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Characterization of wheat-alien translocations conferring resistance to diseases and pests: current status *

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Summary

Wild relatives of common wheat, *Triticum aestivum*, and related species are an important source of disease and pest resistance and several useful traits have been transferred from these species to wheat. C-banding and *in situ* hybridization analyses are powerful cytological techniques allowing the detection of alien chromatin in wheat. C-banding permits identification of the wheat and alien chromosomes involved in wheat-alien translocations, whereas genomic *in situ* hybridization analysis allows determination of their size and breakpoint positions. The present review summarizes the available data on wheat-alien transfers conferring resistance to diseases and pests. Ten of the 57 spontaneous and induced wheat-alien translocations were identified as whole arm translocations with the breakpoints within the centromeric regions. The majority of transfers (45) were identified as terminal translocations with distal alien segments translocated to wheat chromosome arms. Only two intercalary wheat-alien transloctions were identified, one induced by radiation treatment with a small segment of rye chromosome 6RL (*H25*) inserted into the long arm of wheat chromosome 4A, and the other probably induced by homoeologous recombination with a segment derived from the long arm of a group 7 *Agropyron elongatum* chromosome with *Lr19* inserted into the long arm of 7D. The presented information should be useful for further directed chromosome engineering aimed at producing superior germplasm.

Introduction

Genetic erosion caused by modern cultivation procedures has narrowed the genetic base of many crops, including common wheat, *Triticum aestivum* L. Many wild relatives and related species can be succesfully crossed with bread wheat (Sharma & Gill, 1983; Baum et al., 1992; Jiang et al., 1994a; Sharma, 1995). These species represent a large reservoir of useful traits that can be exploited for wheat improvement. The buffered polyploid nature of common wheat tolerates chromosome engineering at a much higher level than do diploid species. Many agronomically interesting traits, including resistance to diseases and pests, stress and salt tolerance, and winterhardiness have been transferred from these species to wheat (for review see Zeller & Hsam, 1983; Gale & Miller, 1987, Knott, 1987; McIntosh, 1991; Islam & Shepherd, 1992; Jiang et al., 1994a).

The chromosomes of hexaploid common wheat can be grouped into seven homoeologous sets, each group consisting of three pairs from each of the A, B, and D genomes. Homoeologous chromosomes in wheat have similar gene contents and can replace and compensate for each other in nullisomic-tetrasomic combinations (Sears, 1952b, 1966b). Similarly, alien chromosomes can compensate for the loss of homoeologous wheat chromosomes. Compensating translocations between homoeologous wheat and alien chromosomes, chromosome arms, or chromosome segments are agronomically desirable, whereas noncompensating translocations cause duplications and deficiencies that usually prevent their use in cultivar improvement.

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The method for transferring genes from related species to wheat largely depends on the evolutionary distance between the species involved. Species belonging to the primary gene pool of common wheat share homologous genomes. This group includes landraces of *T. aestivum*, the wild and cultivated forms of *T. turgidum* L., and the donor species of the A and D genomes of bread wheat, *T. monococcum* L., with the varieties *boeoticum* and *urartu*, and *Aegilops tauschii* Coss. Gene transfer from these species can be achieved by direct hybridization, homologous recombination, backcrossing, and selection. Many genes conferring resistance to diseases and pests have been transferred using this method and several of them are still being exploited in cultivar improvement (McIntosh, 1991).

The secondary gene pool of common wheat includes the polyploid *Triticum/Aegilops* species that have at least one homologous genome in common with *T. aestivum*. Gene transfer from these species by homologous recombination is possible, if the target gene is also located on a homologous chromosome. This group also includes the tetraploid species *T. timopheevii* Zhuk. with its varieties *timopheevii* Zhuk. and *araraticum* Jakubz. and the diploid S-genome species belonging to the *Aegilops* section *Sitopsis*, which are related to the B genome of *T. aestivum*. These species have contributed several resistance genes that are used in cultivar improvement (McIntosh, 1991).

Species belonging to the tertiary gene pool are more distantly related. Their chromosomes are not homologous to those of wheat. Chromosome pairing and recombination in common wheat is largely governed by the gene *Ph1*, located on the long arm of chromosome 5B, which ensures that only homologous chromosomes can pair and recombine (Riley & Chapman, 1958; Sears & Okamoto, 1958; Sears, 1976). Other strategies need to be employed, because gene transfer from these species cannot be achieved by homologous recombination.

For the transfer of whole chromosome arms, the centricbreakage-fusion mechanism of univalents at meiotic metaphase I can be exploited (Sears, 1952a). Univalents have a tendency to break at the centromere, followed by fusion of the broken arms. When an alien target chromosome and its homoeologous wheat chromosome are simultaneously univalent, compensating whole arm translocations can be recovered at fairly high frequencies (Lukaszewski, 1993; Marais & Marais, 1994).

To transfer alien segments that are smaller than complete chromosome arms, two strategies are commonly used. Sears (1956) used ionizing radiation treatment to induce chromosome breaks and thereby transferred a gene conditioning resistance to leaf rust caused by *Puccinia recondita* f. sp. *tritici* Rob. ex Desm. from *Ae. umbellulata* Zhuk. to wheat. The second approach for transferring small, nonhomologous alien segments was pioneered by Riley et al. (1968a, b). By disrupting normal meiotic chromosome pairing using a high-pairing line of *Ae. speltoides* Tausch a gene conditioning resistance to stripe rust caused by *P. striiformis* f. sp. *tritici* Westend. from *Ae. comosa* ssp. *comosa* Sm. in Sibth. et Sm. was transferred to wheat by induced homoeologous recombination.

Both radiation treatment and induced homoeologous recombination have been widely used for transferring alien chromatin with novel genes to wheat. The products were characterized by meiotic chromosome pairing, monosomic analysis, telocentric mapping, and by analyzing morphological and biochemical traits. Recently, more sensitive cytological methods were developed, which allow the identification and monitoring of alien chromatin transfers to wheat. Chromosome banding methods, especially C-banding, permit a fast and reliable identification of all 21 chromosome pairs of the A, B, and D genomes of wheat and can also be used to identify many chromosomes from related species (Gill et al., 1991). *In situ* hybridization (ISH), using total genomic DNA from a donor species in combination with an excess amount of unlabeled genomic blocking DNA from the wheat recipient as probe (GISH), allows determination of translocation breakpoints and the sizes of transferred alien segments (Le et al., 1989).

We have used these methods for characterizing wheat-alien translocations and we recently, reported on radiation-induced transfers (Friebe et al., 1995c). More recently, several new wheat-alien transfers were characterized. In the present review, we summarize the available data on spontaneous and induced wheat-alien genetic transfers. These data will allow further directed chromosome engineering aimed at producing agronomically superior germplasms. Translocation chromosomes were designated according to the nomenclature proposed by Gill et al. (1991) and Raupp et al. (1995), where 'S' = genetically short arm, 'L' = genetically long arm, 'T' = translocation, 'Ti' = intercalary translocation, '·' = centromeric breakpoint, '-' = interstitial breakpoint, '/' = unknown breakpoint, and the number sign '#' is used to distinguish between different chromosomes belonging to the same homoeologous group).

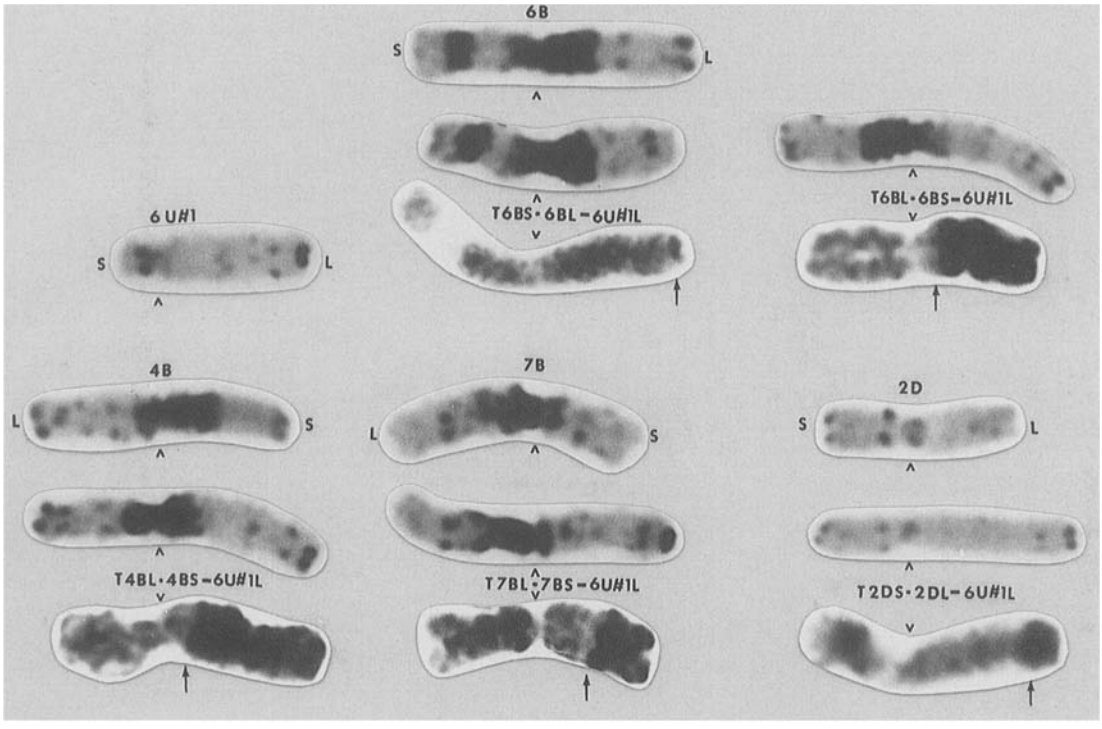

Figure 1. C-banding and GISH patterns of the chromosomes involved in the *Lr9* transfer derived from *Ae. umbellulata* (arrows indicate translocation breakpoinst, arrowheads point to the centromeres, modified after Friebe et al., 1995a)

Transfers derived from *Aegilops* species

Lr9 *from* Ae. umbellulata *(Transfer)*

Radiation treatment, for inducing chromosome breakage and recombining alien chromatin with that of wheat, was first used by Sears (1956), who transferred *Lr9* for leaf rust resistance (Soliman et al., 1963; McIntosh et al., 1965) from the long arm of a group 6 *Ae. umbellulata* chromosome, 6U#1 (Athwal & Kimber, 1972), to wheat. At least 17 different leaf rust resistant wheat-*Ae. umbellulata* translocations were produced. However, only one line, designated Transfer, involved homoeologous chromosome arms and showed normal male and female transmission (Sears, 1972). This compensating translocation was first believed to be an intercalary translocation, but was later shown to be also a terminal transfer of a 6UL segment to the distal region of 6BL (Sears, 1961, 1966a, 1981).

Five of these translocations still maintained at the University of Columbia, MO, USA, were analyzed by C-banding and GISH. Lines T40 (P92–40.1–1), T41 (P92–41.1–1), T44 (P92–44.1–1), T47 (P92–47.1–1), and T52 (P92–52.1–1) were identified as T6BL·6BS–6U#1L, T4BL·4BS–6U#1L, T2DS·2DL–6U#1L, T6BS·6BL–6U#1L (Transfer), and T7BL·7BS–6U#1L, respectively (Figure 1) (Friebe et al., 1995a). The breakpoints and sizes of the transferred *Ae. umbellulata* segments determined by GISH are given in Table 1. The sizes of the transferred 6UL segments range from 0.41 μm in T6BS·6BL–6U#1L to 5.08 μm in T4BL·4BS–6U#1L. These results are in agreement with earlier reports based on meiotic chromosome pairing (Sears, 1956, 1966a, 1972). Recently, molecular markers closely linked to *Lr9* were identified (Schachermayr et al., 1994; Autrique et al., 1995). *Lr9* from Transfer was used in some soft red winter wheat cultivars (e.g. Arthur 71) in the United States but never intensively, probably because the translocation reduces grain yield. Virulence for *Lr9* occurred in the United States in 1971 (Shaner et al., 1972; McIntosh et al., 1995b), indicating that alien genes provide no assurance of durable resistance.

