Development and identification of a complete set of *Triticum aestivum – Aegilops geniculata* chromosome addition lines[1]

Bernd R. Friebe, Neal A. Tuleen, and Bikram S. Gill

Abstract: The production and identification of a complete set of intact *Aegilops geniculata* chromosome and telosome additions to common wheat is described. All U^g and M^g genome chromosomes were tentatively assigned to their homoeologous groups based on C-banding, meiotic metaphase I pairing analyses and plant morphologies. Thirteen disomic and one monosomic wheat–Ae. geniculata chromosome additions were identified. Furthermore, two monotelosomic (MtA7U^{g}L, MtA7M^{g}L) and nine ditelosomic (DtA1U^{g}S, DtA1U^{g}L, DtA2U^{g}S, DtA1M^{g}L, DtA2M^{g}L, DtA3M^{g}S, DtA5M^{g}S, DtA6M^{g}L, DtA7M^{g}S) wheat–Ae. geniculata additions were recovered. C-banding and meiotic pairing analyses revealed that all added U^g and M^g genome chromosomes are structurally unaltered compared to the *Ae. geniculata* parent accession. Chromosome 4M^g has a strong gametocidal gene that, when transferred to wheat, causes extensive chromosome breakage mainly in gametes lacking it. The relationships of *Ae. geniculata* chromosomes with those of the diploid progenitor species and derived polyploids is discussed.

Key words: *Triticum aestivum*, *Aegilops geniculata*, chromosome addition lines, C-banding, genome evolution.

Résumé : La production et la caractérisation d'un jeu complet d'additions chromosomiques et télomériques intactes de l'*Aegilops geniculata* chez le blé sont décrites. Tous les chromosomes des génomes U^g et M^g ont été assignés à leurs groupes homéologues en fonction de leur bandes C, de leur appariement en métaphase I de la méiose et de la morphologie des plantes. Treize lignées disomiques et une lignée monosomique blé–*Ae. geniculata* d'addition chromosomique ont été identifiées. De plus, deux lignées d'addition monotélosomiques (MtA7U^{g}L, MtA7M^{g}L) et neuf lignées d'addition ditélosomiques (DtA1U^{g}S, DtA1U^{g}L, DtA2U^{g}S, DtA1M^{g}L, DtA2M^{g}L, DtA3M^{g}L, DtA5M^{g}S, DtA6M^{g}L, DtA7M^{g}S) blé–*Ae. geniculata* ont été obtenues. La révélation des bandes C et l'analyse des appariements méiotiques ont révélé que tous les chromosomes additionnels provenant des génomes U^g et M^g étaient identiques au plan de la structure par rapport à ceux présents chez l'accession parentale de l'*Ae. geniculata*. Le chromosome 4M^g portait un gène à fort effet gamétocide qui, lorsque transféré chez le blé, cause beaucoup de cassures chromosomiques principalement chez les gamètes chez lesquels il était absent. Les relations entre les chromosomes de l'*Ae. geniculata* et ceux de l'espèce diploïde donatrice ainsi que les espèces polyploïdes dérivées sont discutées.

Mots clés : *Triticum aestivum*, *Aegilops geniculata*, lignées d'addition chromosomique, bandes C, évolution du génome.

[Traduit par la Rédaction]

Introduction

Aegilops geniculata Roth (syn. *Ae. ovata* L. *pro parte*) (van Slageren 1994) is a tetraploid ($2n = 4x = 28$) species with the genome formula $U^gU^gM^gM^g$, where the U^g genome was derived from the U genome of the diploid species *Ae. umbellulata* Zhuk. ($2n = 2x = 14$, UU) and the M^g genome originated from the M genome of *Ae. comosa* Sm. in Sibth. & Sm. ($2n = 2x = 14$, MM) (Kihara 1937, 1946, 1954; Kimber and Abu-Bakar 1981; Kimber et al. 1988). *Ae. geniculata* has a wide distribution and is native to the Mediterranean, Middle East, and southern parts of Russia and Ukraine.

