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C-banding and in-situ hybridization analyses of *Agropyron intermedium*, a partial wheat × *Ag.* intermedium amphiploid, and six derived chromosome addition lines*

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Summary. C-banded karyotypes of *Agropyron intermedium* ($2n=6x=42$, E_1E_2X), a partial amphiploid *Triticum aestivum* – *Ag. intermedium* ($2n=8x=56$, TAF46), and six derived chromosome addition lines, were analyzed. In *Ag. intermedium*, diagnostic C-bands were present on 14 pairs of chromosomes, designated from A to N, while the remaining seven pairs, designated O to U, either lacked, or had only faint, C-bands and were not always identified unambiguously. All seven *Ag. intermedium* chromosome pairs of the partial amphiploid TAF46, and the added *Ag. intermedium* chromosomes present in the six derived addition lines, were identified by their characteristic C-banding patterns. Chromosome morphology and banding patterns were similar to those of the corresponding chromosomes present in the parent *Ag. intermedium* accession, suggesting that these chromosomes were not structurally rearranged. In-situ hybridization, using a 18*s*.26*s* rDNA probe, showed that the *Ag. intermedium* chromosomes 1Ai-1 and 5Ai-1 present in the addition lines L3 and L5 were carrying actively transcribed nucleolus organizer regions. The results are discussed with respect to the genomic relationships of these chromosomes.

Key words: Wheat-*Agropyron* derivatives – C-banding – In-situ hybridization

Introduction

Wild species of the genus *Agropyron* (P.B.) are an important source for improving the genetic variability of hexaploid wheat, *Triticum aestivum* L. em Thell. Among the possible improvements are resistance to wheat streak mosaic and barley yellow dwarf viruses (Sharma et al. 1984; Brettell et al. 1988; Xin et al. 1988; Friebe et al. 1991), resistance to rusts (Sharma and Knott 1966; Wienhues 1966; Knott 1968; Cauderon et al. 1973; Friebe et al. 1992), and tolerance to salt stress (Dewey 1960; McGuire and Dvořák 1981; Forster et al. 1988; Littlejohn 1988).

Agropyron intermedium (Host) P.B. (= *Thinopyrum intermedium* (Host) Barkworth and Dewey) is a hexaploid species ($2n=6x=42$), genomically E_1E_2X, where the E_1 and E_2 genomes are related to the E genome of *Agropyron elongatum* (Host) P.B. (= *Thinopyrum elongatum* (Host) Dewey), and the J genome of *Ag. bessarabicum* (= *Th. bessarabicum*). The origin of the third X genome is still unclear (Dvořák 1981 a, b; Dewey 1984; Wang 1985).

Cauderon (1966) and Cauderon et al. (1973) reported the production of a partial amphiploid, designated TAF46 ($2n=8x=56$), containing seven chromosome pairs from *Ag. intermedium* added to the full chromosome complement of *T. aestivum*. TAF46 was used to produce six *T. aestivum* – *Ag. intermedium* disomic chromosome addition lines. The and Baker (1970) reported that the *Ag. intermedium* chromosome present in the addition line L1 compensates for the loss of wheat chromosome pair 7D, while the *Ag. intermedium* chromosome present in the L2 addition line compensates for the loss of chromosome pair 3A in derived substitution lines, indicating homoeology of these chromosomes for groups 7 and 3, respectively. The homoeologous relationships of all added *Ag. intermedium* chromosomes have been established using chromosomal, morphological, isozyme, and storage protein markers (Figueiras et al. 1986; Forster et al. 1987).

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Fig. 1. C-banded mitotic metaphase chromosomes of *Ag. intermedium* accession no. 75

Giemsa C-banding and in-situ hybridization (ISH) have been used in chromosome identification and in analyzing the evolutionary relationships within the *Triticeae* (for review see Gill and Sears 1988). In this paper we describe the C-banding patterns of *Ag. intermedium* and of the *Ag. intermedium* chromosomes present in the partial amphiploid TAF46 and in the six derived chromosome addition lines. In addition, nucleolar activity of the added *Ag. intermedium* chromosomes was analyzed by ISH analysis. The results are discussed with respect to the genomic affinities of individual *Ag. intermedium* chromosomes.