Table 1. Transfers derived from *Aegilops* species

Germplasm	Alien species	Alien target genes	Description	Size of alien translocation	Size of missing segment	Fraction length of translocation breakpoint	Mode of transfer	Type	Contribution to agriculture
Transfer (T47)	*Ae. umbellulata*	*Lr9*	T6BS·6BL–6U#1L	0.41 μm	0.51 μm of 6BL	0.92	Irradiation	C	+
T40	*Ae. umbellulata*	*Lr9*	T6BL·6BS–6U#1L	4.65 μm	3.29 μm of 6BS	0.23	Irradiation	N	—
T41	*Ae. umbellulata*	*Lr9*	T4BL·4BS–6U#1L	5.08 μm	2.90 μm of 4BS	0.23	Irradiation	N	—
T44	*Ae. umbellulata*	*Lr9*	T2DS·2DL–6U#1L	1.66 μm	0.19 μm of 2DL	0.71	Irradiation	N	—
T52	*Ae. umbellulata*	*Lr9*	T7BL·7BS–6U#1L	2.84 μm	1.13 μm of 7BS	0.48	Irradiation	N	—
2A/2M#4/2	*Ae. speltoides*	*Lr28*	T4AS·4AL–7S#2S				Homoeologous recombination	C	—
2A/2M#3/8	*Ae. speltoides*	*Lr28*	T4AS·4AL–7S#2S				Homoeologous recombination	C	—
C95.24	*Ae. speltoides*	*Sr32*	T2AL·2S#1L–2S#1S				Homoeologous recombination	C	—
C82.1	*Ae. speltoides*	*Sr32*	T2BL/2S#1S				Homoeologous recombination	C	—
C82.2	*Ae. speltoides*	*Sr32*	T2DL–2S#1L·2S#1S				Homoeologous recombination	C	—
RL5711	*Ae. speltoides*	*Lr35/Sr39*	T2B/2S#2				Homoeologous recombination	C	—
CI17884	*Ae. speltoides*	*Gb5*	T7AS–7S#1S·7S#1L	8.54 μm	0.63 μm of 7AS*	0.85	Irradiation	C	—
R1A	*Ae. longissima*	*Pm13*	T3BL·3BS–3Sl#1S				Homoeologous recombination	C	—
R1D	*Ae. longissima*	*Pm13*	T3DL·3DS–3Sl#1S				Homoeologous recombination	C	—
Compair	*Ae. comosa*	*Yr8/Sr34*	T2DS–2M#1L·2M#1S				Homoeologous recombination	N	—
2A–2M#4/2	*Ae. comosa*	*Yr8/Sr34*	T2AS–2M#1L·2M#1S				Homoeologous recombination	N	—
2D–2M#3/8	*Ae. comosa*	*Yr8/Sr34*	T2DS–2M#1L·2M#1S				Homoeologous recombination	C	—

C = compensating, N = non-compensating, ++ = significant, + = some, — = none * size of the wheat segment present

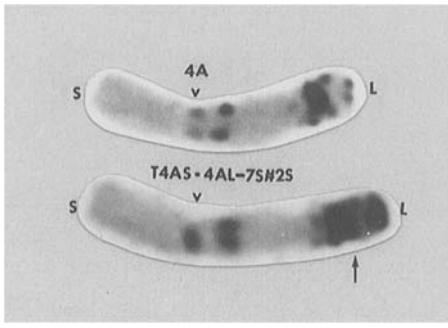

Figure 2. C-banding patterns of the chromosomes involved in the *Lr28* transfer derived from *Ae. speltoides* (Friebe et al., unpublished)

Lr28 *from* Ae. speltoides

Riley and co-workers used a high pairing line of *Ae. speltoides* for inducing homoeologous recombination to transfer *Yr8*, a gene for stripe rust resistance, from *Ae comosa* ssp. *comosa* to wheat (Riley et al., 1968a, b). *Yr8* is present in a 2D/2M translocation line designated Compair. Besides the Compair-translocation, several other stripe rust resistant wheat-*Ae. comosa* translocations were produced (Miller et al., 1988) and two of them, 2D/2M#3/8 and 2A/2M#4/2 were shown to have a leaf rust resistance gene, *Lr28*, derived from *Ae. speltoides* (McIntosh et al., 1982). The chromosomal location of *Lr28* was determined by monosomic analysis, and by telocentric mapping, this gene was mapped 39 centimorgans from the centromere in the long arm of wheat chromosome 4A (McIntosh et al., 1982).

C-banding analysis confirmed these results and showed that in lines 2D/2M#3/8 and 2A/2M#4/2, the subterminal C-band 4AL2.3 is larger than that in *T. aestivum* cv. Chinese Spring (Figure 2) (Gill et al., 1991) and other wheat cultivars. (Friebe & Gill, 1994). RFLP analysis showed that the probes pTksuG10 and pPSR1051, which are group 4L markers, and pCDO1400, a group 7S marker, are present in line 2A/2M#4/2, whereas the adjacent distal group 7 short arm probe pPSR160, was missing in line 2D/2M#3/8, mapping the breakpoint in 4AL2.6 (Mickelson-Young, unpublished data).

Chromosome 4A of *T. turgidum* and *T. aestivum* is involved in a cyclical translocation with chromosomes 5A and 7B (Naranjo et al., 1987, 1988: Liu et al., 1992: Devos et al., 1995; Mickelson-Young et al., 1995). The distal region of the 4AL arm was derived from 7BS. Because the *Lr28* transfer was produced by homoeologous recombination, the transferred segment having *Lr28* most likely derived from the short arm of the *Ae. speltoides* chromosome 7S#2, resulting in the translocation chromosome T4AS·4AL–7S#2S.

Lr28 is not associated with deleterious characters and is present in cultivar Sunland released in Australia. Whereas this gene is widely effective in Australia, South Asia, and Europe, most *P. recondita* f. sp. *tritici* isolates in North America are virulent (McIntosh et al., 1995b).

Sr32 *from* Ae. speltoides

Sears used homoeologous recombination to transfer a gene conditioning resistance to stem rust (*P. graminis* f. sp. *tritici* Eriks. & Henn.), *Sr32*, from a group 2 *Ae. speltoides* chromosome, 2S#1, to wheat chromosomes 2A, 2B, and 2D (C82.1 = P80–14.1–2, C82.2 = P80–139.1–4, C82.3 = P80–132.2–2, C82.4 = P80–153.1–2) (McIntosh, 1991). The translocation involving chromosome 2A (C95.24, obtained from Dr. E. R. Sears in 1969) had adherent glumes, whereas the 2B–2#1S and 2D–2#1S translocations did not show this character. C-banding analysis revealed that the translocation chromosome in line C82.1 consists of the complete short arm of the *Ae speltoides* chromosome 2S#1 and most of the long arm of chromosome 2B of wheat with the breakpoint between the centromere and the proximal C-band 2BL1.5 (Figure 3). The C-banding patterns of the 2A–2S#1S and 2D–2S#1S translocation chromosomes present in lines C95.24 and C82.2 are very similar to each other, both consisting of the complete short arm of 2S#1, most of the long arm of 2S#1 (with two small, but diagnostic distally located C-bands), and small unbanded segments derived from either 2AL (C95.24) or 2DL (C82.2), respectively (Figure 3). *Sr32* has not been used in cultivar improvement (McIntosh et al., 1995b).

Lr35 *and* Sr39 *from* Ae. speltoides

Kerber and Dyck (1990) transferred *Lr35* for adult-plant leaf rust resistance, and *Sr39* for stem rust resistance by homoeologous recombination from an *Ae. speltoides* chromosome, 2S#2, to wheat chromosome 2B. The breakpoint in the T2B/2S#2 tranlocation chromosome could not be determined by C-banding analysis. The translocation chromosome probably consists of segments derived from both arms of 2S#2 (Figure 4).

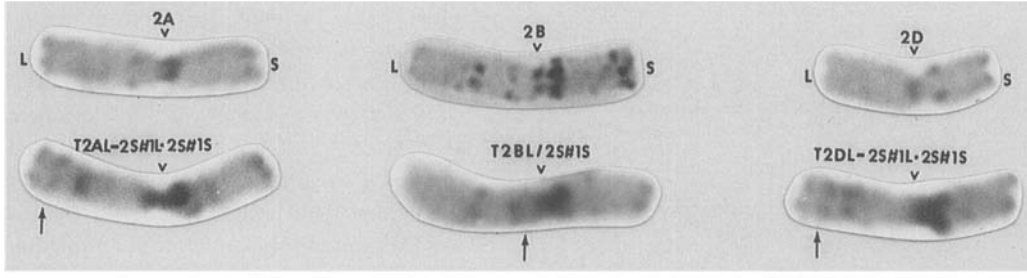

Figure 3. C-banding patterns of the chromosomes involved in the *Sr32* transfer derived from *Ae. speltoides* (Friebe et al., unpublished)

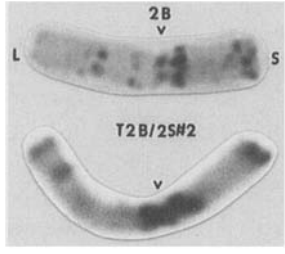

Figure 4. C-banding patterns of the chromosomes involved in the *Lr35/Sr39* transfer derived from *Ae. speltoides* (Friebe et al., unpublished)

Lr36 *from* Ae. speltoides

Ae. speltoides-derived genes conferring resistance to leaf rust were also transferred by Dvorak and co-workers to wheat chromosomes 1B and 6B (Dvorak, 1977; Dvorak & Knott, 1980, 1990). The gene on chromosome 6BS was designated *Lr36* (McIntosh, 1991). Neither *Lr35/Sr39* nor *Lr36* have been exploited in cultivar improvement (McIntosh et al., 1995b).

Yr8/Sr34 *from* Ae. comosa *ssp.* comosa *(Compair)*

The wheat-*Ae. comosa* translocation in Compair has *Yr8* for stripe rust resistance, and in addition *Sr34* for stem rust resistance (McIntosh et al., 1982). *Yr8* and *Sr34* are also present in the independently produced wheat-*Ae. comosa* translocation lines 2D/2M#3/8 and 2A/2M#4/2 (McIntosh et al., 1982; Miller et al., 1988).

C-banding analysis confirmed the 2D/2M translocation in Compair and showed the translocation to consist of the complete short arm of 2M, a large part of the long arm of 2M, and a distal segment with a telomeric C-band derived from 2DS (Figure 5). The C-banding pattern of the wheat-*Ae. comosa* translocation present in 2D/2M#3/8 is very similar to the Compair-translocation and can also be described as T2DS–2M#1L·2M#1S. In line 2A/2M#4/2 the translocation chromosome was identified as T2AS–2M#1L·2M#1S, lacking the telomeric C-band but showing a small but diagnostic C-band derived from the 2AS arm. C-banding confirmed the structure of the translocation chromosomes determined earlier from meiotic pairing analysis (Miller et al., 1988). Because all three translocations were produced by homoeologous recombination, they should involve homoeologous chromosome arms. However, C-banding analysis revealed that in each case the breakpoints are located in the longer arm of the *Ae. comosa* chromosome 2M#1, whereas the wheat segments were derived from the short arms of either chromosome 2D or 2A. These results might reflect a rearranged structure of chromosome 2M#1. *Yr8* and *Sr34* have not been exploited in cultivar improvement (McIntosh et al., 1995b).