Ae. geniculata is a valuable source for disease and pest resistance (Gill et al. 1985), which can be used for improving cultivated bread wheat, *Triticum aestivum* L. em Thell ($2n = 6x = 42$, AABBDD) (Friebe et al. 1996*b*). Mettin et al. (1977) attempted to increase the protein content of bread wheat by transferring *Ae. geniculata* chromosomes to the winter wheat cultivar Poros, but only three chromosome addition lines and two putative wheat – *Ae. geniculata* translocation lines were obtained (Friebe and Heun 1989).

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B.R. Friebe[2] and B.S. Gill. Department of Plant Pathology, Wheat Genetics Resource Center, Throckmorton Hall, Kansas State University, Manhattan, KS 66506–5502, U.S.A.
N.A. Tuleen. Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843–2474, U.S.A.

[1]Contribution No. 98-144-J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, KS 66506–5502, U.S.A.

[2]Author to whom all correspondence should be addressed. (e-mail: friebe@ksu.edu)

Here we report the development and identification of thirteen disomic, one monosomic, and nine ditelosomic *Ae. geniculata* chromosome additions to 'Chinese Spring' wheat.

Materials and methods

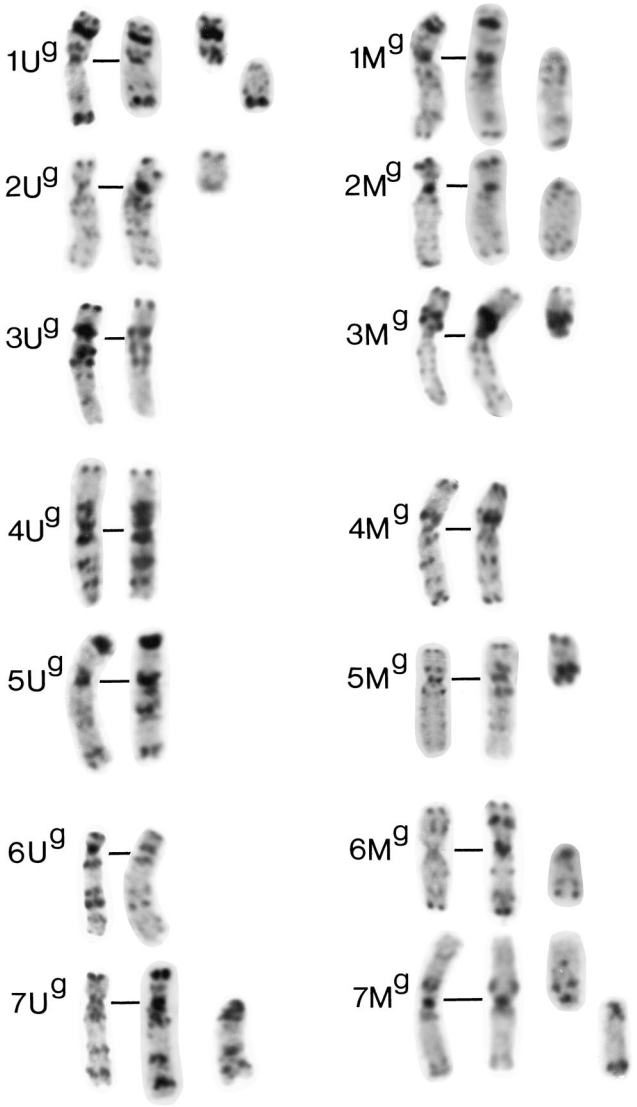
Plants of the *Ae. geniculata* accession TA2899 (line #2 collected in Israel and kindly provided by Dr. G.E. Hart, Texas A & M University) were crossed as male parents to *T. aestivum* cv. Chinese Spring (CS). The F_1 was backcrossed with CS and one BC_1 plant was obtained with $2n = 8x = 56$ chromosomes in root tip meristems. This plant formed $19^{II} + 1^{IV} + 14^{I}$ at meiotic metaphase I, indicating that a spontaneous wheat–wheat translocation had occurred. Spikes from this plant were emasculated, pollinated with CS, and a large number of BC_2 seeds were obtained. These backcross seeds were germinated and seedlings with 43–46 chromosomes were saved. The meiotic pairing in these plants was determined in pollen mother cells (PMCs), and the plants with more than 43 chromosomes or 43 chromosome plants with a quadrivalent, were backcrossed again with CS. The BC_3 seeds resulting from these pollinations were germinated, plants with 43 chromosomes were saved, and their meiotic pairing behavior determined. Plants that formed a quadrivalent after the second backcross were either eliminated, or a large number of BC_3 seeds was produced allowing the selection of plants with added *Ae. geniculata* chromosomes, but lacking the wheat–wheat translocation. Plants with added *Ae. geniculata* telosomes were recovered in the offspring of monosomic addition plants. Disomic addition plants for complete *Ae. geniculata* chromosomes or telosomes were obtained in the self-pollinated progenies of monosomic chromosome addition or telosomic addition plants.

