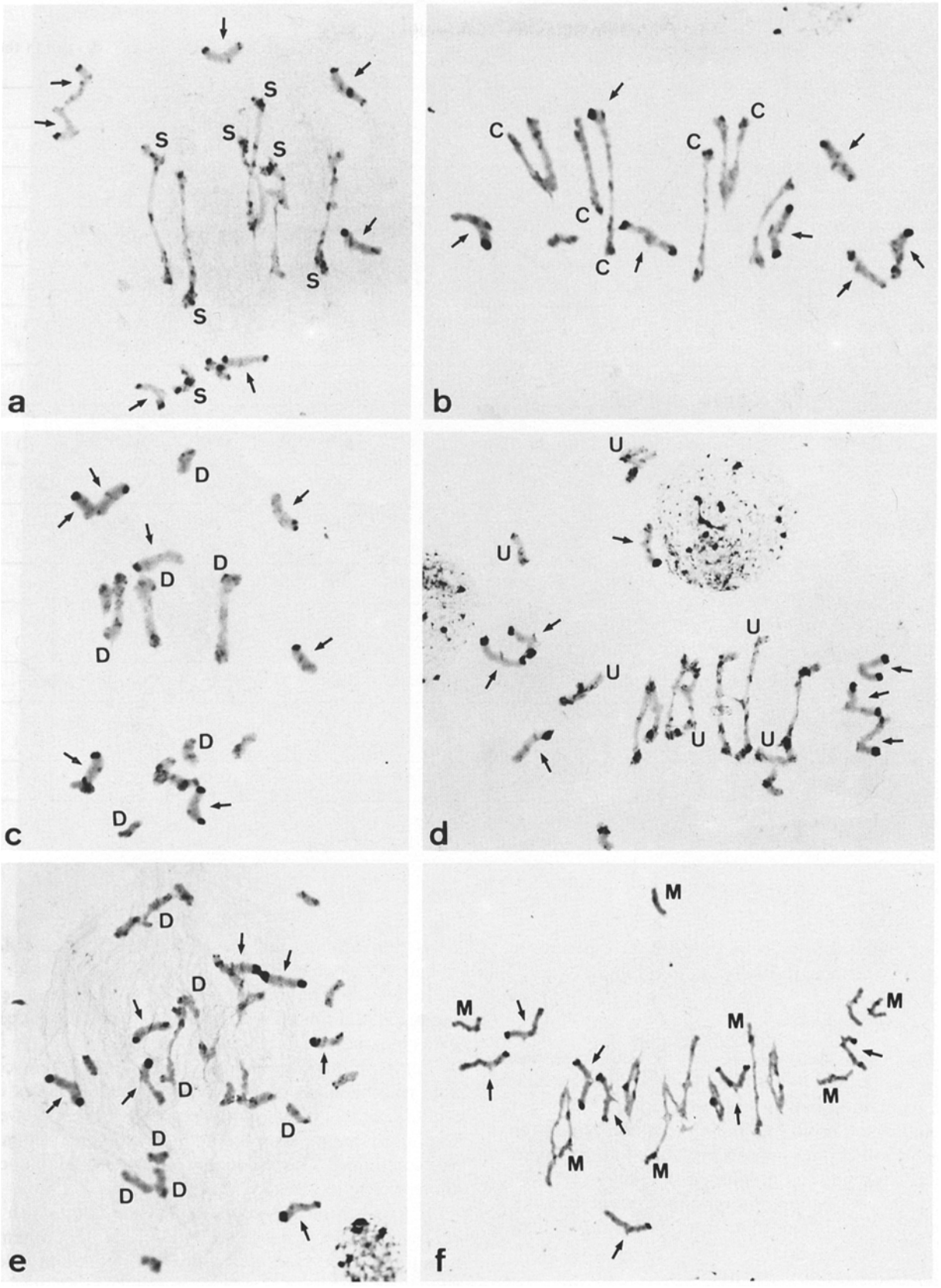

Fig. 1 a–f. C-banded metaphase-I cells of intergeneric *Aegilops* × *Secale cereale* hybrids: **a** *Ae. variabilis* × *S. cereale* (U*S*R), **b** *Ae. cylindrica* × *S. cereale* (DCR), **c** *Ae. ventricosa* × *S. cereale* (DNR), **d** *Ae. triaristata* (6×) × *S. cereale* (*UMN*R), **e** *Ae. juvenalis* × *S. cereale* (*DMU*R), **f** *Ae. crassa* (6×) × *S. cereale* (*DDM*R). In all cases the chromosomes of one genome are indicated by its *symbol* whereas the remaining chromosomes are *unmarked*; *arrows* indicate rye chromosomes

Table 2. Mean number and ranges (in brackets) of *Aegilops-Aegilops* and *Aegilops-Secale* associations per metaphase-I cell in the hybrids analysed

Female parent	Type of association						
	Aegilops-Aegilops				*Aegilops-rye*		
	U-U	U-*S*	*S-S*	Total	U-R	*S*-R	Total
Ae. variabilis (UU*SS*)	0.16 (0–1)	2.20 (0–5)	0.49 (0–1)	2.89 (0–6)	0.13 (0–1)	0.10 (0–1)	0.20 (0–1)
	U-U	U-*M*	*M-M*	Total	U-R	*M*-R	Total
Ae. triaristata (4×) (UU*MM*)	0.37 (0–1)	2.77 (0–6)	1.03 (0–3)	4.24 (1–8)	0.13 (0–1)	0.11 (0–1)	0.24 (0–1)
		C-D	D-D	Total	C-R	D-R	Total
Ae. cylindrica (DDCC)		3.65 (2–5)	2.93 (1–6)	6.59 (4–9)	0.08 (0–1)	0.22 (0–2)	0.30 (0–2)
		D-N	N-N	Total	D-R	N-R	Total
Ae. ventricosa (DDNN)		2.72 (0–5)	0.38 (0–1)	3.11 (0–5)	0.08 (0–1)	0.02 (0–1)	0.10 (0–1)