Gb5 *from* Ae. speltoides

Wells and co-workers (Lay et al., 1971; Wells et al., 1973, 1982) transferred *Gb5* conditioning resistance to greenbug (*Schizaphis graminum* Rond. (syn. *Toxoptera graminum* Rond.)), (Tyler et al., 1985, 1986, 1987), from a group 7 *Ae. speltoides* chromosome to 7A of wheat. The same irradiation experiment also led to the recovery of the wheat-*Agropyron intermedium* (Host) Beauvois (syn. *Thinopyrum intermedium* (Host) Barkworth & Dewey)) translocation T4DL·4Ai#2S, with *Wsm1* for resistance to wheat streak mosaic virus. C-banding and ISH patterns, using the highly repetitive rye DNA probe pSc119, suggested that *Gb5* was located on an *Ae. speltoides* chromosome 7S#1, substituting for wheat chromosome 7A in germplasms CI17883, CI17884, and CI17885 (Friebe et al., 1991a). However, meiotic pairing analysis in hybrids showed that the short arm of this chromosome paired with the short arm of wheat chromosme 7A in 97% of pollen mother cells (Lukaszewski, personal communication; Friebe et al., 1995c; Gill et al., 1996) Therefore,*Gb5* must be

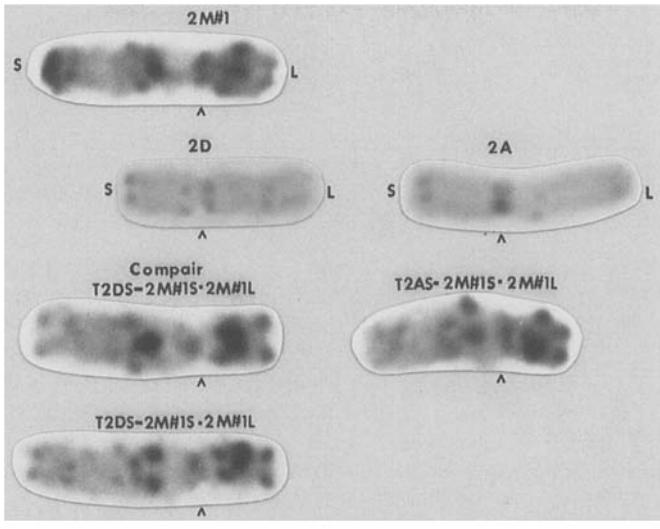

Figure 5. C-banding patterns of the chromosomes involved in the *Yr8/Sr34* transfer derived from *Ae. comosa* (Friebe et al., unpublished)

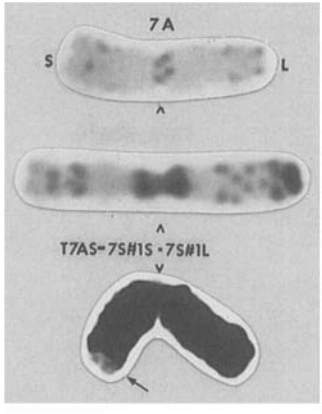

Figure 6. C-banding and GISH patterns of the chromosomes involved in the *Gb5* transfer derived from *Ae. speltoides* (modified after Friebe et al., 1995c)

located on a wheat-*Ae. speltoides* translocation chromosome described as T7S#1L·7S#1S–7AS, consisting of the complete long arm of 7S#1, most of the short arm of 7S#1, and a very small, 0.63 μm, distal segment derived from 7AS. The breakpoint is at FL 0.85 (Figure 6, Table 1). *Gb5* has not been exploited in wheat improvement (McIntosh, 1991).

Pm12 *from* Ae. speltoides

Miller et al. (1987) transferred *Pm12*, conferring resistance to powdery mildew (*Erysiphe graminis* DC., (syn. *Blumeria graminis* (DC. E. O. Speer) f. sp. *tritici*, from *Ae. speltoides* to wheat chromosome 6A. *Pm12* has not contributed to cultivar improvement (McIntosh 1991).

Pm13 *from* Ae. longissima

Ceoloni et al. (1988, 1992) used induced homoeologous recombination to transfer *Pm13* conferring resistance to powdery mildew, from the short arm of chromosome $3S^l$#1 of *Ae. longissima* Schweinf. et Muschl. to wheat chromosome arms 3BS and 3DS. The $3S^l$#1S arm has a prominent diagnostic telomeric C-band, which is also present in the T3BL·3BS–$3S^l$#1S (R1A) and T3DL·3DS–$3S^l$#1S (R1D) translocation chromosomes (Figure 7). The C-banding patterns of these translocations indicate that the breakpoints are located very close to the telomeres in the short arms. Recently meiotic pairing and RFLP analyses showed that the sizes of the transferred $3S^l$#1 segments in these translocations were different (Donini et al., 1995). *Pm13* is now being introduced into advanced durum and bread wheat lines (Ceoloni et al., 1996).

Pch1 *and* Sr38/Lr37/Yr17 *from* Ae. ventricosa *(Roazon, Rendevous, VPM1)*

Doussinault and co-workers transferred *Pch1* for resistance to eyespot caused by *Pseudocercosporella herpotrichoides* (Fron) Dreighton from *Ae. ventricosa* Tausch to wheat (Doussinault et al., 1983). *Pch1* is located on chromosome arm 7DL (Jahier et al., 1979, 1989; Worland et al., 1988) and is closely linked with

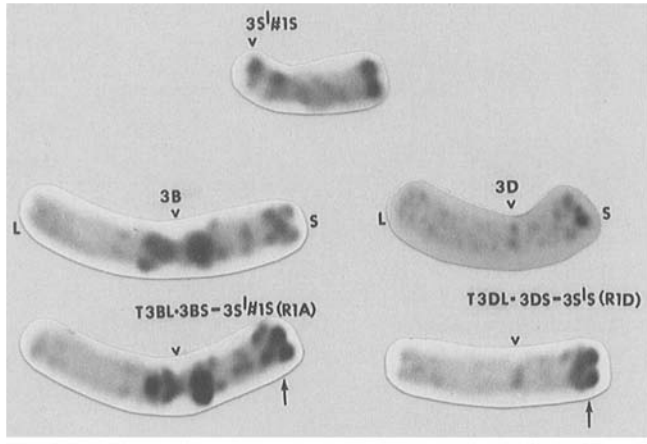

Figure 7. C-banding patterns of the critical chromosomes involved in the *Pm13* transfer derived from *Ae. longissima* (Friebe et al., unpublished)

an *Ae. ventricosa* derived gene, *Ep-D1b*, for endopeptidase (McMillan et al., 1986; Koebner et al., 1988; Law et al., 1988; Vahl & Müller, 1991). The C-banding patterns of the translocated 7DL arms (the cytologically shorter arms) in cultivars Rendevous and Roazon are similar to 7DL of Chinese Spring wheat (Martin, 1991). This is caused by the similarities in C-banding patterns of chromosome 7D of *Ae. ventricosa* and 7D of *T. aestivum*, making it impossible to visualize this translocation by C-banding or GISH. *Pch1* has been used in wheat improvement and was transferred to several germplasms and cultivars (Roazon, VPM1, and Rendevous in Europe; and Madsen and Hyak in the United States).

Bariana & McIntosh (1993, 1994) and Bonhomme et al. (1995) showed that VPM1 also had *Ae. ventricosa*-derived genes *Lr37* for leaf rust resistance, *Sr38* for stem rust resistance, and *Yr17* for stripe rust resistance, which were derived from chromosome 6M^{v} and mapped to the short arm of wheat chromosome 2A. The rust resistance genes are being used in cultivars (Trident, Sunbri) in Australia.

Transfers derived from *Triticum timopheevii* ssp. *timopheevii* and ssp. *araraticum*

Sr36/Pm6 *from* T. timopheevii *ssp.* timopheevii

T. timopheevii var. *timopheevii* is the source of stem rust resistance gene *Sr36*, which was transferred to wheat chromosome 2B (Allard and Shands, 1954; Nyquist, 1957, 1962). *Sr36* is closely linked with the powdery mildew resistance gene, *Pm6,* which also originated from *T. timopheevii* ssp. *timopheevii* (McIntosh & Gyarfas, 1971; McIntosh & Luig, 1973; Jorgensen & Jensen, 1973; McIntosh, 1991). The C-banding pattern of the T2B/2G#1 translocation present in the Australian derivative Timvera, suggests that segments derived from both arms of 2G#1 are present, but did not locate the exact breakpoints in this translocation (Figure 8). Genetic analysis indicated that *Sr36* is located in the short arm, wheareas *Pm6* mapped in the long arm of the translocation chromosome (McIntosh, unpublished data). The *Sr36/Pm6* transfer has been used in germplasms in North America (Arthur and its derivatives Hand, Kenosha, Roughrider, Vernum, Wisconsin Supremo), Australia (Timvera, Mendos, Timgalen, Cook, Songlen), South Africa (Dipka, Flamink, Gouritz) and in Kenya and Ethiopia (McIntosh et al., 1995b).

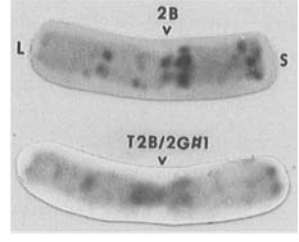

Figure 8. C-banding patterns of the chromosomes involved in the *Sr36/Pm6* (Timvera) transfer derived from *T. timopheevii* ssp. *timopheevii* (Friebe et al., unpublished)

Sr37 *from* T. timopheevii *ssp.* timopheevii

Sr37 was transferred to wheat chromosome 4B (Gyarfas, 1968; McIntosh & Gyarfas, 1971; McIntosh,

Table 2. Transfers from *Triticum timopheevii*

Germplasm	Alien species	Alien target genes	Description	Size of alien translocation	Size of missing segment	Fraction length of translocation breakpoint	Mode of transfer	Type	Contribution to agriculture
C747	*T. timopheevii* ssp. *timopheevii*	*Sr36/Pm6*	T2B/2G#1				Homoeologous recombination	C	++
Line W	*T. timopheevii* ssp. *timopheevii*	*Sr37*	T4B/4G#1				Homoeologous recombination	C	—
Thatcher/*Lr18*	*T. timopheevii* ssp. *timopheevii*	*Lr18*	T5BS·5BL–5G#1L				Homoeologous recombination	C	—
RL6087	*T. timopheevii* ssp. *araraticum*	*Sr40*	T2BL/2G#2S				Homoeologous recombination	C	—

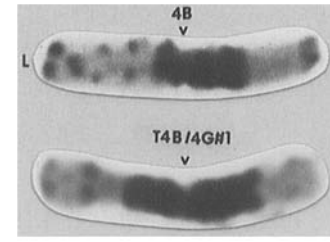

Figure 9. C-banding patterns of the chromosomes involved in the *Sr37* transfer derived from *T. timopheevii* ssp. *timopheevii* (Friebe et al., unpublished)

1991). *Sr37* was considered to be located on chromosome 4G present in a 4G(4B) substitution line (SrTt–2) (Dvorak, 1983), although meiotic pairing analysis suggested that this chromosome was involved in a translocation with chromosome 4B (McIntosh, unpublished data). The short arm of the T4B/4G#1 translocation chromosome is lacking the telomeric 4BS C-band, but has an additional small diagnostic C-band derived from the short arm of 4G (Figure 9). Because of similarities in C-banding patterns of 4B and 4G, however, the exact breakpoint in this translocation could not be determined. *Sr37* has not contributed to cultivar improvement (McIntosh et al., 1995b).

Lr18 *from* T. timopheevii *ssp.* timopheevii

T. timopheevii ssp. *timopheevii* contributed the leaf rust resistance gene *Lr18* that was transferred to the long arm of wheat chromosome 5B (McIntosh, 1983), and is associated with a *T. timopheevii* derived telomeric band of the 5GL arm (Yamamori, 1994). The translocation chromosome consists of the short arm of 5B, part of the long arm of 5B, and a terminal segment derived from 5G#1, T5BS·5BL–5G#1L (Fig, 10). *Lr18* has not been used intensively in wheat cultivars (McIntosh et al., 1995b).

Sr40 *from* T. timopheevii *ssp.*araraticum

Stem rust resistance gene *Sr40*, was transferred from *T. timopheevii* ssp. *araraticum* to the short arm of wheat chromosome 2B (Dyck, 1992). The short arm of the translocation chromosome has a prominent telomeric C-band derived from 2G#2, whereas the C-banding pattern of the long arm is similar to 2BL of wheat, thus confirming the T2BL/2G#2S translocation (Figure 11). However, the exact translocation breakpoint could

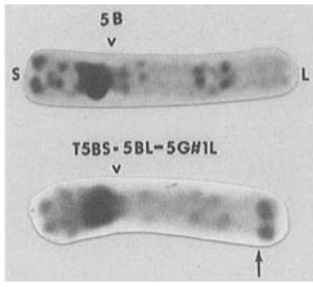

Figure 10. C-banding patterns of the chromosomes involved in the *Lr18* transfer derived from *T. timopheevii* ssp. *timopheevii* (Friebe et al., unpublished)

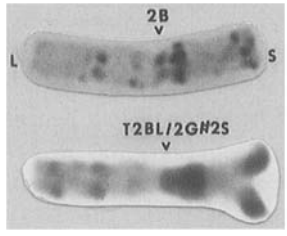

Figure 11. C-banding patterns of the chromosomes involved in the *Sr40* transfer derived from *T. timopheevii* ssp. *araraticum* (Friebe et al., unpublished)

not be determined. *Sr40* has not been used in wheat improvement (McIntosh et al., 1995b).