Materials and methods

The material analyzed consisted of the partial amphiploid, *T. aestivum* cv. 'Vilmorin 27' – *Ag. intermedium* designated TAF46, disomic chromosome addition lines designated L1, L2, L3, L4, L5, L7, and *Ag. intermedium* accession no. 75, that was used as the male parent in the production of these lines.

Chromosome identification was according to the C-banding technique described by Gill et al. (1991). Chromosome measurements were on 20 C-banded *Ag. intermedium* chromosomes of TAF46 using wheat chromosome 3B as a standard. For ISH, pTa 71 was used containing one unit of 18*s*.26*s* rRNA (8.9 kb) from *T. aestivum* (Gerlach and Bedbrook 1979). The probe was labelled by nick translation with biotinylated dUTP. Details for slide preparation, ISH, and detection of hybridization sites were as described by Rayburn and Gill (1985) and Mukai et al. (1990). Chromosome designations of the *Ag. intermedium* chromosomes present in TAF46 and in the derived chromosome addition lines were according to their homoeology followed by the number 1 to distinguish them from other *Ag. intermedium* chromosomes belonging to the same homoeologous group. Chromosomes of the *Ag. intermedium* accession no. 75 were designated with letters from A to U since their homoeologous relationships have not yet been established.

Results

C-banded karyotype of Ag. intermedium

C-banding analysis was carried out on seven plants of *Ag. intermedium* accession no. 75. Characteristic C-bands are present in 14 of the 21 chromosome pairs, designated A–N (Figs. 1, 2). The remaining seven pairs of chromosomes, designated O–U, are either lacking or have only faint C-bands, making it difficult to distinguish between them.

C-banding polymorphism was observed for many chromosomes, and in cases where these chromosomes were identified unambiguously they are shown as pairs in Fig. 2 (chromosomes C, D, G, H, J, K, U). In addition, at least one deletion was found in chromosome D, which resulted in the complete loss of the distally located euchromatic region of its short arm. Although the number of plants available for this analysis was small, a large amount of C-band polymorphism as well as structural modifications were observed. Undetected variation might also be present, since several chromosomes were similar in size, arm ratio, and banding pattern.

C-banded karyotype of TAF46 and the addition lines

A C-banded mitotic metaphase cell of the partial amphiploid TAF46 is shown in Fig. 3. The C-banding patterns of the wheat and *Ag. intermedium* chromosomes present in the partial amphiploid and of the six *Ag. intermedium* chromosomes in the addition lines are shown in Fig. 4. Chromosome length data and arm ratios of the *Ag. intermedium* chromosome are given in Table 1. In the cultivar 'Vilmorin 27', chromosomes 5B and 7B are involved in a reciprocal translocation, forming the translocation chromosomes T5BS · 7BS and T5BL · 7BL, with the breakpoints being located within the centromeric re-