	U-U	*U-MN*	*MN-MN*	Total	*U*-R	*MN*-R	Total
Ae. triaristata (6×) (*UUMMNN*)	0.14 (0–1)	1.90 (1–4)	3.90 (1–6)	5.98 (3–9)	0.04 (0–1)	0.04 (0–1)	0.08 (0–1)
	D-D	*D-UM*	*UM-UM*	Total	*D*-R	*UM*-R	Total
Ae. juvenalis (*DDMMUU*)	0.13 (0–1)	1.68 (0–3)	2.58 (1–5)	4.44 (1–7)	0.04 (0–1)	0.10 (0–1)	0.14 (0–1)
		DD-M	*DD-DD*	Total	*DD*-R	*M*-R	Total
Ae. crassa (6×) (*DDDDMM*)		2.27 (1–5)	6.49 (3–9)	8.77 (6–12)	0.05 (0–1)	0.01 (0–1)	0.06 (0–1)

curately analysed in order to establish intraspecific and intergeneric genome relationships (see Table 2).

Rye-rye associations

In most hybrids carrying only one R genome, intragenomic associations shaped like rod bivalents, such as those reported in haploids of rye (Neijzing 1985), were occasionally observed (see Table 1). In such associations all of the rye chromosomes are involved at similar frequencies. When two R genomes are present in a DNRR hybrid, the associations between the rye chromosomes are strictly homologous (data from Cuñado et al. 1986).

Aegilops-Aegilops associations

In the *Ae. uniaristata* × rye (NR) hybrid, N chromosomes show intragenomic associations (see Table 1) at frequencies similar to those reported in haploids of *Ae. longissima* (S^1S^1) (Riley and Chapman 1957) and *Ae. caudata* (CC) (Chapman and Riley 1964).