Transfer derived from *Haynaldia villosa*

Chen and co-workers (Chen et al., 1995) transfered the powdery mildew resistance gene *Pm21* from *Haynaldia villosa* (L.) Schur. (syn. *Dasypyrum villosum* (L.) Candargy) to common wheat. The translocation chromosome consists of the short arm of the *H. villosa* chromosome 6V#1 translocated to the long arm of wheat chromosome 6A, with the breakpoint at the centromere, T6AL·6V#1S.

Transfers derived from *Agropyron* species

Lr19/Sr25 *from* A. elongatum *(Agatha)*

Knott and co-workers (Sharma & Knott, 1966; Knott, 1968, Dvorak & Knott, 1977) used radiation treatment to transfer leaf rust resistance gene *Lr19* and stem rust resistance gene *Sr25* (McIntosh et al., 1977) from the long arm of a group 7 *A. elongatum* (Host) Beauvois (syn. *Thinopyrum elongatum* (Host) Dewey)) chromosome to the long arm of wheat chromosome 7D. The breakpoints are located in the cytologically shorter arms of 7D and 7Ae#1, which were shown to be homoeologous to the genetically long arms of group 7 chromosomes (Werner et al., 1992; Kim et al., 1993). The T7DS·7DL–7Ae#1L translocation present in cultivar Agatha (Figure 12) has a size of 2.55 μm, replacing a 2.62 μm long distal segment of 7DL (Table 3) (Friebe et al., 1994b).

The *A. elongatum* segment in Agatha also has an undesirable gene(s) for yellow flour pigmentation. Knott (1980, 1984, 1989) used EMS-treatment to produce lines with reduced pigmentation. Two lines were obtained and designated Agatha–28 and Agatha–235. C-banding and GISH patterns of the Agatha–28 translocation chromosome are very similar to those of the original Agatha translocation (Figure 12), indicating that reduced pigmentation is probably caused by a mutation in the pigmentation gene. However, in Agatha–235, the transferred *A. elongatum* segment is smaller (1.99 μm) and is inserted between FLs 0.31 and 0.75 in the long arm of 7D. The translocation chromosome can be described as T7DS·7DL–7Ae#1L–7DL (Figure 12 Table 3). This line only expresses leaf rust resistance, presumably *Sr25* was lost along with the gene for yellow pigmentation (Friebe et al., 1994b).

Putative homoeoalleles of *Lr19* and *Sr25* were transferred from *A. distichum* (Thun.) Löve (syn. *Thinopyrum distichum* (Thun.) Löve) to wheat (Marais et al., 1988; Marais, 1992a, b). According to Marais & Marais (1990) the cultivar Indis has a translocation chromosome with most of the long arm of wheat chromosome 7D replaced by a *T. distichum* segment . The C-banding and GISH patterns of the translocation chromosome present in Indis are very similar to those of the translocation present in Agatha (Figure 12). The alien segment has similar proximal and subterminal C-bands and the breakpoint is also located in a similar region. Furthermore, in common with Agatha, the transferred alien segment in Indis has genes for yellow endosperm pigmentation and both translocation chromosomes have a segregation-distortion factor(s) (Zhang & Dvorak, 1990; Marais, 1990). These results suggest that the Agatha- and Indis-translocations were derived from the same *Agropyron/Thinopyrum* source.

Genes *Lr19/Sr25* were also transferred to wheat by induced homoeologous recombination (Sears 1973, 1977). Transfers 7Ag#1, 7Ag#2, 7Ag#3, and 7Ag#7, together with Agatha were backcrossed to several Australian wheat cultivars. The degree of preferential transmission for the first three lines and Agatha depend-

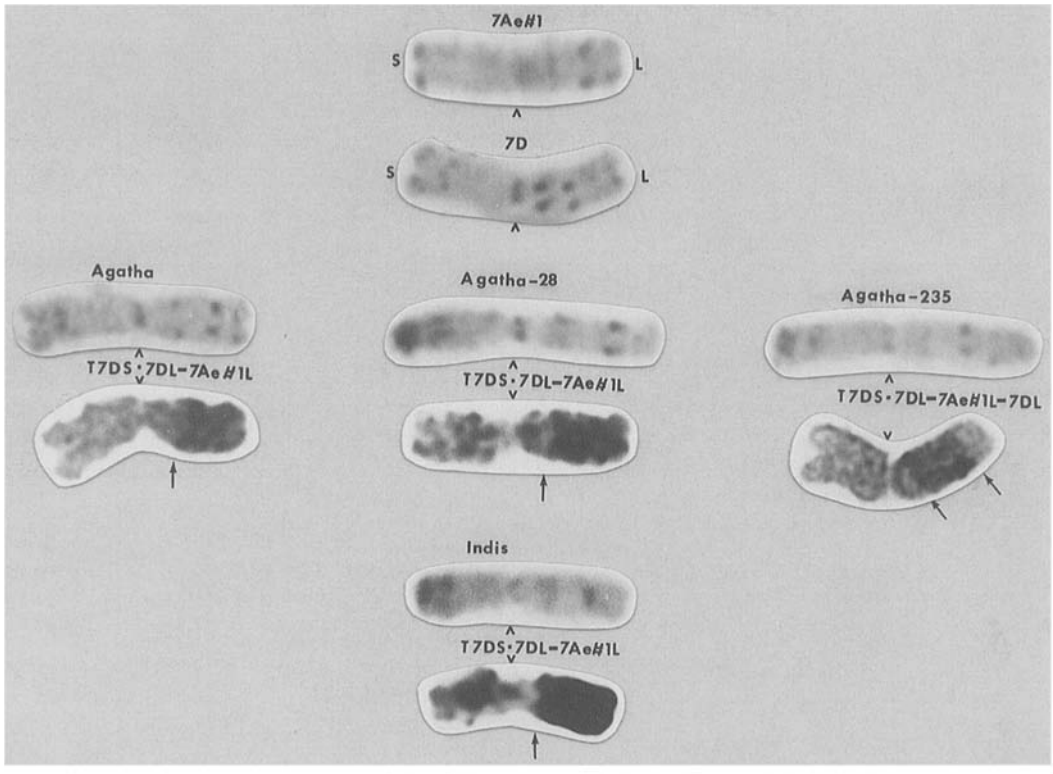

Figure 12. C-banding and GISH patterns of the chromosomes involved in the *Lr19/Sr25* transfer derived from *A. elongatum* (modified after Friebe et al., 1994b)

ed upon the recurrent parent, whereas the segment of 7Ag#7 was not preferentially transmitted (McIntosh et al., 1995b). C-banding analysis suggests that transfer 7Ag#7 might have a terminal wheat segment.

Lr19 was used in wheat cultivars in Sweden (Sunnan) and in Mexico (Oasis 86) (McIntosh et al., 1995b). However, the association of *Lr19* with undesirable yellow flour pigmentation has so far, prevented its broader use in wheat improvement. Lines with reduced levels of pigmentation obtained from Agatha (Knott, 1980, 1984, 1989) and Indis (Marais, 1992a) may have greater potential in wheat breeding. Virulence for *Lr19* was recently detected in *P. recondita* f. sp. *tritici* in Mexico (Huerta-Espino & Singh, 1994).

Lr29 *from* A. elongatum

Sears (Sears 1973, 1977) transfered *Lr29* for leaf rust resistance from 7Ae#1 of *A. elongatum*, the source of *Lr19/Sr25*, to wheat by homoeologous recombination. *Lr29* was located on the 7Ae#1S arm and is present in the 7Ag#11 transfer (McIntosh et al., 1995b). C-banding analysis confirmed the T7DL–7Ae#1L·7Ae#1S translocation in line RL6080 (Thatcher*6/7Ag#11), and located the breakpoint in the distal region of the T7DL–7Ae#1L arm (Figure 13). *Lr29* has not been exploited in cultivars (McIntosh et al., 1995b).

Sr43 *from* A. elongatum

Knott and co-workers also transferred *Sr43* for stem rust resistance from a group 7 *A. elongatum* chromosome to wheat chromosome 7D using homoeologous recombination (Knott et al., 1977; Kibirige-Sebunya & Knott, 1983). ISH analysis using species-specific repetitive DNA sequences identified the translocation chromosomes as T7DL–7Ae#2L·7Ae#2S, T7DS·7DL–7Ae#2L, and T7DS·7Ae#2L (Kim et al., 1993). In common with the *Lr19/Sr25* transfers, *Sr43* is associated with distorted inheritance and yellow flour pigmentation, which distracts from its use in resistance breeding.

Table 3. Transfers derived from *Agropyron* species

Germplasm	Alien species	Alien target genes	Description	Size of alien translocation	Size of missing segment	Fraction length of translocation breakpoint	Mode of transfer	Type	Contribution to agriculture
Agatha	*A. elongatum*	*Lr19/Sr25*	T7DS·7DL–7Ae#1L	2.55 μm	2.62 μm of 7DL	0.32	Irradiation	C	+
Agatha–28	*A. elongatum*	*Lr19/Sr25*	T7DS·7DL–7Ae#1L	2.73 μm	2.71 μm of 7DL	0.29	EMS-induced	C	—
Agatha–235	*A. elongatum*	*Lr19*	T7DS·7DL–7Ae#1L–7DL	1.99 μm	1.29 μm of 7DL	0.31 0.75	EMS-induced	C	—
7Ag#11	*A. elongatum*	*Lr29*	T7DL–7Ae#1L·7Ae#1S				Homoeologous recombination	C	—
Indis	*Th. distichum*	*Lr19/Sr25*	T7DS·7DL–7Ae#1L				Spontaneous	C	+
Agent	*A. elongatum*	*Sr24/Lr24*	T3DS·3DL–3Ae#1L	1.26 μm	1.38 μm of 3DL	0.70	Spontaneous	C	++
Teewon	*A. elongatum*	*Sr24/Lr24*	T1BL·1BS–3Ae#1L			0.50 in the satellite of 1BS	Irradiation	N	—
K2046	*A. elongatum*	*Sr26*	T6AS·6AL–6Ae#1L	2.48 μm	3.63 μm of 6AL	0.09	Irradiation	C	++
CI15322	*A. elongatum*	WSMR	T4DS·4DL–1Ae#1L	1.31 μm	0.73 μm of 4DL	0.67	Irradiation	N	—
875-94-2	*A. elongatum*	*Cmc2*	T5BL·6Ae#2S	6Ae#2S	5BS	0	Spontaneous	C	—
WGRC27	*A. intermedium*	*Wsm1*	T4DL·4Ai#2S	4Ai#2S	4DS	0	Irradiation	C	—
T4	*A. intermedium*	*Lr38*	T3DL·3DS–7Ai#2L	2.78 μm	0.67 μm of 3DS	0.46	Irradiation	N	—
T7	*A. intermedium*	*Lr38*	T6DS·6DL–7Ai#2L	4.19 μm	1.45 μm of 6DL	0.32	Irradiation	N	—
T24	*A. intermedium*	*Lr38*	T5AL·5AS–7Ai#2L	4.20 μm	0.88 μm of 5AS	0.35	Irradiation	N	—
T25	*A. intermedium*	*Lr38*	T1DS·1DL–7Ai#2L	2.55 μm	0.82 μm of 1 DL	0.59	Irradiation	N	—
T33	*A. intermedium*	*Lr38*	T2AS·2AL–7Ai#2L	2.42 μm	1.40 μm of 2AL	0.62	Irradiation	N	—
86–187	*A. intermedium*	*Sr*	T7DS–7Ai#1L·7Ai#1S				Homoeologous recombination	N	—
TC6	*A. intermedium*	BYDR	T7DS–7Ai#1S·7Ai#1L			0.33	Tissue culture	C	—
TC7	*A. intermedium*	BYDR	T1BS–7Ai#1S·7Ai#1L			0.37	Tissue culture	N	—
TC14	*A. intermedium*	BYDR	T7DS–7Ai#1L·7Ai#1S			0.56	Tissue culture	N	—

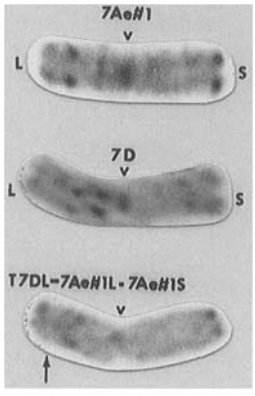

Figure 13. C-banding patterns of the chromosomes involved in the *Lr29* transfer derived from *A. elongatum* (Friebe et al., unpublished)

Lr24/Sr24 *from* A. elongatum *(Agent, Teewon)*

Agent is a spontaneous wheat-*A. elongatum* translocation line with leaf rust and stem rust resistance genes *Lr24* and *Sr24* (Smith et al., 1968; McIntosh et al., 1977). C-banding and GISH analyses identified the translocation chromosome as T3DS·3DL–3Ae#1L, with the breakpoint at FL 0.70 (Figure 14). The 3Ae#1L segment in this translocation has a size of 1.26 μm, replacing 1.38 μm of the 3DL arm of wheat (Table 3) (Jiang et al., 1994a).