The C-banding protocol described by Gill et al. (1991) was used for chromosome identification. The homoeology of the *Ae. geniculata* chromosomes was determined by comparing them with the standard karyotypes of the diploid U-genome progenitor species *Ae. umbellulata* (Friebe et al. 1995*b*) and the M-genome diploid *Ae. comosa* (Friebe et al. 1996*a*) and by plant characteristics of the corresponding chromosome addition lines. To verify the identity of the added *Ae. geniculata* chromosomes considered to belong to the U genome, meiotic metaphase I pairing was analyzed in testcross combinations with the corresponding ditelosomic addition lines of CS–*Ae. umbellulata* (Friebe et al. 1995*b*) and CS–*Ae. peregrina* (Hack. in J. Fraser) Marie & Weller ($2n = 4x = 28$, $U^pU^pS^pS^p$) (Friebe et al. 1996*c*). Furthermore, meiotic metaphase I pairing was analyzed in F_1 hybrids of the *Ae. geniculata* addition lines with the *Ae. geniculata* parent accession TA2899 and with *Ae. biuncialis* Vis. ($2n = 4x = 28$, $U^bU^bM^bM^b$). The purpose of the first cross was to determine if the *Ae. geniculata* chromosomes in the addition lines were unaltered relative to the chromosomes of the *Ae. geniculata* parent accession. The second testcross was used to detect chromosomal rearrangements between the U^g/U^b and M^g/M^b genome chromosomes of *Ae. geniculata* and *Ae. biuncialis*. Photomicrographs were taken with a Zeiss photomicroscope III, using Kodak Imagelink HQ microfilm 1461.

Results

Ae. geniculata has seven pairs each of the U^g- and M^g-genome chromosomes. Thirteen complete *Ae. geniculata* chromosomes were isolated in CS wheat as disomic addition lines. At present, chromosome $6U^g$ is only available in monosomic condition. Furthermore, nine ditelosomic (DtA1U^{g}S, DtA1U^{g}L, DtA2U^{g}S, DtA1M^{g}L, DtA2M^{g}L, DtA3M^{g}S, DtA5M^{g}S, DtA6M^{g}L, and DtA7M^{g}S) and two monotelosomic addition lines (MtA7U^{g}L and MtA7M^{g}L) were identified (Fig. 1). The cytogenetic integrity of the wheat genome and the added *Ae. geniculata* chromosomes in the different addition lines was verified by C-banding and meiotic pairing analysis. The genomic affinity and cytogenetic identification of individual chromosomes of *Ae. geniculata* in the different addition lines was determined by C-banding, meiotic pairing analysis and plant morphology. These results are described below.

Fig. 1. C-banding patterns of *Aegilops geniculata* chromosomes and telosomes added to *Triticum aestivum* cv. Chinese Spring (chromosomes shown on the left were taken from the *Ae. geniculata* parent accession TA2899).