In hybrids carrying two different *Aegilops* genomes, variations in the mean frequency of associations per cell were observed, ranging from 2.01 in *Ae. ovata* × rye to 6.59 in *Ae. cylindrica* × rye (Table 1). These differences were considered to be an estimation of the degree of evolutionary relationships between the genomes involved since most of the associations are of an intergenomic nature although a low frequency of intragenomic associations were also observed (Table 2).

It is worth mentioning that in hybrids in which 3 different species sharing the same origin and genome constitution (UU*MM*) are involved (Kimber and Feldman 1987) we found variations in the mean number of intergenomic associations per cell i.e. 2.01 in *Ae. ovata* × rye, 4.24 in *Ae. triaristata* × rye and 5.39 in *Ae. biuncialis* × rye (Table 1). Therefore, the evolutionary affinities

between the U and *M* genomes seem to be different in each parental species. Accumulated changes in one or two genomes from the origin of each species to date may be responsible for the results obtained. Alternatively, donor species of *M* genomes may be different since it is accepted that these species share the U genome from *Ae. umbellulata* (Kimber and Yen 1989).

Hybrids carrying three different *Aegilops* genomes do not show an increase in the number of associations as compared with the triploid hybrids mentioned above despite having an additional genome (Table 1). Only the hybrid in which *Ae. crassa* (6x) is the female parental shows a higher frequency of intergenomic associations, probably due to the existence of two D genomes (Tables 1, 2; Fig. 1f).

In most polyploid hybrids, the number of chromosomes involved in multivalents exceeded the number of *Aegilops* genomes displayed in them (Table 1; Fig. 1a–c, f). These configurations are probably due to the existence of different translocations between chromosomes belonging to different genomes and/or homoeology groups such as has been proposed by several authors (Tanaka 1955; Cuñado et al. 1986). These interchanges seem to be frequent in *Ae. biuncialis* and *Ae. cylindrica* since in their crosses with rye, trivalents, quadrivalents and pentavalents were observed in the corresponding hybrids (Table 1; Fig. 1b). On the other hand, these translocations might also explain the existence of intragenomic associations in some of the hybrids mentioned above (Table 2).

Finally, Miller and Riley (1972) and Naranjo et al. (1979) reported that in wheat-rye combinations, homoeologous associations between wheat chromosomes increased when the dosage of rye genomes increased. However, when the frequencies of associations between *Aegilops* chromosomes in two different *Ae. ventricosa*-rye hybrids (DNR and DNRR) were compared no significant differences between them were found ($t=1.98$; $df=5$) (Table 1). Therefore, the R genomes had no observed dosage effect on homoeologous *Aegilops* associations.

Aegilops-rye associations

The mean number of associations per cell ranged from 0.06 in the *Ae. ovata* × rye hybrid to 0.30 in the *Ae. triuncialis* × rye hybrid (Table 1), with the associations always being rod bivalents. These low frequencies indicate a negligible relationship between *Aegilops* and *S. cereale* genomes. It was also observed that the frequencies of *Aegilops-Secale* associations do not increase with increasing ploidy level although the number of chromosomes involved is higher (Tables 1, 2). In these situations a high number of *Aegilops* chromosomes might favour, as a consequence of their close relationships, the opportunity of association between them to the detriment of the rye chromosomes.

Table 3. Percentages of *Aegilops*-rye associations for each of the different rye chromosome groups in the hybrids analysed

Female parent	Rye chromosomes				
	1R	2R+ 3R	5R	6R	4R+ 7R
Ae. uniaristata (NN)	27.27	18.18	18.18	0.00	36.36
Ae. triuncialis (UUCC)	6.67	6.67	33.33	6.67	46.67
Ae. variabilis (UUSS)	2.70	2.70	38.71	12.90	41.93
Ae. triaristata (4×) (UU*MM*)	5.88	0.00	35.29	5.88	52.94
Ae. ovata (UU*MM*)	16.67	0.00	33.33	0.00	50.00
Ae. biuncialis (UU*MM*)	6.06	21.21	36.36	3.03	33.33
Ae. triaristata (6×) (*UUMMNN*)	0.00	0.00	25.00	25.00	50.00
Ae. ventricosa (DDNN)	30.00	20.00	20.00	0.00	30.00
Ae. cylindrica (DDCC)	10.00	15.00	25.00	16.67	33.33
Ae. juvenalis (*DDMMUU*)	6.67	0.00	26.27	20.00	46.47
Ae. crassa (6×) (*DDDDMM*)	0.00	0.00	0.00	20.00	80.00
Total	10.09	11.01	28.90	10.09	39.91