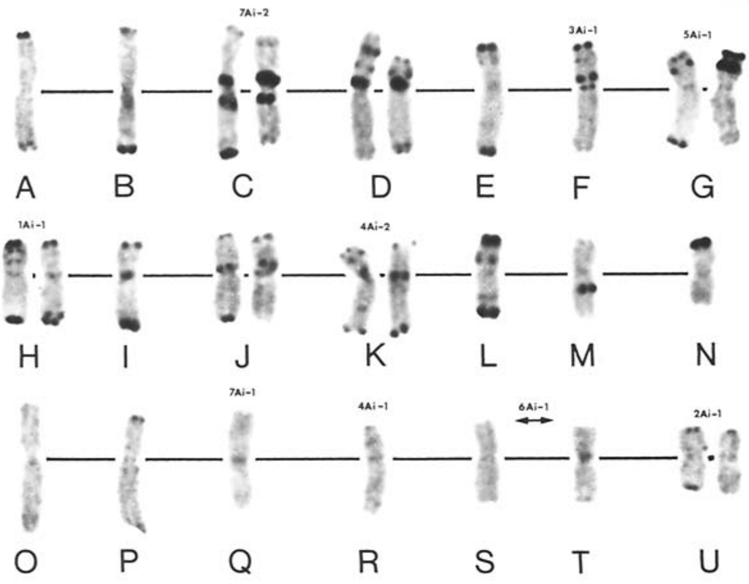

Fig. 2. C-banded karyotype of *Ag. intermedium* accession no. 75

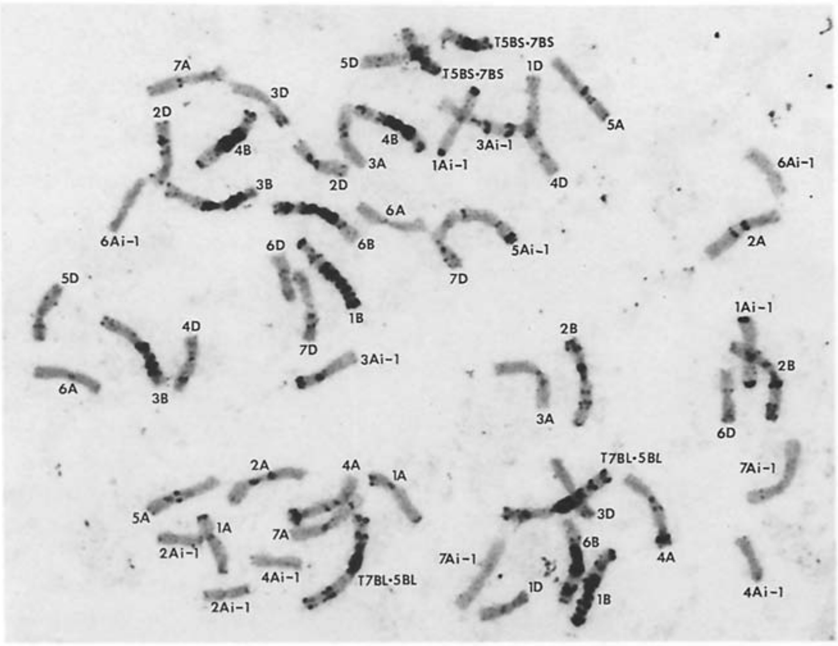

Fig. 3. C-banded mitotic metaphase chromosomes from a 2n = 55 chromosome plant (monosomic for chromosome 5Ai-1) of the partial amphiploid *T. aestivum* – *Ag. intermedium*

gions. The same translocation chromosomes were also observed in all six derived addition lines.

All seven *Ag. intermedium* chromosome pairs can be identified by their characteristic C-banding patterns:

Chromosome 1Ai-1. Present in addition line L3, is submetacentric and shows large telomeric C-bands in both arms and two small interstitial bands in the short arm. Occasionally, a small satellite was observed in the short arm.

Chromosome 2Ai-1. Present in the partial amphiploid TAF46, but not in any of the addition lines. Since the homoeologous relationships of all the other *Ag. intermedium* chromosomes have been established, and assigned to groups 1, 3, 4, 5, 6 and 7, it was postulated that this chromosome is homoeologous to group 2 of the *Triticeae* (Forster et al. 1987). Chromosome 2Ai-1 is a small, slightly submetacentric chromosome, with small but distinct telomeric C-bands in both arms.

Chromosome 3Ai-1. Present in L2, is submetacentric and shows large proximally and terminally located C-bands in the short, and faint interstitial and telomeric C-bands in the long, arm.

