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Relationships between the chromosomes of *Aegilops umbellulata* and wheat

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Abstract A comparative genetic map of *Aegilops umbellulata* with wheat was constructed using RFLP probes that detect homoeoloci previously mapped in hexaploid bread wheat. All seven *Ae. umbellulata* chromosomes display one or more rearrangements relative to wheat. These structural changes are consistent with the sub-terminal morphology of chromosomes 2 U, 3 U, 6 U and 7 U. Comparison of the chromosomal locations assigned by mapping and those obtained by hybridization to wheat/*Ae. umbellulata* single chromosome addition lines verified the composition of the added *Ae. umbellulata* chromosomes and indicated that no further cytological rearrangements had taken place during the production of the alien-wheat aneuploid lines. Relationships between *Ae. umbellulata* and wheat chromosomes were confirmed, based on homoeology of the centromeric regions, for 1 U, 2 U, 3 U, 5 U and 7 U. However, homoeology of the centromeric regions of 4 U with wheat group-6 chromosomes and of 6 U with wheat group-4 chromosomes was also confirmed, suggesting that a re-naming of these chromosomes may be pertinent. The consequences of the rearrangements of the *Ae. umbellulata* genome relative to wheat for gene introgression are discussed.

Key words *Aegilops umbellulata* · Co-linearity · Comparative mapping · Translocations · *Triticum aestivum* · Wheat

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Introduction

Alien germplasm is an important source of novel genes for wheat improvement. In 1956, Sears transferred the leaf rust resistance gene, *Lr9*, from *Aegilops umbellulata* Zhuk., a wild Mediterranean grass, to wheat using radiation-induced recombination. The *Lr9* resistance gene is introgressed on chromosome arm 6BL and has, as yet, not been overcome in a range of wheat-growing areas (McIntosh et al. 1995). *Ae. umbellulata* has also been identified as a source of resistance to powdery mildew, Hessian fly, and greenbug (Gill et al. 1985).

Following the construction of six individual *Ae. umbellulata* chromosome disomic additions and one monosomic addition, assigned A to G, to the hexaploid wheat variety Chinese Spring (CS) (Kimber 1967), several attempts have been made to identify the relationships between the wheat and *Ae. umbellulata* chromosomes. Shepherd (1973) established that two *Ae. umbellulata* chromosomes, A and B, are associated with the production of prolamins, which in wheat are coded for by genes on the homoeologous group-1 and -6 chromosomes. A homoeologous relationship between *Ae. umbellulata* chromosome B and the wheat group-1 chromosomes was confirmed by the good compensating ability of chromosome B for 1A, 1B and 1D (Kimber 1968). However, the relationship between *Ae. umbellulata* chromosome A and the wheat group-6 chromosomes was ambiguous. Although it was possible to substitute *Ae. umbellulata* chromosome A for the wheat group-6 chromosomes, only incomplete genetic compensation was obtained (Kimber 1968). Based on pairing data (Athwal and Kimber 1972) it was nevertheless decided that *Ae. umbellulata* chromosome A was homoeologous to the wheat group-6 chromosomes. The identity of *Ae. umbellulata* chromosome C as 5 U was based on the phenotype of the CS/C addition line, the normal morphology and vigour of the 5A, 5B and 5D disomic substitutions, and the presence

of a distinct secondary constriction and small satellite on chromosome C, similar to that on chromosome 5D in *Ae. squarrosa* (= *T. tauschii*) (Chapman and Riley 1970). *Ae. umbellulata* chromosome D compensated well for the wheat group-2 chromosomes and was identified as 2 U (Riley et al. 1971). Monosomic addition line F was perceived to have homoeology with wheat group 4, and disomic additions E and G were both classified as 7U. No addition line was available for chromosome 3U. Since then, a complete set of whole-chromosome and telosomic addition lines, with the exception of 6U^{v}S and 7U^{v}S, have been developed for the U^{v} genome of *Ae. peregrinum*, which is structurally similar to the U genome of *Ae. umbellulata* (Friebe et al. 1996). It was clear, however, that the homoeologous relationships of the U and U^{v} genomes with those of wheat were not complete. Analysis of *Ae. umbellulata* and *Ae. peregrinum* addition lines with a limited number of RFLP probes, and isozyme markers with known location in wheat, indicated that a syntenic relationship between wheat and *Ae. umbellulata* chromosomes existed only for 2U, while all other U chromosomes were involved in at least one translocation (Yang et al. 1996). Rearrangements between chromosomes 6U and 1U, 3U and 7U, 4U and 5U, and 4U and 6U, relative to wheat, characterised both the U and U^{v} genomes. Furthermore, this study demonstrated that the centromeric regions of 4U and 4U^{v}, and 6U and 6U^{v} were homoeologous to the centromeric regions of wheat homoeologous group -6 and -4 chromosomes, respectively.

In order to more closely resolve the relationships between the wheat and *Ae. umbellulata* chromosomes, a genetic map was constructed in a cross between two *Ae. umbellulata* accessions using probes previously employed to map wheat loci. A simultaneous analysis of the *Ae. umbellulata* addition lines 1U, 2U, 4U, 5U, 6U and 7U was carried out to investigate whether any further rearrangements had been generated during the production of the addition lines.

Materials and methods

Plant material

The wheat variety Chinese Spring (CS), disomic single-chromosome addition lines for 1U, 2U, 5U, 6U and 7U added to CS, and a CS/4U monosomic single-chromosome addition line (Kimber 1967) were used to determine the chromosomal location of RFLP loci in *Ae. umbellulata*. A cross made by T. E. Miller between two *Ae. umbellulata* accessions ($2n = 2x = 14$; UU), A (JIC2010001) and C (JIC2010003) from the John Innes Centre (JIC) cereal collection, was used to produce the mapping population. The mapping population consisted of 122 F_2 progenies from the cross A × C.