On the other hand, taking into account ploidy level and the number of chromosomes involved in the hybrids shown in Table 2, it is clear that the frequencies of associations between *Aegilops* and the rye genomes are similar (Table 2). Only when the N genome of *Ae. ventricosa* and *Ae. triaristata* (6x) is involved is this frequency lower (Table 2).

Finally, on the basis of their morphological features and C-banding patterns five rye chromosome groups could be distinguished, namely: 1R, 2R-3R, 5R, 6R and 4R-7R (see for description, Giráldez et al. 1979). Table 3 shows the percentages of *Aegilops*-rye chromosome associations in all of the intergeneric hybrids analysed. From this table it is apparent that not all rye chromosomes have an equal probability of association with *Aegilops* chromosomes, neither within each hybrid nor among different hybrids.

Discussion

The polyploid species of *Aegilops* have evolved through hybridisation and chromosome doubling with closely related species. However, most of these species form only bivalents at metaphase I (Chennaveeraiah 1960; Cermeño et al. 1985; Cuñado 1992). This fact could be explained by assuming that the chromosomes of *Aegilops* genomes are actually so differentiated from each other

that they are unable to associate. If so, the existence of multivalents formed by chromosomes numbering more than the number of *Aegilops* genomes in *Aegilops* × rye hybrids (see Table 1) could be explained by the existence of different translocations between chromosomes from different genome and/or homoeology groups (Tanaka 1955; Cuñado et al. 1986). On the contrary, high levels of chromosome associations were observed in the hybrids between polyploid *Aegilops* species and their possible ancestors (see Kimber and Feldman 1987, for references) and in the intergeneric *Aegilops* × rye hybrids analysed here (Tables 1, 2). Therefore, structural changes may not solely explain the diploid-like meiosis found in most polyploid species of *Aegilops* and, consequently, it seems more likely that this meiosis was produced by a genetic suppression of homoeologous associations at metaphase I (AbuBakar and Kimber 1982; McGuire and Dvorak 1982).

Effect of R genome on homoeologous associations

In wheat × rye hybrids the rye genome interferes with the diploidising system and thus increases homoeologous chromosome associations (see Gupta and Fedak 1986). Nevertheless, Miller and Riley (1972) concluded that this promoting effect was so weak that several doses of rye genome were necessary to counter the effect of the *Ph* locus of chromosome 5B being even in single dosage. With regard to the *Aegilops* × rye hybrids analysed here, the levels of homoeologous associations between the *Aegilops* chromosomes observed are much higher than those reported in polyhaploids of some *Aegilops* species (Matsumura 1940; Chapman and Miller 1977; Shigenobu and Sakamoto 1977; Fedak 1983) (Tables 1, 2). Therefore, the rye genome seems to induce *Aegilops* homoeologous associations although no dosage effect was detected (Table 1). This fact may be attributed to a minor effectiveness of the genetic control in the hemizygous condition that restricts homoeologous associations in polyploid *Aegilops* species with respect to the analogous system in wheat (Gupta and Fedak 1985b). Thus, the presence of only one R genome would almost certainly lead to the maximum level of *Aegilops* associations allowed.

Relationships between the genomes of polyploid Aegilops species

Frequencies of associations at metaphase I between chromosomes of *Aegilops* may be useful in determining the relative affinity of the genomes present in the intergeneric hybrids and in comparing them to that existing between their putative diploid parents.