Sears (1973, 1977) used induced homoeologous recombination for transferring *Lr24* (and *Sr24*) to wheat, and several compensating translocations involving wheat chromosomes 3B and 3D were obtained. All the recombinant lines are either 3Ae#1–3D or 3Ae#1–3B (transfers #10 and #13) terminal translocations with breakpoints in different regions of the 3Ae#1L arm. Most of the 3D–3Ae#1 translocations produced by induced homoeologous recombination carry a gene for red grain color derived from 3Ae#1, but white grained recombinants were obtained from transfers #3 and #14 (McIntosh, unpublished data).

Lr24 and *Sr24* were also transferred to wheat using radiation treatment of TAP 48, a wheat-*A. elongatum* chromosome addition line having the *A. elongatum* chromosome 3Ae#1. A translocation line was released under the name Teewon (Sebesta et al., 1995a). C-banding and GISH analyses identified the wheat-*A. elongatum* translocation in Teewon as T1BL·1BS–3Ae#1L (Figure 14). The breakpoint is located in the middle of the 1BS satellite (Jiang et al., 1994b). The T1BL·1BS–3Ae#1L translocation does not carry the gene for red grain color. The Agent translocation and the recombinant lines produced by Sears (1973, 1977) are compensating translocations and, thus, are expected to be more suitable for cultivar improvement than the noncompensating T1BL·1BS–3Ae#1L translocation present in the Teewon and various Amigo derivatives (The et al., 1992). Recently, molecular markers closely linked to *Lr24* were identified (Schachermayr et al., 1995).

Lr24 is largely ineffective in North America, South America and South Africa but remains effective and is being used in cultivars in Australia. *Sr24* has been overcome in South Africa and in India but is still effective in North America and in Australia (McIntosh et al., 1995b).

Sr26 *from* A. elongatum

Knott (1961, 1968) used radiation treatment for transferring gene *Sr26* for stem rust resistance, from the long arm of a group 6 *A. elongatum* chromosome to the long arm of wheat chromosome 6A. C-banding and GISH analyses confirmed the T6AS·6AL–6Ae#1L translocation (Figure 15) (Friebe et al., 1994b). The breakpoint is located in the 6AL arm close to the centromere, at a fraction length of 0.09. The size of the transferred *A. elongatum* segment is 2.48 μm, replacing a 3.63 μm distal segment of 6AL (Table 3). The *Sr26* transfer has contributed to cultivar improvement and is still in use in cultivars in Australia, although it does cause a significant reduction in yield (McIntosh, 1991, The et al., 1988; McIntosh et al., 1995b).

Wheat streak mosaic resistance from A. elongatum

Sebesta and co-workers (Sebesta & Bellingham, 1963; Sebesta et al., 1972) used radiation to transfer a gene for wheat streak mosaic resistance (WSMR) (Martin et al., 1976; Pfannenstiel & Niblett, 1978) from *A. elongatum* to wheat. C-banding and GISH analyses revealed that the resistance gene came from the long arm of a group 1 *A. elongatum* chromosome, 1Ae#1, translocated to wheat chromosome 4D in germplasm CI15322 in the form of a noncompensating T4DL·4DS– 1Ae#1L translocation (Figure 16) (Jiang et al., 1993). The 1Ae#1L segment in this translocation has a size of 1.31 μm, replacing a 0.73 μm distal segment of 4DL, with the breakpoint at FL 0.67 (Table 3). CI15322 had a second complete *A. elongatum* chromosome, 1Ae#2, substituting for wheat chromosome 1D.

Recently, lines with only the T4DL·4DS–1Ae#1L translocation chromosome were produced. These lines

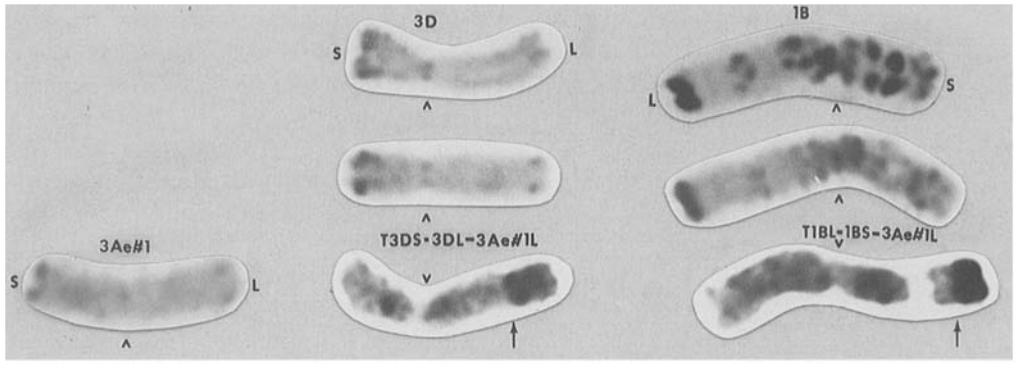

Figure 14. C-banding and GISH patterns of the chromosomes involved in the *Lr24/Sr24* transfers derived from *A. elongatum* (modified after Jiang et al., 1994a and b)

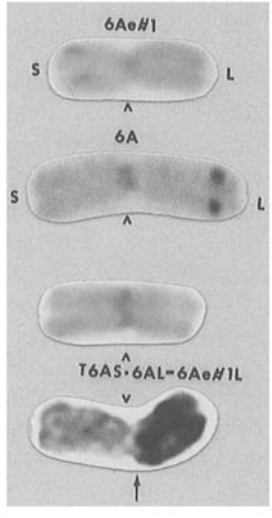

Figure 15. C-banding and GISH patterns of the chromosomes involved in the *Sr26* transfer derived from *A. elongatum* (modified after Friebe et al., 1994b)

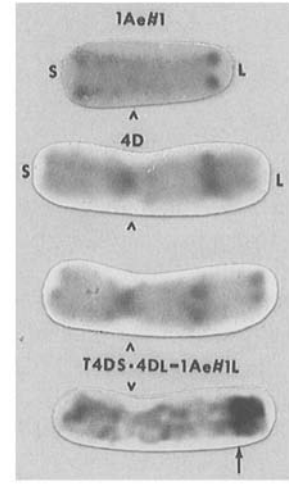

Figure 16. C-banding and GISH patterns of the chromosomes involved in the WSMR transfer derived from *A. elongatum* (modified after Jiang et al., 1993)

did not share the same high level of resistance to wheat streak mosaic virus compared with the parent line CI15322, suggesting that the 1Ae#1 arm has more than one gene for wheat streak mosaic virus resistance and that not all are present in the 1Ae#1L segment translocated to wheat chromosome 4D. This gene has not been used in wheat improvement.

Cmc2 *from* A. elongatum

Larson & Atkinson (1970, 1972, 1973) transferred a gene (designated *Cmc2*) conferring resistance to wheat curl mite (*Eriophyes tulipae*, (syn. *Aceria tulipae* Keifer)) colonization from a group 6 *A. elongatum* chromosome to wheat. *Cmc2* is available in non-compensating translocations involving wheat chromosomes 5B (T5BL·6Ae#2S, Whelan et al., 1983, 1986; Kim et al., 1992) (Figure 17) and 6A (T6AS·6Ae#2S, Whelan & Lukow, 1990), and in a spontaneous compensating T6DL·6Ae#2S translocation (Whelan, 1988; Whelan & Hart, 1988; Whelan & Conner, 1989). *Cmc2* has not been intensively used in wheat improvement.

Wsm1 *from* A. intermedium

By irradiating F_1 seeds from the cross CI15092 (a 4Ai#2(4A) substitution line)/*Ae. speltoides*//Fletcher x Centurk with fast neutrons, Wells and co-workers (Kota, 1980: Lay et al., 1971; Wells et al., 1973, 1982) transferred *Wsm1* for wheat streak mosaic resistance from the short arm of a group 4 *A. intermedium*

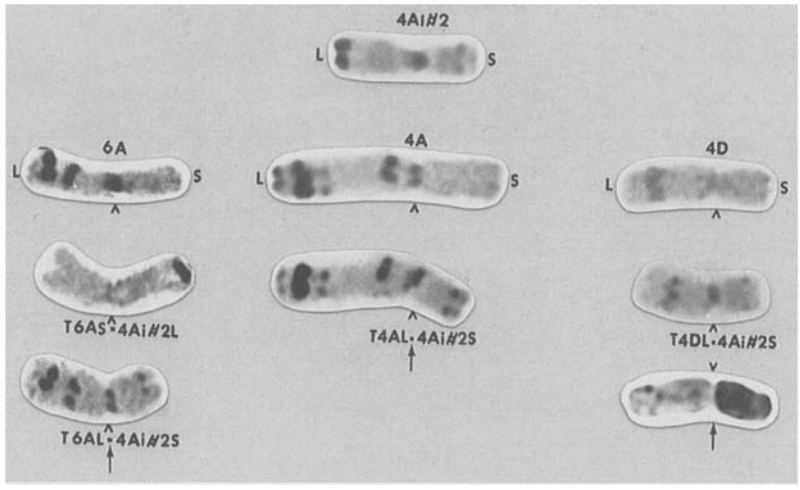

Figure 18. C-banding and GISH patterns of the chromosomes involved in the *Wsm1* transfer derived from *A. intermedium* (modified after Friebe et al., 1991a)

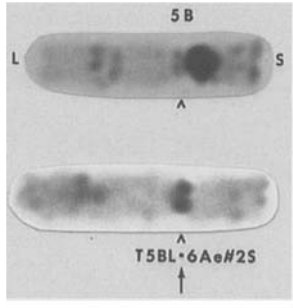

Figure 17. C-banding patterns of the chromosomes involved in the *Cmc2* transfer derived from *A. elongatum* (Friebe et al., unpublished)

chromosome to wheat. C-banding and GISH identified one reciprocal translocation in germplasm CI17883, with the translocated chromosomes T6AS·4Ai#2L and T6AL·4Ai#2S, and one compensating translocation, T4DL·4Ai#2S, in germplasm CI17884 (Figure 18, Table 3) (Friebe et al., 1991a). The latter line also had a wheat-*Ae. speltoides* translocation chromosome T7AS–7SS·7SL, conferring resistance to greenbug (*Gb5*). Germplasm, KS93WGRC27, has only the T4DL·4Ai#2S translocation, and consequently performs better agronomically (Gill et al., 1995). *Wsm1* is now being introduced into advanced breeding lines.

Wsm1 was also transferred to wheat using induced homoeologous recombination (Wang & Liang, 1977; Wang et al., 1977; Liang et al., 1979). C-banding analysis indicated that the translocation chromosome in line CI17766 involved the short arm of 4Ai#2 and the long arm of wheat chromosome 4A (Fig 18) (Friebe et al., 1991a). GISH analysis revealed that the breakpoint in this translocation is located in the middle of the short arm of the translocation chromosome (Wang & Zhang, 1995).

Lr38 *from* A. intermedium

Wienhues (1960, 1966, 1967, 1971, 1973, 1979) used either X-ray or ^{60}Co treatments to transfer *Lr38* for leaf rust resistance, from the long arm of a group 7 *A. intermedium* chromosome (7Ai#2) to wheat. C-banding and GISH analyses identified five different leaf rust resistant wheat-*A. intermedium* translocations involving the wheat chromosomes 2A (T33 = W49), 5A (T24), 1D (T25), 3D (T4), and 6D (T7) (Friebe et al., 1992b, 1993a). The translocation chromosomes can be described as T2AS·2AL–7Ai#2L, T5AL·5AS–7Ai#2L, T1DS·1DL–7Ai#2L, T3DL·3DS–7Ai#2L, and T6DS·6DL–7Ai#2L (Figure 19). The sizes of the transferred 7Ai#2L segments in these translocations are 2.42 μm, 4.20 μm, 2.55 μm, 2.78 μm, and 4.19 μm, respectively (Table 3). All five translocations involve nonhomoeologous chromosome arms and, therefore, are noncompensating. Preliminary field trials showed that these lines have reduced grain yield (Dyck & Friebe, 1993). *Lr38* has not contributed to cultivar improvement and is now being transferred to wheat using induced homoeologous recombination.