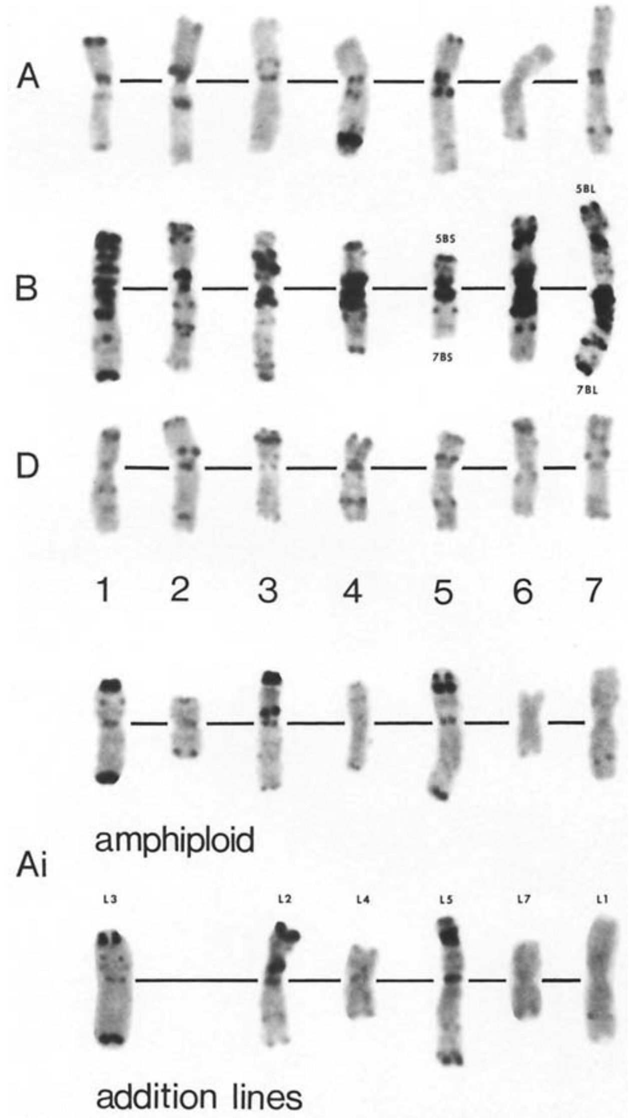

Fig. 4. C-banded karyotype of the partial amphiploid *T. aestivum – Ag. intermedium* and C-banding patterns of the *Ag. intermedium* chromosomes present in the six derived chromosome addition lines

Table 1. Chromosome lengths, standard deviations, arm ratios and *Ag. intermedium*/3 B lengths ratios of the *Ag. intermedium* chromosomes present in the partial amphiploid TAF46 (data based on measurements of 20 C-banded chromosomes)

Chromosome	Chromosome length	Standard deviation	Arm ratio	*Ag. intermedium*/3B length ratio
1Ai-1	7.6 μm	1.0 μm	1.4	0.69
2Ai-1	5.3 μm	0.7 μm	1.2	0.48
3Ai-1	8.3 μm	0.7 μm	1.3	0.76
4Ai-1	5.1 μm	0.5 μm	1.1	0.47
5Ai-1	8.0 μm	0.7 μm	1.5	0.72
6Ai-1	5.8 μm	0.4 μm	1.2	0.53
7Ai-1	8.4 μm	0.9 μm	1.1	0.76

Chromosome 4Ai-1. Present in L4, is small, almost metacentric and possesses very small telomeric C-bands in both arms. In addition, another very small C-band is present in the distal region of the short arm.

Chromosome 5Ai-1. Present in line L5, is a submetacentric SAT chromosome and has a secondary constriction and a small satellite in the short arm. Telomeric C-bands are present in both arms, and several small interstitial C-bands are observed in the long arm.

Chromosome 6Ai-1. Present in line L7, is metacentric and similar in size to chromosomes 2Ai-1 and 4Ai-1 but does not show any C-bands.

Chromosome 7Ai-1. Present in line L1, is almost metacentric and shows a very small C-band in the proximal half of the short arm and in the distal region of the long arm.

In-situ hybridization analysis

The 18*s*.26*s* rDNA probe was used to confirm the presence of nucleolus organizer regions (Nors) on chromosomes 1Ai-1 and 5Ai-1 in the L3 and L5 addition lines. Five pairs of ISH sites were observed in L3 (Fig. 5) as well as in line L5 (Fig. 6a).