Genomic integrity of the addition lines

The C-banding patterns of the wheat chromosomes in the *Ae. geniculata* addition lines are similar to standard CS, indicating that the wheat–wheat translocation present in the BC_1 plant was successfully eliminated. However, a heteromorphic chromosome 6D with a telomeric C-band in the long arm was segregating in some of the lines. The C-

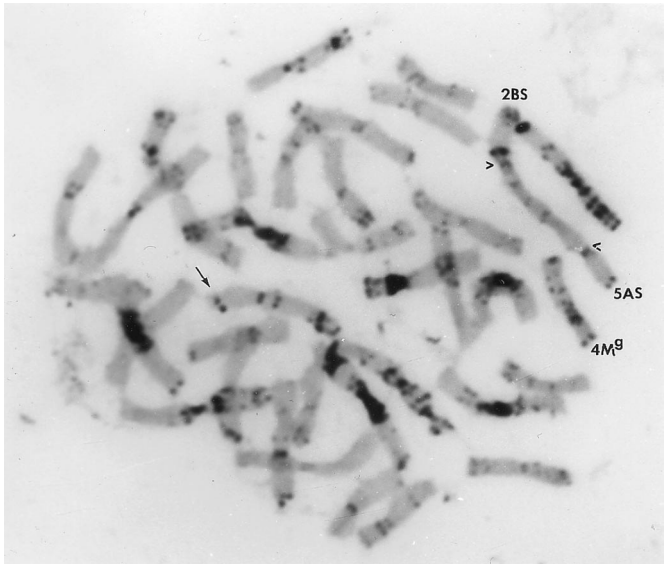
Table 1. Metaphase I pairing in testcross combinations of disomic M^g- and U^g-genome chromosome additions (DA) of *Ae. geniculata* with the *Ae. geniculata* parent accession.

Testcross combinations	No. of PMCs	No. of PMCs with 1 ring″
CS × *Ae. geniculata*	120	0
DA1M^g × *Ae. geniculata*	42	30
DA2M^g × *Ae. geniculata*	45	37
DA3M^g × *Ae. geniculata*	135	103
DA4M^g × *Ae. geniculata*	52	43
DA5M^g × *Ae. geniculata*	50	31
DA6M^g × *Ae. geniculata*	67	50
DA7M^g × *Ae. geniculata*	29	23
DA4U^g × *Ae. geniculata*	38	25

banding patterns of the added *Ae. geniculata* chromosomes are identical to those of the corresponding chromosomes in the *Ae. geniculata* parent accession TA2899 (Fig. 1). This indicates that no aberrations occurred in the *Ae. geniculata* chromosomes during the isolation of the addition lines. The integrity of the added M^g chromosomes was further verified by meiotic metaphase I pairing of testcross plants of the M^g additions with the *Ae. geniculata* parent accession TA2899. A ring bivalent was observed in more than 50% of the PMCs in the seven 36 chromosome hybrids (Table 1), indicating that the added M^g-genome chromosomes are not structurally rearranged. No ring bivalent was observed in the control CS × *Ae. geniculata* hybrid (Table 1).

However, genetically induced cytological instability was observed in the 4U^g addition line. During the selection procedure for recovering *Ae. geniculata* chromosomes, it was noted that self-pollination of plants monosomic for chromosome 4M^g produced a large number of offspring with chromosomal rearrangements, i.e., dicentric, ring, telocentric, and acrocentric chromosomes (Fig. 2), indicating the presence of a gametocidal gene on chromosome 4M^g. Further details on the gametocidal action of this chromosome will be published elsewhere.

Fig. 2. Chromosome aberrations observed in the offspring of a monosomic addition plant for the *Aegilops geniculata* chromosome 4M^g. The centromeres of a dicentric chromosome involving 2B and 5A of wheat are marked with arrowheads and an additional rearrangement is present in the short arm of wheat chromosome 4A marked with an arrow. Note that the plant is monosomic for chromosome 4M^g.



Cytogenetic identification based on chromosome morphology and C-banding homologies

All of the U^g-genome and most of the M^g-genome chromosomes in the addition lines were cytogenetically identified based on comparative chromosome morphology and C-banding pattern homologies. In this process, the genomic affinity of the *Ae. geniculata* chromosomes in individual addition lines was also determined. The U^g genome chromosomes of *Ae. geniculata* are similar in size, arm ratio, and C-banding pattern compared to those of the diploid progenitor species *Ae. umbellulata* (Friebe et al. 1995*b*). These similarities were used to assign the U^g-genome chromosomes in the addition lines to the various homoeologous groups of wheat (Fig. 1). However, C-banding analysis did not detect an apparent structural change in chromosomes 4U^g and 4U (of *Ae. umbellulata*) (see below).