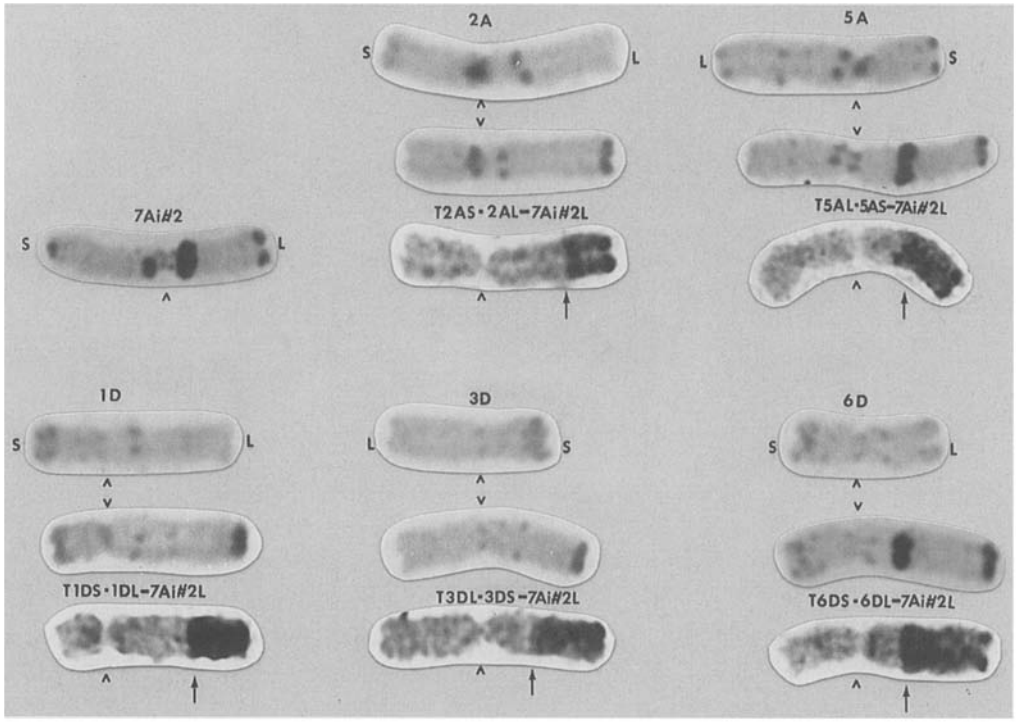

Figure 19. C-banding and GISH patterns of the chromosomes involved in *Lr38* transfers derived from *A. intermedium* (modified after Friebe et al., 1992 and 1993a)

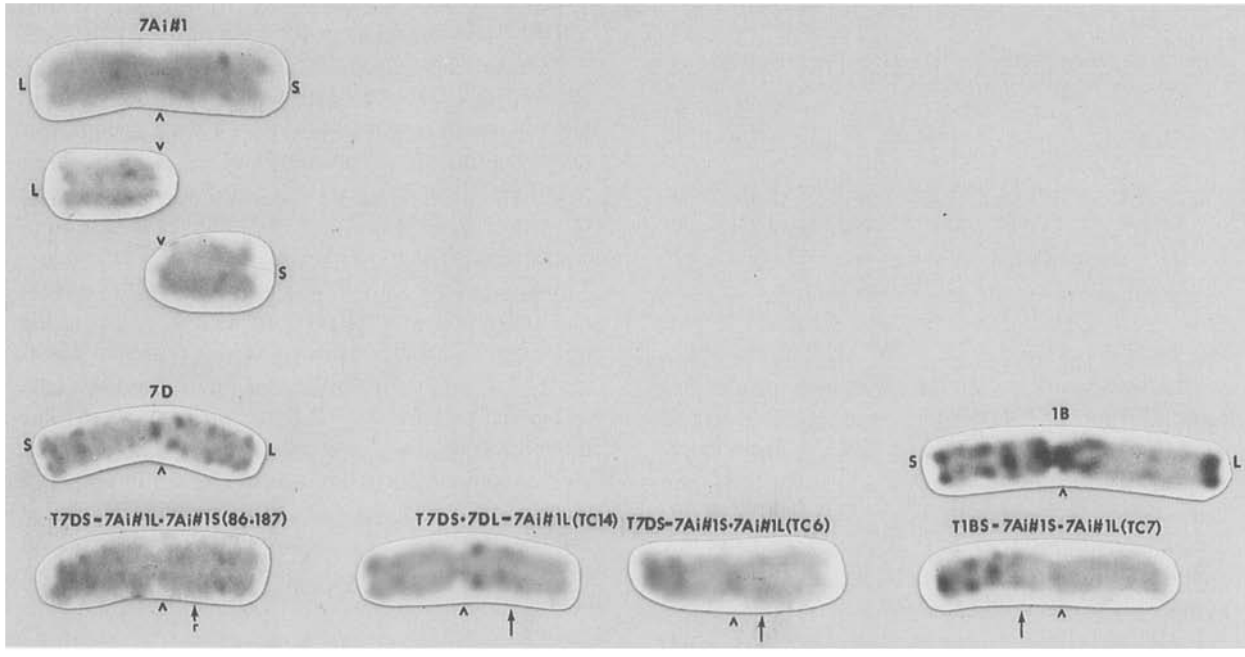

Figure 20. C-banding patterns of the chromosomes involved in the SrAgi and BYDR transfers derived from *A. intermedium* (Friebe et al., unpublished)

SrAgi *and BYD from* A. intermedium

McIntosh used induced homoeologous recombination to transfer gene *SrAgi* for stem rust resistance from a group 7 *A. intermedium* chromosome addition line produced by Cauderon (1966) and Cauderon et al. (1973) (L1 = TAF2 = 7Ai#1, Friebe et al., 1992a) to wheat. *SrAgi* was derived from the short arm of 7Ai#1represented in the ditelosomic chromosome addition line TAF2d, having a small but diagnostic C-band in the distal region of this arm. The 7Ai#1S arm, conditioning purple coleoptiles, is cytologically slightly longer than the genetically L arm. C-banding and GISH identified the wheat chromosome involved in line 86.187 as T7DS–7Ai#1L·7Ai#1S (Figure 20) *SrAgi* has been redesignated *Sr44*.

The genetically long arm of chromosome 7Ai#1, having a small and proximally located C-band, is the source of barley yellow dwarf resistance (BYDR) that was transferred to wheat by tissue culture (Brettel et al., 1988; Banks et al., 1995). Three different wheat-*A. intermedium* translocation types were identified by C-banding, GISH, and RFLP analyses: T1BS–7Ai#1S·7Ai#1L (with the breakpoint at FL 0.37, line TC7), T7DS–7Ai#1S·7Ai#1L (with the breakpoint at FL 0.33; lines TC5, TC6, TC8, TC9, TC10), and T7DS·7DL–7Ai#1L (with the breakpoint at FL 0.56; line TC14, having also a 6G(6B) substitution derived from *T. timopheevii*) (Hohmann et al., 1996). A line with the *T. timopheevii* cytoplasmic male sterility nuclear restoration system was used in the development of these derivatives (P. Banks, personal communication).

Transfers derived from cultivated rye, *Secale cereale*

Lr26/Sr31/Yr9/Pm8

Kattermann (1937, 1938) obtained a spontaneous wheat-rye substitution line in which the wheat chromosome 1B was replaced by rye chromosome 1R. The derived T1BL·1R#1S translocation also occurred spontaneously (Figure 21) (Mettin et al., 1973; Zeller, 1973). The 1RS arm in this translocation has *Lr26* for leaf rust resistance, *Sr31* for stem rust resistance, *Yr9* for stripe rust resistance, and *Pm8* for powdery mildew resistance (Bartos & Bares, 1971; Bartos et al., 1973). The 1RS arm not only compensates for the loss of the wheat arm 1BS, but also confers a heterotic effect on grain yield (Rajaram et al., 1983). However, lines with the T1BL·1R#1S translocation may have reduced quality, because doughs made from them tend to be sticky (Zeller et al., 1982) especially with overmixing. Shepherd and co-workers produced 1RS recombinant lines using homoeologous recombination (Koebner and Shepherd, 1986; Koebner et al., 1986). The 1RS segments in these translocations differ in size (Rogowski et al., 1991, 1992, 1993) and some may show an improved storage protein composition. The T1BL·1R#1S translocation, together with the T1AL·1R#2S translocation (see*Gb2/Sr/Pm17*), is the most successful wheat-alien translocation and is still in use worldwide for hexaploid wheat improvement (Lukaszewski, 1990; Villareal et al., 1991). The T1BL·1R#1S translocation conferring *Pm8* resistance was also transferred from the CIMMYT cv. Veery to tetraploid wheat (Friebe et al., 1987, 1989, 1993b) and can be used for improving durum wheat. In contrast to the rust resistance genes, *Pm8* is not expressed in all genetic backgrounds (Friebe et al., 1989) due to the presence of a suppressor, *SuPm8*, located in wheat chromosome arm 1AS (Ren et al., 1996a, b). The frequency of suppression is low in European wheat backgrounds, but much higher in materials generated in Mexico.

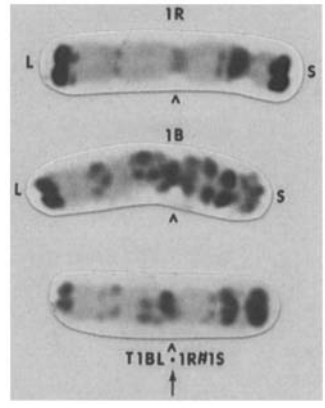

Figure 21. C-banding patterns of the chromosomes involved in the *Lr26/Sr31/Yr9/Pm8* transfer derived from *S. cereale* (modified after Friebe et al., 1989)

Gb2/Sr/Pm17 *(Amigo)*

Sebesta and co-workers used X-ray treatment to transfer *Gb2* for greenbug resistance from Insave F. A. rye, via the octoploid triticale cultivar Gaucho, to wheat and a wheat-rye translocation cultivar was released

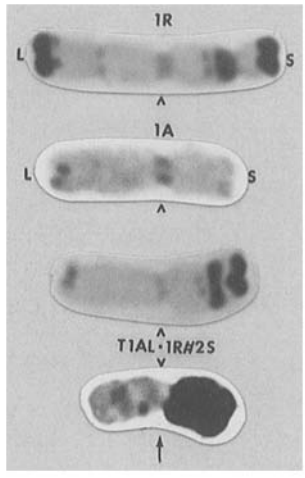

Figure 22. C-banding and GISH patterns of the chromosomes involved in the *Gb2/Pm17* transfer derived from *S. cereale* (modified after Friebe et al., 1995c)

under the name Amigo (Wood et al., 1974; Sebesta & Wood, 1978; Sebesta et al., 1995b). The wheat-rye translocation in Amigo consists of the short arm of rye chromosome 1R translocated to the long arm of wheat chromosome 1A, with the breakpoint within the centromeric region (Figure 22) (Hollenhorst & Joppa, 1981, 1983; Zeller & Fuchs, 1983; Lapitan et al., 1986). The centromeric breakpoint in T1AL·1R#2S suggests that this translocation may have originated from centricbreakage-fusion. The 1RS arm in T1AL·1R#2S has gene *Pm17* (Lowry et al., 1984; Heun et al., 1990) conditioning resistance to powdery mildew that is different from *Pm8* present in T1BL·1RS#1 translocations. Amigo is also resistant to stem rust, but it is not known if this gene is different from *Sr31*. Recently, *Pm17* was transferred to the 1RS arm of the wheat-rye translocation chromosome T1BL·1RS#1 (Hsam et al., 1995).