Four major rDNA gene clusters are known to be present in the chromosome complement of hexaploid wheat and these have been located on the short arms of chromosomes 1B, 6B, 5D, and 1A. A minor rDNA locus has also been reported on the long arm of chromosome 7D (Mukai et al. 1991). Therefore, the four pairs of ISH sites, observed in the addition lines L3 and L5, can be assigned to the Nors of wheat chromosomes 1B, 6B, 5D, and 1A. The remaining ISH sites are not caused by the minor rDNA site of 7DL, but by Nors located on the short arms of the added *Ag. intermedium* chromosomes 1Ai-1 in L3 and 5Ai-1 in L5. The ISH signal intensity of Nor chromosomes in L3 was 6B > 1B > 1Ai-1 > 5D > 1A, while that of line L5 was 6B > 5Ai-1 > 1B > 5D > 1A.

Because of their distinctive labeling, most Nor loci can also be identified in the interphase nucleus (Fig. 6b, see also Mukai et al. 1991), permitting direct visualization of the activity of different Nor loci in the same nucleus. Analysis of interphase nuclei show that the Nors of chromosomes 1Ai-1 and 5Ai-1 are often associated with nucleoli indicating they are active in organizing nucleoli (Fig. 6b). Nucleolar activity of chromosomes 1Ai-1 and 5Ai-1 is also indicated by the presence of secondary constrictions in the short arms of these chromosomes.

Discussion

Ag. intermedium is an autoallo-hexaploid species genomically E_1E_2X, where the E_1- and E_2-genomes are known

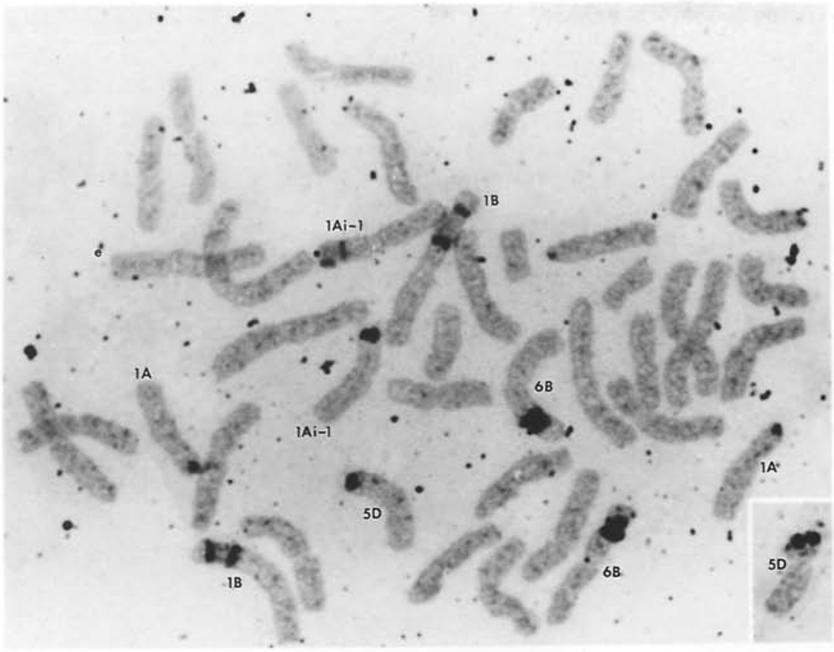

Fig. 5. In-situ hybridization labeling patterns of mitotic metaphase chromosomes of the *T. aestivum* – *Ag. intermedium* chromosome addition line 1Ai-1 using the 18*s*.26*s* rDNA probe