The C-banding patterns and the amount of C-heterochromatin of the M^g-genome chromosomes of *Ae. geniculat*a are similar to those of the M-genome chromosomes of the diploid progenitor species *Ae. comosa* subsp. *comosa* (Friebe et al. 1996*a*). Accordingly, the homoeologous identification of chromosomes 1M^g, 6M^g, and 7M^g was based on this similarity (Fig. 1). Chromosomes 2M^g and 5M^g have similar arm ratios and C-banding patterns and could not be distinguished. The remaining *Ae. geniculata* chromosomes 3M^g and 4M^g differ in C-banding patterns from the corresponding chromosomes of *Ae. comosa* subsp. *comosa*. Their tentative assignment to homoeologous groups 3 and 4 was based on chromosome arm ratio only. However, unambiguous assignments of these chromosomes to homoeologous groups were based on meiotic pairing and morphological trait homologies (see below).

Genomic affinities and cytogenetic identification based on meiotic pairing

The relationship of the U^g-genome chromosomes of *Ae. geniculata* with the corresponding U-genome chromosomes derived from the diploid progenitor species *Ae. umbellulata* was analyzed by meiotic metaphase I paring in testcross combinations of the U^g chromosome additions with the appropriate ditelosomic *Ae. umbellulata* addition lines. Because plants with ditelosomic additions for 4US are late-heading dwarfs, the 4U^g addition line was testcrossed with the 4U^pS and 4U^pL ditelosomic additions derived from *Ae. peregrina*. The short and long arm telosomes of the *Ae. umbellulata* chromosomes 1U, 2U, 5U, and 7U and the long arm telosome 6U^pL paired in the form of a heteromorphic rod bivalent (t1″) (Table 2). These data provided conclusive evidence of genomic affinity and cytogenetic identification and also indicated that the corresponding U^g chromosome arms in *Ae. geniculata* are structurally unaltered (Table 2). Similarly, the short arm telosome 4U^pS paired with the 4U^gS arm. However, no pairing was observed between the 4U^pL

Table 2. Metaphase I pairing in testcross combinations of disomic and monosomic U^g-genome chromosome additions (DA and MA, respectively) of *Ae. geniculata* with the corresponding ditelosomic U- and U^p-genome additions derived from *Ae. umbellulata* and *Ae. peregrina*.

Testcross combinations	PMCs examined	Percent with t1″
DA1U^g × DA1US	68	32
DA1U^g × DA1UL	131	19
DA2U^g × DA2US	73	14
DA2U^g × DA2UL	111	45
DA4U^g × DA4U^pS	128	47
DA4U^g × DA4U^pL	100+	0
DA5U^g × DA5US	129	18
DA5U^g × DA5UL	44	89
MA6U^g × DA6U^pL	41	93
DA7U^g × DA7US	88	16
DA7U^g × DA7UL	24	67

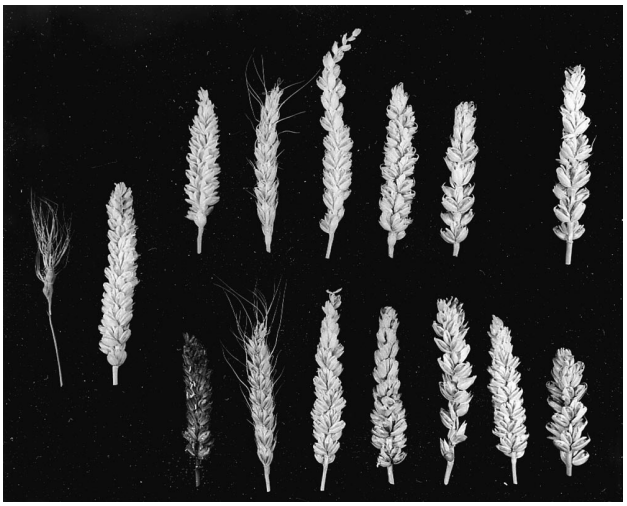
and 4U^gL arms, suggesting that the latter was modified. To determine if chromosome 4U^g had been altered during its isolation, the corresponding addition line was pollinated with the *Ae. geniculata* parent accession. The presence of a ring bivalent at meiotic metaphase I of the 36-chromosome F_1 plant indicated that chromosome 4U^g added to CS wheat is unaltered (Table 1).