The et al. (1992) reported that in addition to *Gb2* and *Pm17*, Amigo also carries the leaf rust and stem rust resistance genes *Lr24* and *Sr24* that are known to be derived from the long arm of a group 3 *A. elongatum* chromosome. GISH analysis confirmed the presence of *A. elongatum* chromatin in Amigo and identified the translocation chromosome as T1BL·1BS–3Ae#1L (Jiang et al., 1994b). The T1BL·1BS–3Ae#1L translocation was derived from the cultivar Teewon, one of the parent lines of Amigo.

Gb6 *transfer*

Sebesta and co-workers transferred *Gb6* for greenbug resistance using radiation treatment from Insave F. A. rye to wheat (Porter et al., 1991, 1994). Line GRS1201 has the compensating wheat-rye translocation T1AL·1R#3S, whereas germplasm GRS1205 has a complete but modified rye chromosome 1R#3, and GRS1204 is homozygous for a reciprocal wheat-rye translocation with the translocation chromosomes T2AL·2AS–1R#3S and T2AS–1R#3S·1R#3L (Figure 23, Table 4) (Friebe et al., 1995b). *Gb6* is located on the 1R#3S segment in these translocations and conditions resistance to greenbug biotypes E and G, both of which are virulent on plants with *Gb2*, located on the T1AL·1R#2S translocation present in the cultivar Amigo. At present, it is not known whether *Gb2* and *Gb6* are different alleles of the same locus or different genes. The compensating T1AL·1R#3S translocation present in germplasm GRS1201 should be a superior source of *Gb6* and hence should be used in crop improvement.

Russian wheat aphid resistance

Marais et al. (1994) transferred a gene for resistance to Russian wheat aphid (*Diuraphis noxia* Mordvilko) from the short arm of 'Turkey 77' rye chromosome 1R (1R#4S) exploiting homologous recombination to place it in the 1RS arm of the T1BL·1R#1S translocation chromosome derived from Veery. In addition to the resistance to RWA one of the selected homozygous recombinant lines also contained *Sr31* and *Lr26*.

Lr25/Pm7 *(Transec)*

Transec, produced by Driscoll and co-workers (Driscoll & Jensen, 1963, 1964, 1965; Driscoll & Anderson, 1967; Driscoll, 1968), is a derivative of the Cornell Wheat Selection 82a1–2–4–7. This line had a complex cytogenetic structure. It was nullisomic for the long arm of wheat chromosome 2B, and this nullisomy was compensated by the presence of a pair of rye telocentric chromosomes conditioning resistance to leaf rust (*Lr25*) and powdery mildew (*Pm7*). It also had a segment derived from the long arm of rye chromosome 5R with the hairy neck peduncle gene (*Hp*) translocated to the long arm of wheat chromosome 4B (Driscoll & Sears, 1965). Because the rye telocentric chromosomes compensated for the loss of the 2BL arm of wheat, it was assumed that they were derived from

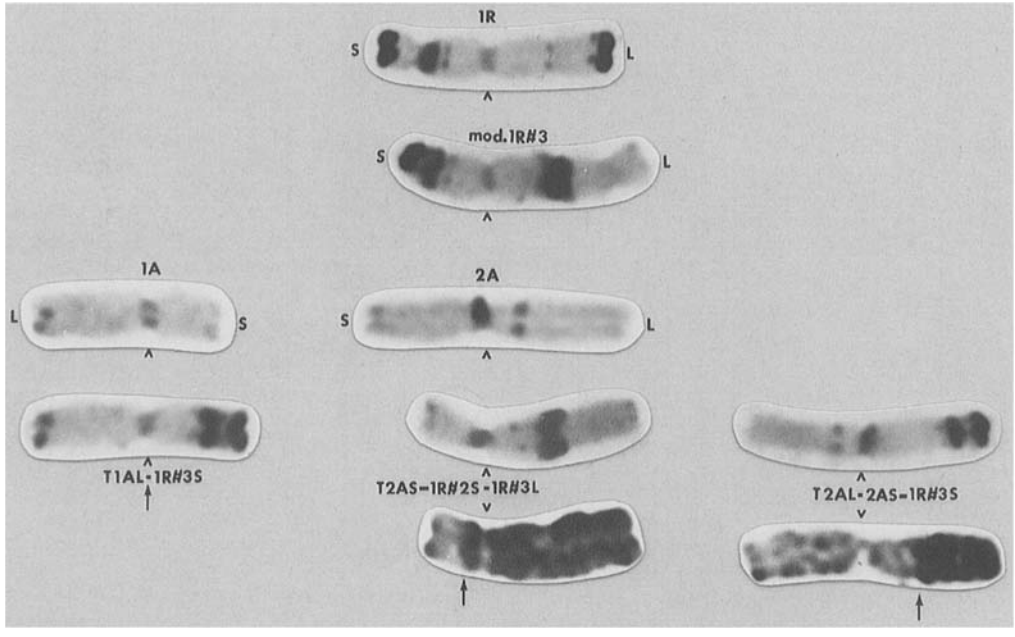

Figure 23. C-banding and GISH patterns of the chromosomes involved in the *Gb6* transfer derived from *S. cereale* (modified after Porter et al., 1994 and Friebe et al., 1995b)

the long arm of 2R. Transec was selected in the irradiated progeny of the cross, 82a1–2–4–7 × Chinese Spring, as a line having 2n = 42 and expressing the *Lr25* and *Pm7* resistances, but lacking the hairy neck phenotype.

The breakpoint in the Transec translocation, was located 1 cM from the centromere in the long arm of chromosome 4B by telocentric mapping (Driscoll & Bielig, 1968), whereas the *Hp* gene in the 82a1–2–4–7 parent mapped 30 cM from the centromere (Driscoll & Sears, 1965). Because the breakpoint in Transec mapped closer to the centromere, it was assumed that the entire 5RL segment was lost and replaced by a segment derived from the 2RL rye telosome.

C-banding analysis confirmed the presence of a wheat-rye translocation involving wheat chromosome 4B, but suggested that the rye segment in Transec, having a prominent subtelomeric C- band, was derived from the distal region of 5RL instead of 2RL (Heun & Friebe, 1990; Friebe et al., 1995c). However, analysis of meiotic chromosome pairing in testcross combinations with the wheat-(Chinese Spring)-rye (Imperial) chromosome addition lines 2R and 5R showed that the Transec- translocation chromosome paired only with the long arm of 2R, and not with 5RL (Figure 24). Therefore, the wheat-rye translocation chromosome in Transec can be described as T4BS·4BL–2R#1L, agreeing with the earlier report of Driscoll & Bielig (1968). GISH analysis located the breakpoint in the 4BL arm at a fraction length of 0.61 with the 2RL segment having a size of 2.40 μm and replacing 1.03 μm of the 4BL arm (Table 4). However, because homology at the chromosome ends is enough to ensure meiotic pairing, it cannot be excluded that the Transectranslocation has

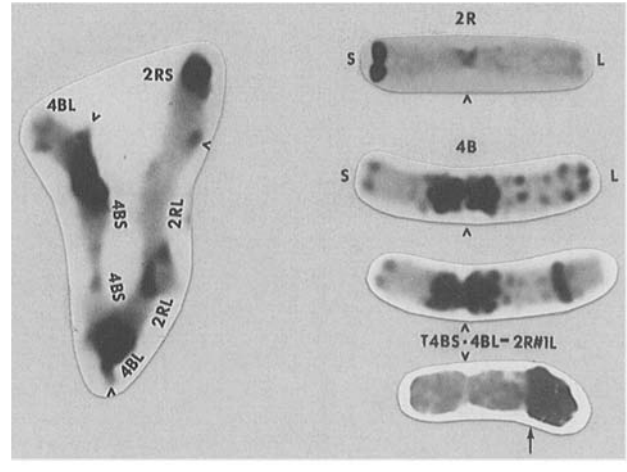

Figure 24. C-banding and GISH patterns of the chromosomes involved in the *Lr25/Pm7* transfer derived from *S. cereale* (modified after Friebe et al., 1995c)

Table 4. Transfers derived from *Secale cereale*

Germplasm	Alien species	Alien target genes	Description	Size of alien translocation	Size of missing segment	Fraction length of translocation breakpoint	Mode of transfer	Type	Contribution to agriculture
WGRC14	*S. cereale*	Pm8/Sr31 Lr26/Y49	T1BL·1R#1S	1RS	1BS	0	Spontaneous	C	++
Amigo	*S. cereale*	Gb2/Pm17	T1AL·1R#2S	1RS	1AS	0	Irradiation	C	++
	A. elongatum	Sr24/Lr24	T1BL·1BS–3Ae#1L			0.50 in the satellite of 1BS	Irradiation	N	
GRS 1201	*S. cereale*	Gb6	T1AL·1R#3S	1RS	1AS	0	Irradiation	C	—
GRS 1204	*S. cereale*	Gb6	T2AL·2AS–1R#3S T2AS–1R#3S·1RL#3			0.39 in S 0.27 in L	Irradiation	N	—
Transec	*S. cereale*	Lr25/Pm7	T4BS·4BL–2R#1L	2.40 μm	1.03 μm of 4BL	0.61	Irradiation	N	—
ST–1	*S. cereale*	Lr45	T2AS–2R#3S·2R#3L	1.71 μm	1.58 μm	0.39	Irradiation	C	—
WRT238	*S. cereale*	Sr27	T3AS·3R#1S	3RS	3AL	0	Irradiation	N	—
90M126–2	*S. cereale*	Sr27	T3AL·3R#1S	3RS	3AS	0	Irradiation	C	—
90M129–9	*S. cereale*	Sr27	T3BL·3R#1S	3RS	3BS	0	Irradiation	C	—
WGRC28	*S. cereale*	Pm20	T6BS·6R#3L	6RL	6BS		Spontaneous	N	—
KS85HF011	*S. cereale*	H21	T2BS·2R#2L	2RL	2BL		Tissue culture	C	—
88HF16	*S. cereale*	H25	T6BS·6BL–6R#1L	6.95 μm		0.11	Irradiation	N	—
88HF79	*S. cereale*	H25	T4BS·4BL–6R#1L	3.88 μm		0.46	Irradiation	N	—
88HF89	*S. cereale*	H25	T4AS·4AL–6R#1L–4AL	0.70 μm	none	0.06 0.19	Irradiation	N	—

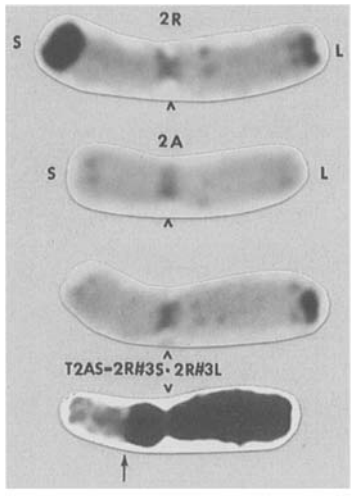

Figure 25. C-banding and GISH patterns of the chromosomes involved in the *Lr45* transfer derived from *S. cereale* (modified after McIntosh et al., 1995)

an additional intercalary segment derived from 5RL. *Lr25* and *Pm7* have not contributed to wheat improvement (McIntosh et al., 1995b).

Lr45 *transfer*

Mukade et al., (1970) transferred a gene for leaf rust resistance from the rye cultivar, Petkus, to wheat using X-rays. C-banding and GISH analyses located the leaf rust resistance gene, designated *Lr45,* on the wheat-rye translocation chromosome T2AS–2R#3S·2R#3L (Figure 25), which consists of the long arm of 2R, a 1.71 μm long segment of the short arm of 2R, and a distal 2.68 μm long segment of 2AS. Because meiotic pairing analysis, as discussed above, revealed that the rye segment in the Transec translocation, having *Lr25*, was derived from 2RL it remains to be shown that the leaf rust resistance gene *Lr45* in the T2AS–2R#3S·2R#3L translocation line is different from *Lr25*.The breakpoint is at FL 0.39 (Table 4) (McIntosh et al., 1995a). Although the T2AS–2R#3S·2R#3L translocation is of the compensating type, its male transmission frequency is reduced. The large size of the rye segment in this translocation has, so far, prevented its exploitation in cultivar improvement.