It has been accepted that the diploid donors of the *Ae. triuncialis* genomes, namely *Ae. umbellulata* (UU) and *Ae. caudata* (CC), are very closely related species so that one could be derived from the other or from a common ancestor (Miller 1981). Likewise, Lucas and Jahier (1988) reported a close relationship between the diploid ancestors of genomes of *Ae. cylindrica, Ae. caudata* and *Ae. squarrosa* (DD). The high frequency of *Aegilops* associations observed in *Ae. triuncialis* × *S. cereale* and *Ae. cylindrica* × rye hybrids confirms that the genomes present in these tetraploid species are very closely related (Table 1). The same results also indicate that the D and C genomes of *Ae. cylindrica* are more closely related than the U and *C* genomes of *Ae. triuncialis*, which is unlike the results obtained from the diploid species (Lucas and Jahier 1988). This fact could due to the diploidizing system of *Ae. cylindrica* being less effective in the hemizygous condition than that of *Ae. triuncialis* and thus a higher level of homoeologous associations would be possible in the former. Another possible cause might be that structural modifications occurred from the origin of these *Aegilops* polyploids; in fact, translocations seem to have taken place in *Ae. triuncialis* and *Ae. cylindrica* (Table 1; Fig. 1 b). Nevertheless, the structural and/or molecular differentiations seem to have had a major effect in *Ae. triuncialis* because there has been a reduction of affinity between their U and *C* genomes.

The relationship between *Ae. umbellulata* and *Ae. longissima*, the possible donors of the U and *S* genomes of *Ae. variabilis* (UU*SS*) (Yen and Kimber 1990), seems to be very remote (McGuire 1986). This is supported by the frequencies of the associations observed in the *Ae. variabilis* × *S. cereale* hybrid (Tables 1, 2). The intragenomic associations found in this hybrid could be explained either by associations between homologous segments dispersed throughout the U and *S* chromosomes of *Ae. variabilis* or by translocations that occurred during the evolution of this tetraploid species (Furuta 1981; Kawahara 1986).

The *M* genomes of *Ae. biuncialis, Ae. triaristata* (4x) and *Ae. ovata* seem to be modified forms of the genome found in *Ae. comosa* (Kimber and Feldman 1987). Nevertheless, Kimber et al. (1988) analysed chromosome associations in several hybrids between *Ae. ovata* and remaining polyploid species sharing the *M* genome and pointed out that their modified *M* genomes were different. Likewise, Nakai and Tsuji (1984) concluded from studies of acid phosphatase isozymes that the *M* genome of *Ae. ovata* was closely related to that of *Ae. comosa* (MM) but different to the *M* genome of *Ae. biuncialis* and *Ae. triaristata* (4x). This conclusion is supported by the association frequencies between *Aegilops* chromosomes found in the hybrids between these species and rye (Table 1). Therefore, substantial differences in the relationships between the U and M genomes of each species exist that could be imputed to the different origin of the *M* genome, in some cases from *Ae. comosa* (MM) and

other from *Ae. uniaristata* (NN). However, the number of chromosome associations observed in the hybrids between these two diploid species and *Ae. umbellulata* (UU) suggests that the relationships of the M and N genomes with U genomes are similar (Lucas and Jahier 1988). Therefore, there must have been more than one diploid ancestor of the *M* genome, and the genomes of these tetraploid species must have also been modified during their evolution. One piece of evidence for this is that multivalents originated by translocations were observed in all of the hybrids of genomic constitution U*M*R (Table 1). The interchanges seem more numerous in *Ae. biuncialis* since in its hybrid with rye, quadrivalents and pentavalents are also observed in addition to a high frequency of trivalents, whereas in the *Ae. ovata* × *S. cereale* hybrid the frequency of trivalents is very low and no more complex configurations appear (Table 1). Therefore, it will be necessary to reinvestigate which is the donor of the M-modified genome of each polyploid species, and it also seems that the allocation of the same symbol (*M*) to these genomes is unjustified.