For analyzing the relationships of the added *Ae. geniculata* chromosomes with the U^b- and M^b-genome chromosomes of *Ae. biuncialis*, the U^g and M^g additions were crossed with *Ae. biuncialis*, and metaphase I pairing was analyzed in the 36-chromosome F_1 plants. In testcross combinations involving chromosomes 1U^g, 2U^g, 5U^g, 7U^g, 2M^g, 5M^g, and 7M^g, a ring bivalent was observed at varying frequencies. These data confirmed the genomic affinities and further indicated homology of the M^g-genome chromosomes with M^b-genome chromosomes of *Ae. biuncialis*. In the F_1 hybrids involving chromosomes 4U^g, 1M^g, 3M^g, 4M^g, and 6M^g, no ring bivalent was observed in more than 100 PMCs analyzed (Table 3). These data suggest that the 4U^b, 1M^b, 3M^b, 4M^b, and 6M^b chromosomes of *Ae. biuncialis* are rearranged compared with the corresponding chromosomes of *Ae. geniculata*.

Table 3. Metaphase I pairing in testcross combinations of disomic U^g-genome chromosome additions (DA) of *Ae. geniculata* with *Ae. biuncialis*.

Testcross combinations	PMCs examined	Percent PMCs with 1 ring″
Control		
CS × *Ae. biuncialis*	100+	0
Crosses with U^g additions		
DA1U^g × *Ae. biuncialis*	216	16
DA2U^g × *Ae. biuncialis*	176	15
DA4U^g × *Ae. biuncialis*	146	0
DA5U^g × *Ae. biuncialis*	72	47
DA7U^g × *Ae. biuncialis*	111	29
Crosses with M^g additions		
DA1M^g × *Ae. biuncialis*	230	0
DA2M^g × *Ae. biuncialis*	141	18
DA3M^g × *Ae. biuncialis*	147	0
DA4M^g × *Ae. biuncialis*	220	0
DA5M^g × *Ae. biuncialis*	123	11
DA6M^g × *Ae. biuncialis*	158	0
DA7M^g × *Ae. biuncialis*	143	17

Fig. 3. Spike morphologies of the *Triticum aestivum* cv. Chinese Spring-*Aegilops geniculata* disomic chromosome addition lines (DA). Left to right (center): *Ae. geniculata*, *Triticum aestivum* cv. Chinese Spring; (top row) Da1U^g, DA2U^g, DA3U^g, DA4U^g, DA5U^g, DA7U^g; (bottom row) DA1M^g, DA2M^g, DA3M^g, DA4M^g, DA5M^g, DA6M^g, DA7M^g.



Genetic identification based on plant morphology

Spike morphologies of the *Ae. geniculata* addition lines are shown in Fig. 3. Some of the morphological features are unique to specific homoeologous groups and are invaluable aids in genetic identification of chromosome addition lines.

The disomic addition line 1M^g has black glumes but otherwise is similar to CS. Seed set may be reduced when plants are grown under less than ideal light conditions. Spikes of the ditelosomic addition line 1M^gL are similar to CS with white glumes. This locates the gene for black glumes on the short arm of chromosome 1M^g and confirms the homoeology of this arm to group 1 short arms of Triticeae, for which this trait is an excellent marker.

The spike morphology of disomic addition line 2M^g is similar to those of all of the homoeologous group 2 chromosomes of the Triticeae that have been added to CS wheat, in having short awns and tenacious glumes. The ditelosomic addition line 2M^gL is similar to the whole chromosome addition and confirms the genetic homoeology of 2M^gL with the group 2 long arms of the analyzed Triticeae species.