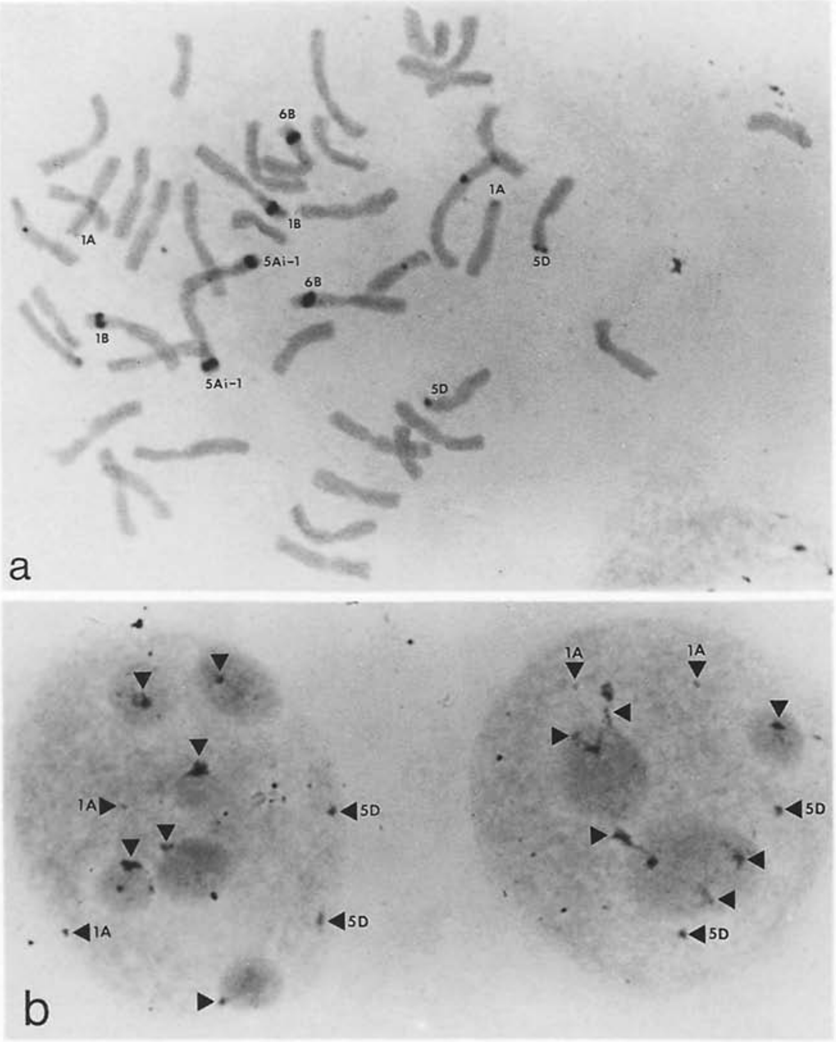

Fig. 6a, b. In-situ hybridization labeling patterns with the 18*s*.26*s* probe. **a** Mitotic metaphase chromosomes of the addition line 5Ai-1. **b** Nucleolar activity in the interphase nucleus of different nucleolar organizer regions chromosomes in the 5Ai-1 addition line to be related to the E genome of *Ag. elongatum* and the J genome of *Ag. bessarabicum* (Dvořák 1981a; Dewey 1984).

The overall C-banding pattern of the *Ag. intermedium* accession no. 75 is different from that of a Caucasian *Ag. intermedium* line described by Aizatulina et al. (1989). Only some chromosomes are similar in morphology and C-banding pattern; chromosomes C and D of line 75 resemble chromosomes 1 and 10 of the *Ag. intermedium* karyotype reported by Aizatulina et al. (1989). These differences in C-banding patterns reflect the large amount of polymorphism as well as the structural modifications which are present in this species.

The C-banding patterns and morphologies of chromosomes 1Ai-1, 3Ai-1, 4Ai-1, 5Ai-1, 6Ai-1, and 7Ai-1 present in the disomic addition lines are identical to the corresponding chromosomes present in the partial amphiploid TAF46, indicating that these chromosomes are not structurally rearranged. Chromosomes 1Ai-1, 2Ai-1, 3Ai-1, 4Ai-1, 5Ai-1, 6Ai-1, and 7Ai-1 are similar to the chromosomes designated H, U, F, R, G, S, or T and Q in *Ag. intermedium* accession 75. These results suggest that the alien chromosomes present in wheat-alien chromosome addition lines are not structurally rearranged compared to the corresponding chromosomes of the alien donor species.

Several *Ag. intermedium* chromosomes show superficial resemblance to some chromosomes of different diploid *Agropyron* species. Endo and Gill (1984) analyzed the C-banding patterns of several diploid *Agropyron* species. Their analysis revealed characteristic differences in C-banding patterns between the chromosome complement of *Ag. elongatum* and *Ag. bessarabicum*, indicating that these genomes are not completely equivalent. Whereas *Ag. elongatum* chromosomes have relatively small telomeric and interstitial C-bands, larger and only telomeric C-bands are characteristic of the chromosome complement of *Ag. bessarabicum*. However, results from karyotypic homology based on comparative chromosome size and C-banding patterns of *Ag. intermedium* chromosomes with those of the supposed ancestral species *Ag. elongatum* and *Ag. bessarabicum* were inconclusive.