It has been reported that *Ae. triaristata* (6x) (*UUMMNN*) originated from hybridization between *Ae. triaristata* (4x) (UU*MM*) and *Ae. uniaristata* (NN) (Kimber and Feldman 1987). Studies on the relationships between the presumptive diploid ancestors of the genomes of this hexaploid species indicated that *Ae. comosa* and *Ae. uniaristata* are more closely related to each other than to *Ae. umbellulata* (Lucas and Jahier 1988). Results from the *Ae. triaristata* (6x) × *S. cereale* hybrid agree with this conclusion since the frequencies of associations between the *M* and *N* chromosomes are higher than those between these two genomes and the *U* genome, in spite of the greater number of chromosomes involved in the latter case (Table 2) (Fig. 1 d).

In *Ae. juvenalis* there are three modified genomes (*D*, *M* and *U*) from *Ae. squarrosa*, *Ae. comosa* and *Ae. umbellulata*, respectively (Kihara 1963). From an analysis of hybrids between those diploid species it is evident that the relationship of *Ae. squarrosa* with *Ae. umbellulata* and *Ae. comosa* is closer than between the two latter species (Lucas and Jahier 1988). However, the number of chromosome associations observed in the *Ae. juvenalis* × *S. cereale* hybrid indicates that the *U* and *M* genomes are closer to each other than to the *D* genome (Table 2), due perhaps to substantial modifications occurring in the three genomes of *Ae. juvenalis* such as was suggested by Zhao and Kimber (1984). Furthermore, the frequency of associations between the *U* and *M* genomes in this hybrid is higher than that observed in the hybrid in which *Ae. ovata* is involved, although in the former case the *D* genome might compete with the *U* and *M* genomes to associate (Tables 1, 2). In conclusion, the *U* and *M* genomes of *Ae. juvenalis* seem to be more closely related than the *Ae. ovata* genomes.

Several authors have concluded that the two *D* genomes of *Ae. crassa* (6x) (*DDDDMM*) became differentiated during their evolution from the D genome present in *Ae. squarrosa*, although they are very similar to each other (Zhao and Kimber 1984; Gupta and Fedak 1985 b). Our results are in agreement with this hypothesis since in the *Ae. crassa* (6x) × rye hybrid a high frequency of associations between the two *D* genomes is observed (Table 2; Fig. 1 f).

One the other hand, chromosome association frequencies from the hybrids of *Ae. crassa* (6x) and *Ae. ventricosa* with rye might indicate that the relationships of the M and N genomes with the D genome are distant but similar (Tables 1, 2). However, in the hybrid with *Ae. crassa* (6x) there are two closed *D* genomes that pair with each other preferentially so that the opportunity of M chromosomes to associate will be reduced. If we consider this fact, the frequency of associations between the *D* and *M* genomes in the last hybrid is quite high, and consequently the *D* and *M* genomes of *Ae. crassa* (6x) may be closer to each other than are the D and N genomes of *Ae. ventricosa*. These results agree with those of Lucas and Jahier (1988) who found that *Ae. squarrosa* was closely related to *Ae. comosa* but distantly related to *Ae. uniaristata*.

In conclusion, our data show that the patterns of relationships between the genomes present in the majority of polyploid species of *Aegilops* are in concordance with those reported for the proposed diploid parents even though differences do exist in some species. In these latter cases, additional studies are necessary to elucidate whether these differences are due to differentiations that occurred during the evolution of the polyploid species or, to the contrary, that the diploid donors proposed are not the correct ones.

Relationships between Aegilops and Secale cereale genomes

From the results of several authors and from the data presented here it is evident that the genomes of *Aegilops* are very remote from the rye genome (Tables 1, 2), although some genomes, C and M (Hutchinson et al. 1980), seem to be more closely related than others (see N genome in Table 1). Likewise, in hybrids between *S. cereale* and polyploid species of *Aegilops* the mean frequencies of associations between rye and different *Aegilops* genomes are similar except when the N genome is involved, the frequencies then being lower (Tables 1, 2). In addition, different rye chromosomes do not appear to be associated with *Aegilops* ones at the same frequency (Table 3). Therefore, the present results seem to indicate that there may be differences in relationships not only between the R genome and different *Aegilops* genomes but also between different homoeologous groups.

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