Spikes of the disomic addition line 3M^g are tapered and mostly longer than those of CS. The upper 3–4 spikelets usually fail to set seed. The rachis is fragile and often breaks between the second and fourth spikelets at the base of the head.

Spikes of the disomic addition line 4M^g have supernumerary florets, which give the appearance of being more dense than those of CS. The upper 1/4 of the spike usually fails to set seed.

Spikes of the disomic addition line 5M^g are lax at the base and compact at the top. The ditelosomic addition line 5M^{g}S is similar in morphology to CS.

Spikes of the disomic addition line 6M^g are similar in appearance to those of CS, but have reduced seed set in the upper quarter of the spike.

Spikes of the disomic addition line 7M^g are more lax in the basal area of the spike than those of CS.

Spikes of the disomic addition lines 1U^g, 2U^g, 5U^g, and 7U^g are similar to the addition lines derived from *Ae. umbellulata* and *Ae. peregrina.* The spikes of the disomic addition line 3U^g are tapered and longer than those of CS with the upper spikelets being sterile. The spikes of the addition line 4U^g are shorter and more compact than those of CS. Florets in the upper third of the head are mostly sterile. Overall, the morphological traits provided further evidence of genetic homology deduced from C-banding and meiotic pairing analyses.

Discussion

The C-banding patterns of the *Ae. geniculata* chromosomes are similar to those reported earlier (Friebe and Heun 1989). However, because of the lack of knowledge about the homoeologous relationships of the *Ae. geniculata* chromosomes, they were previously designated with letters from A to N (Friebe and Heun 1989). Recently, detailed standard karyotypes based on C-banding and in situ hybridization analyses were established for all of the diploid *Aegilops* species (Badaeva et al. 1996*a*, 1996*b*; Friebe and Gill 1996; Friebe et al. 1992*a*, 1992*b*, 1993, 1995*a*, 1995*b*, 1995*c*, 1996*a*). These studies created the basis for a more detailed analysis of the polyploid species of this genus. Based on the comparison with the standard karyotypes of the diploid progenitor species *Ae. umbellulata* and *Ae. comosa* and plant characteristics of the *Ae. geniculata* addition lines in the present study, all U^g and M^g chromosomes were tentatively assigned to their homoeologous groups. Furthermore, C-banding analysis identified *Ae. comosa* subsp. *comosa* as the donor of the M^g genome of *Ae. geniculata*.

Maan (1977) reported that the cytoplasm of *Ae. geniculata* is similar to that of *Amblyopyrum muticum* (Boiss.) Eig (syn. *Ae. mutica* Boiss.) (2*n* = 2*x* = 14, TT), based on observations of plant characteristics in alloplasmic lines with the genomes of *T. aestivum* and *T. durum* substituted into the cytoplasms of different *Aegilops* species. Similarly, the analyses of plastome and chondriome differentiation in diploid and polyploid *Aegilops* species suggest that a form of *Am. muticum* was the maternal and *Ae. umbellulata* the paternal parent of *Ae. geniculata* (Tsunewaki 1996). The present study confirms that the U^g genome of *Ae. geniculata* was contributed by *Ae. umbellulata*, but revealed evidence that *Ae. comosa* subsp. *comosa* contributed the M^g genome of *Ae. geniculata*. Further studies are needed to evaluate this discrepancy.

A complete set of fourteen *Ae. geniculata* whole chromosomes and nine telosomes were added to CS wheat. C-banding and meiotic metaphase I pairing analyses showed that these chromosomes were not rearranged compared with the corresponding chromosomes of the *Ae. geniculata* parent accession.