Sr27

Acosta (1962) used irradiation treatment to transfer a gene for stem rust resistance from Imperial rye chromosome 3R to chromosome 3A of Chinese Spring wheat. *Sr27* was derived from the short arm of rye chromosome 3R (Rao, 1978). C-banding and isozyme analyses identified the wheat- rye translocation chromosome in WRT238 as T3AS·3R#1S (Marais & Marais, 1994). *Sr27* has not been exploited in wheat cultivars, however, it is present in a complete rye chromosome 3R in many triticale lines produced and distributed by CIMMYT (McIntosh et al., 1995b). Recently, more useful compensating whole arm translocations were produced, where the 3RS arm is translocated to the long arms of wheat chromosomes 3A (T3AL·3R#1S) or 3B (T3BL·3R#1S) (Figure 26) (Marais & Marais, 1994).

Pm20

Friebe and co-workers transferred *Pm20* for powdery mildew resistance, from the long arm of Prolific rye chromosome 6R#3 to the 6RL arm of a T6BS·6R#2L wheat-rye translocation chromosome by homologous recombination (Friebe & Larter, 1988; Heun & Friebe, 1990; Friebe et al., 1994a, 1995d). The T6BS·6R#2L translocation germplasm, produced by Tuleen, is in *T. timopheevii* cytoplasm and has a fertility restoration gene located on the 6R#2L arm. Differences in polymorphic C-bands permitted the localization of *Pm20* close to the telomere of the 6RL arm (Fig 27).*Pm20* is now being introgressed into advanced breeding lines.

H21 *(Hamlet)*

Sears et al. (1992) used tissue culture to transfer gene *H21* for resistance to the Hessian fly, *Mayetiola destructor* (Say) (syn. *Phytophaga destructor* (Say)), from Chaupon rye to wheat (Lapitan et al., 1984). C-banding analysis revealed that *H21* was located in the long arm of rye chromosome 2R (Friebe et al., 1990). In the germplasm Hamlet, the complete 2RL arm is translocated to the short arm of wheat chromosome 2B, with the breakpoint at the centromere (Figure 28). The centromeric breakpoint in T2BS·2R#2L suggests that this translocation may have originated by the centric-breakage fusion mechanism. The T2BS·2R#2L translocation is not associated with reduced baking quality, confers resistance to all known biotypes of the Hessian fly, and is being transferred to advanced breeding lines.

H25

A second gene, *H25*, for Hessian fly resistance was transferred by Sebesta from the rye cultivar Balbo

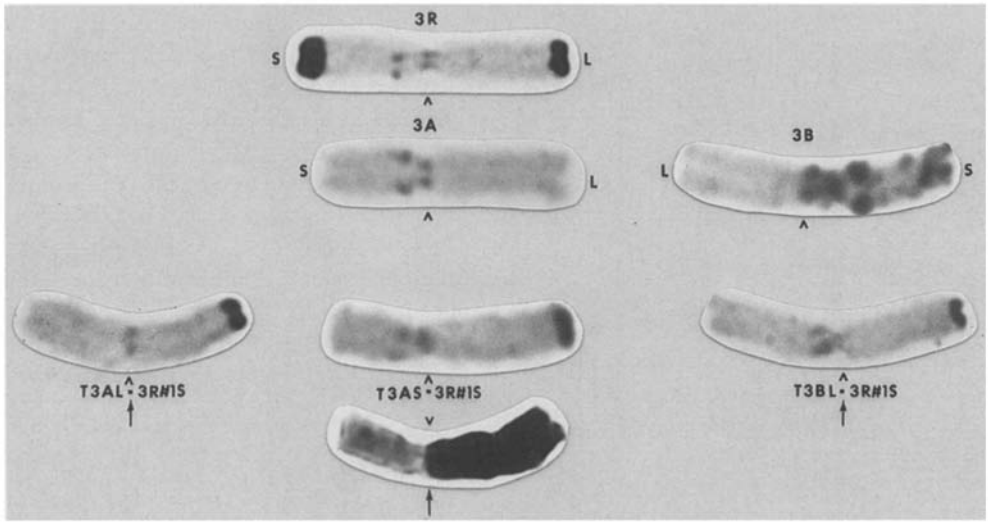

Figure 26. C-banding and GISH patterns of the chromosomes involved in the *Sr27* transfer derived from *S. cereale* (Friebe et al., unpublished)

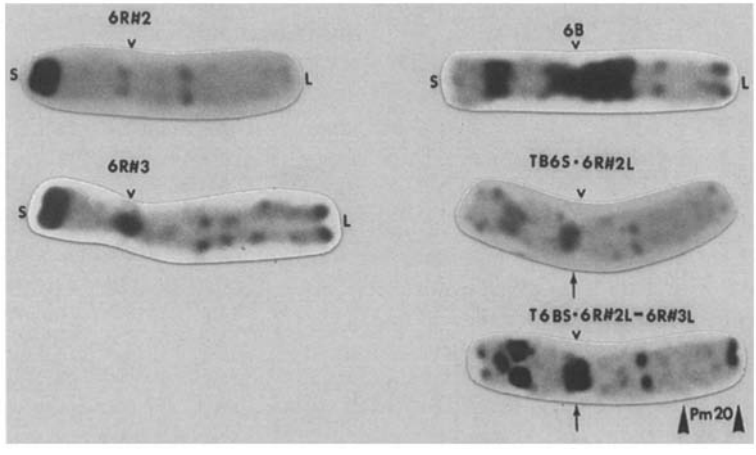

Figure 27. C-banding patterns of the chromosomes involved in the *Pm20* transfer derived from *S. cereale* (modified after Friebe et al., 1994a)

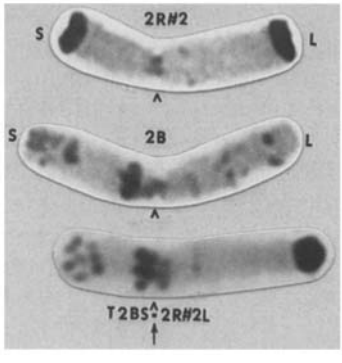

Figure 28. C-banding and GISH patterns of the chromosomes involved in the *H21* transfer derived from *S. cereale* (modified after Friebe et al., 1990)

to wheat using X-rays. *H25* was located in the long arm of rye chromosome 6R. C-banding analysis identified three wheat–6RL translocations involving wheat chromosomes 4B, 6B, and 4A (Figure 29) (Friebe et al., 1991b, c). ISH analysis, using highly repetitive and total genomic rye DNA as probes, was used to identify the breakpoints and sizes of the transferred rye segments (Table 3) (Mukai et al., 1991, 1993). Almost the complete 6RL arm is present in T6BS·6BL–6R#1L (6.95 μm), whereas about half of the 6RL arm (3.88 μm) is present in T4BS·4BL–6R#1L, with the breakpoints at FL's 0.11 and 0.46, respectively. In Ti4AS·4AL–6R#1L–4AL, a 0.70 μm long segment of 6RL is inserted between FL's 0.06 and 0.19 in the long arm of wheat chromosome 4A. Recombination

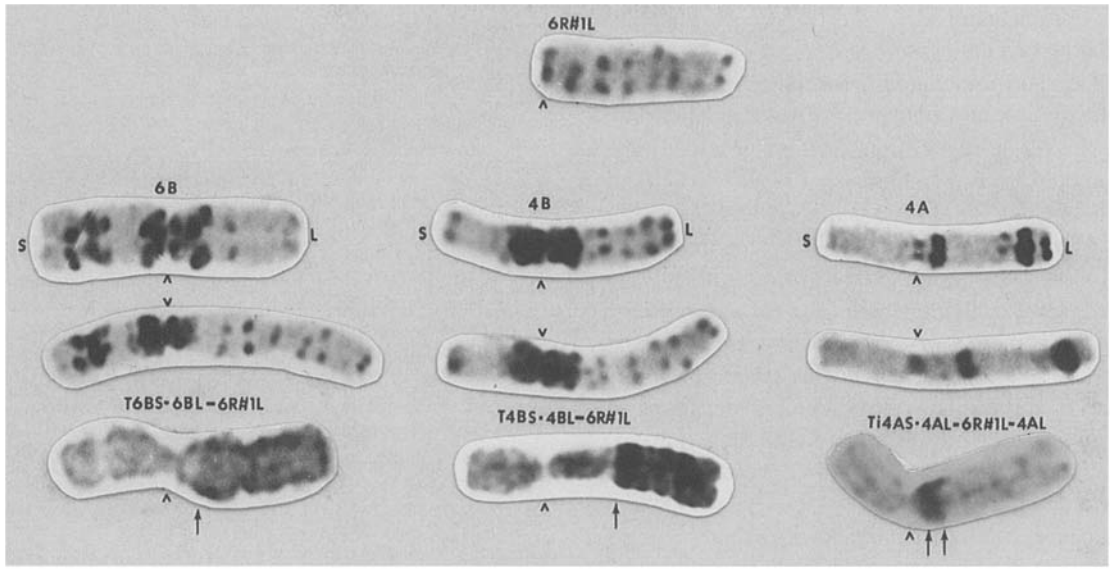

Figure 29. C-banding and GISH patterns of the chromosomes involved in the *H25* transfer derived from *S. cereale* (modified after Friebe et al., 1991c and Mukai et al., 1993)

mapping using a Hessian fly susceptible T6BS·6R#2L translocation line produced by Tuleen, where the 6RL arm is polymorphic for diagnostic C-bands, located the *H25* gene close to the telomere of the 6RL arm (Delaney et al., 1995). Ti4AS·4AL–6RL#1–4AL is the only intercalary wheat-alien translocation produced using radiation treatment. All wheat–6RL translocations are being transferred to advanced breeding lines.

A third gene for resistance to Hessian fly was recently identified and located on the long arm of rye chromosome 3R. This gene is now being transferred to wheat by centric fusion and by radiation treatment (Hatchett and Lukaszewski, personal communication).

Conclusions

Although many wheat-alien translocation lines have been produced, few have made significant contributions to wheat improvement (McIntosh, 1991). The spontaneous Agent translocation with *Lr24/Sr24* and the radiation-induced *Sr26* transfer, both derived from *A. elongatum,* have contributed significantly to cultivar improvement, although the latter translocation causes a reduction of about 10% in yield (The et al., 1988). Furthermore, lines with the *Sr36/Pm6* transfer derived from *T. timopheevii* as well as lines with either *Sr36* or *Pm6* alone are still being used in cultivars.

So far, the most successful wheat-alien transfers are whole arm translocations where the short arm of rye chromosome 1R is translocated to the long arm of either wheat chromosomes 1A or 1B. The 1RS arm in these translocations not only compensates for the loss of the relevant wheat arms 1AS or 1BS, but also has a heterotic effect on grain yield. These are the only wheat-alien translocation lines that have outyielded pure wheat cultivars. The T1AL·1R#2S and T1BL·1R#1S translocations are still used intensively in cultivars worldwide. RFLP analysis revealed that all rye chromosomes, except 1R, have rearrangements compared to those of wheat (Devos et al., 1993). Similar rearrangements that lead to the formation of unbalanced gametes and reduced performance of derived wheat-alien translocation lines might also be present in other related species.

The data presented show that 11 of the 58 wheat-alien translocations analyzed by C-banding and GISH were whole arm translocations with breakpoints within the centromeric regions. The majority of the translocations (45) analyzed were identified as terminal translocations, where an alien segment was translocated to a wheat chromosome arm. Only two intercalary translocations with an alien segment inserted into a wheat chromosome arm were identified. One of these was radiation-induced and resulted in the insertion of a small segment of the telomeric region of 6RL with *H25* for Hessian fly resistance into the proximal region of

wheat chromosome arm 4AL. The second intercalary transfer involved the insertion of a segment of the long arm of a group 7 *A. elongatum* chromosome with *Lr19*, into wheat chromosome arm 7DL. Although an EMS treatment was used, this translocation most likely arose by homoeologous recombination.

The results show that radiation treatment causes random chromosome breaks. The majority of translocations resulting from radiation treatments were formed between nonhomoeologous chromosome arms. These noncompensating translocations are genetically unbalanced, and lead to reduced agronomic performance. In contrast, all wheat-alien translocations produced by induced homoeologous recombination are of a compensating type and, thus have greater agronomic potential.

Because, recombination between homoeologous chromosomes of wheat and related species is drastically reduced in the proximal regions of chromosome arms (Lukaszewski, 1992; Lukaszewski & Curtis, 1992; Werner et al., 1992) it will be difficult to transfer a target gene from these areas using induced homoeologous recombination. In these situations, radiation treatment with strong selection for the recovery of compensating translocations (Sears, 1993) or other strategies such as the use of the chromosome breaking action of gametocidal chromosomes (Endo et al., 1994), might be more successful.

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