Seven chromosome pairs of *Ag. intermedium* are mostly euchromatic (Fig. 2, chromosomes O–U) and show only faint C-bands. Similar, mostly euchromatic chromosomes are neither present in *Ag. elongatum* nor in *Ag. bessarabicum* suggesting that these chromosomes might have been derived from the unknown X genome.

Overall, the *Ag. intermedium* karyotype appears to be quite distinctive from the related diploid species and must have undergone a large amount of structural rearrangement.

Chromosomes 1Ai-1, 3Ai-1, and 5Ai-1 present in TAF46 and in the addition lines L3, L2, and L5 are similar in morphology and C-banding patterns to chromosomes of the diploid species *Ag. bessarabicum* (Endo and Gill 1984, chromosome designated A) and *Ag. elongatum* (Endo and Gill 1984, chromosomes designated G and B). The *Ag. intermedium* chromosomes 2Ai-1, 4Ai-1, 6Ai-1, and 7Ai-1, present in TAF46 and the addition lines L4, L7, and L1, are almost free of C-bands and, except for 7Ai-1, are also significantly smaller which might suggest that these chromosomes too may have been derived from the unknown X genome.

Lapitan et al. (1987) analyzed the ISH patterns of several diploid and polyploid *Agropyron* species using rye repeated-DNA probes pSc74 and pSc119. Whereas pSc119 produced a dispersed labeling pattern in all *Ag. elongatum* chromosomes and mainly telomeric hybridization sites in *Ag. bessarabicum* chromosomes, no hybridization was observed with probe pSc74 in these species. However, it was found that pSc74 hybridizes to the telomeric regions of eight chromosome pairs of *Ag. intermedium*. Since neither *Ag. elongatum* nor *Ag. bessarabicum*, the probable donor species of the E_1 and E_2 genomes of *Ag. intermedium*, showed hybridization with probe pSc74, it was assumed that the chromosome pairs labeled with pSc74 in *Ag. intermedium* have originated from the unknown X genome.

ISH analysis of TAF46 using probes pSc74 and pSc119 revealed no labeling site on any of the *Ag. intermedium* chromosomes (Mukai, unpublished results). This result cannot be explained satisfactorily at present but may perhaps be caused by different stringencies of hybridization in both experiments. Further analyses are necessary to determine the genomic relationships of the *Ag. intermedium* chromosomes present in TAF46 and in the derived chromosome addition lines.

Chromosome 4Ai-1, present in addition line L4, differs in C-banding pattern from a chromosome also derived from *Ag. intermedium*, which specifies resistance to wheat streak mosaic virus and substitutes for chromosomes 4A and 4D of wheat (Friebe et al. 1991). This *Ag. intermedium* chromosome, designated 4Ai-2, is similar in morphology and banding pattern to chromosome K of the *Ag. intermedium* accession 75. Furthermore, the chromosome designated C in the *Ag. intermedium* karyotype shown in Fig. 2 is almost identical in C-banding pattern and morphology to *Ag. intermedium* chromosomes present in the wheat-*Agropyron* chromosome substitution lines developed by Wienhues (1966). This *Ag. intermedium* chromosome, designated 7Ai-2, conditions resistance to leaf, stripe, and stem rust and substitutes for the loss of wheat chromosomes 7A and 7D (Friebe et al. 1992).

Thus, nine out of 21 chromosomes of *Ag. intermedium* have been assigned to the homoeologous groups of the *Triticeae*. Further analyses are necessary to establish the homoeologous relationships of all *Ag. intermedium* chromosomes and to determine their genomic affinities. This information will be valuable in genetic introgression of useful traits from *Ag. intermedium* into wheat as well as in basic studies of genome evolution in the *Triticeae*.

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