Meiotic pairing analysis in testcrosses of the U^g chromosome additions with the ditelosomic U-genome additions derived from *Ae. umbellulata* further showed that the *Ae. geniculata* chromosomes 1U^g, 2U^g, 5U^g, 6U^g, and 7U^g are similar to those present in the diploid progenitor species. The short arm of chromosome 4U^g is similar to the 4U^{p}S arm of *Ae. peregrina*, whereas the 4U^{g}L arm is rearranged compared with the 4U^{p}L of *Ae. peregrina*, thus probably also with the 4UL arm of *Ae. umbellulata.*

Meiotic pairing analysis in testcross combinations of the *Ae. geniculata* additions with *Ae. biuncialis* showed that, except for chromosomes 4U^b, 1M^b, 3M^b, 4M^b, and 6M^b, all chromosomes were structurally unaltered as indicated by the formation of ring bivalents at metaphase I. Whether the rearrangements involving these chromosomes are species-specific or if they reflect chromosome polymorphisms within the two species is not known. Such structural chromosome polymorphism was demonstrated in *Ae. geniculata*, where meiotic pairing analysis detected the presence of up to two reciprocal translocations in 73 accessions analyzed (Furuta 1981).

The U-genome of *Ae. umbellulata* is present in several tetraploid *Aegilops* species and is considered a pivotal genome (Zohary and Feldman 1962; Kimber and Yen 1988). In interspecific hybrids between two tetraploid U-genome species that differ in their second or differential genome (S or M), the U-genome chromosomes are present as pairs and undergo normal meiotic pairing and segregation. The chromosomes of the two differential genomes are present in only one copy, which results in meiotic irregularities. In these hybrids, the pivotal genome is considered to act as a buffer, whereas the two differential genomes may undergo repatterning as the consequence of nonhomologous recombination. Evidence supporting this pivotal-differential evolution pattern came from meiotic pairing analysis, showing that the U genome in polyploid *Aegilops* species is very similar to the U genome of *Ae. umbellulata*, whereas the differential genomes in these polyploids are substantially modified (Feldman 1965*a*, 1965*b*, 1965*c*).

The present study also supports the pivotal–differential evolution theory. Except for the long arm of chromosome 4U^g, all U^g-genome chromosomes are structurally similar to the corresponding U-genome chromosomes of *Ae. umbellulata*, whereas chromosomal rearrangements were detected between group 1, 3, 4, and 6 chromosomes of the M^g/M^b genomes of *Ae. geniculata* and *Ae. biuncialis*. However, there also is evidence that the pivotal U genome in these polyploids has accumulated structural changes (Kimber et al. 1988; Talbert et al. 1993).

The present analysis detected a high frequency of chromosomal instability in the offspring of plants that were monosomic for the *Ae. geniculata* chromosome 4M^g, whereas progenies derived from plants that were disomic for this chromosome were cytologically stable. The chromosomal aberrations occurred at higher frequencies in plants that lacked chromosome 4M^g (24%) but also were detected at lower frequencies in plants mono- or disomic for this chromosome (8%). This behavior suggests that chromosome

$4M^g$ has a gametocidal gene, which preferentially causes chromosome breakage in gametes lacking this gene. Similar gametocidal genes have been reported for other diploid and polyploid *Aegilops* species (for review see Endo 1990; Tsujimoto 1995). Gametocidal genes have been located on group 2 chromosomes of *Ae. sharonensis* Eig ($2n = 2x = 14$, $S^{sh}S^{sh}$), *Ae. longissima* Schweinf. & Muschl. ($2n = 2x = 14$, S^lS^l), *Ae. speltoides* Tausch ($2n = 2x = 14$, SS), *Ae. cylindrica* Host ($2n = 4x = 28$, $D^cD^cC^cC^c$), group 4 chromosomes of *Ae. sharonensis*, *Ae. longissima*, group 3 chromosomes of *Ae. caudata* L. ($2n = 2x = 14$, CC) and *Ae. triuncialis* L. ($2n = 4x = 28$, $U^tU^tC^tC^t$), and on a group 6 chromosome of *Ae. speltoides* (Endo 1990; Tsujimoto 1995). Previous studies showed that gametocidal genes induce chromosome breakage and fragmentation in the postmeiotic interphase before the first pollen mitosis (Nasuda et al. 1998). The resulting breakage-fusion-bridge cycles persist in the derived zygotes and endosperms and later stages of plant development, but eventually cease as the result of healing of the broken chromosome ends. The gametocidal action of chromosome $4M^g$ and its relationship with other gametocidal *Aegilops* genes remains to be established.

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