Probes and primers

Wheat and barley probes, previously used in mapping various Triticeae populations, were obtained from the JIC collection (prefix 'PSR'; putative functions, shown in parenthesis in the locus designations, were assigned according to Smith et al. 1997), Cornell University ('BCD'), NABMGP ('ABC'), Kansas State University ('KSU'), University of Bari ('UBP'), C. Ainsworth (pCSS22 – locus *Xwye835*(*Wx*); pSh2.25 – locus *Xwye838*(*Adpg2*)), P. Carbonero (pST3 – locus *Xpsr489*(*Sus*); pST8 – locus *Xpsr490*(*Ss1*)), G. Fincher (G5 – locus *Xwia858*(*Glb35*); pλc3 – locus *Xwia483*(*Cxp1*)), L. Dennis (3′Adh – locus *Xcsd19*(*Adh*)), A. Breiman (ATP β 4/A – locus *Xtav1931*(β-*Atp*)), J. Scandalios (pCat2.1c – locus *Xpsr484*(*Cat*)), B. Lane (Germin – locus *Xbgl485*(*Ger*)), P. von Wettstein-Knowles (pACP1 – locus *Xwaxc2*(*Acl1.3*)), P. Joudrier (pTd78 – locus *Xmtd862*(*CM16*)) and D. Bringloe (pFed – locus *Xpsr803*(*Fed*)). Primer pairs J13/1 and J13/2 which detect the *Xsfr1* locus were as published by Schachermayr et al. (1994).

Marker analysis and mapping

All methods of DNA extraction, RFLP analysis and mapping were as described by Laurie et al. (1993). Amplification reactions using the J13/1 and J13/2 primers were performed as described by Schachermayr et al. (1994) but using an annealing temperature of 56°C. The genetic maps were constructed using 'Mapmaker v.3.0', supplied by E. S. Lander, Whitehead Institute for Biomedical Research, Cambridge, Massachusetts. All map positions were verified manually by examining recombination events. Genetic distances are expressed in cM (Kosambi).

Results and discussion

Wheat – *Ae. umbellulata* relationship

The chromosomal location of loci detected by 79 probes was determined using the CS/*Ae. umbellulata* single-chromosome addition lines. In total, 102 probes were tested for variation between the parents of the *Ae. umbellulata* mapping population. Sixty eight of these (67%) revealed polymorphisms with at least one of the four restriction enzymes *Eco*RI, *Eco*RV, *Dra*I and *Hin*dIII, and were used for mapping. Forty one of the probes used for mapping had also been located using the CS/*Ae. umbellulata* addition lines. Chromosomal locations for homoeoloci in wheat and *Ae. umbellulata* are presented in Table 1. As a CS/3 U line was not available, all *Ae. umbellulata* locations included in Table 1 for loci detected by wheat homoeologous group-3 probes are based on mapping data unless these probes detected a signal on any of the other CS/U addition lines. No discrepancies were found between the two data sets, which indicated that no major rearrangements had taken place during the production of the addition lines. The genetic maps, and their relationship to the wheat chromosomes, is presented in Fig. 1. The composition of the U genome is discussed below in relation to the D genome of Chinese Spring wheat, which was also taken as the base genome in a comparison of wheat and rye (*Secale cereale*) (Devos et al. 1993). The likely centromere positions have been extrapolated from the position of the wheat centromeres, and chromosomes are orientated tentatively with the short arms at the top (Fig. 1). Because of the

Table 1 RFLP probes detecting homoeoloci in wheat and *Ae. umbellulata*; chromosomal locations in *Ae. umbellulata* were based on CS/U addition-line and map data

Chromosomal location in wheat	Chromosomal location in *Ae. umbellulata*	Probes[c]
1AS 1BS 1DS	1U	*PSR11*[b], *PSR13*, *PSR161*, *PSR168*, PSR596[b], *BCD98*[a,b]
1AL 1BL 1DL	1U	PSR12[b], *PSR121*[a], *PSR162*[b]
1AL 1BL 1DL	6U	*PSR159*, 3′Adh[b], ATP β 4/A[b], *pSh2.25*
1A 1D	6U	PSR1118[b],
2AS 2BS 2DS	2U	*PSR107*, *PSR109*[a,b], *PSR130*[b], *PSR135*, *PSR137*, *PSR146*, PSR332[b], *PSR666*
2AL 2BL 2DL	2U	*PSR101*, *PSR102*[b], *PSR112*, *PSR151*, PSR540[a,b], *PSR571*[b], *PSR630*, PSR687[a,b]
2AL 2BL 2DL	6U	*PSR609*[b], PSR934[a,b], *pTtksuF41*[b], *pTtksuH16*
3AS 3BS 3DS	7U	*PSR598*, *PSR1196*[b], pTtksuG53[a,b]
3AL 3BL 3DL	3U	PSR394[b], *pλc3*[b], G5[a,b], ABC374[b], BCD131[b]
4AL 4BS 4DS	6U	*PSR139*[b], *PSR144*[b], *PSR147*, *PSR155*, *PSR166*, *PSR584*, *PSR921*[b], *Germin*[b]
4AS 4BL 4DL	4U	*PSR104*, *PSR920*, *PSR1318*
4AL 4BL 4DL	4U	*PSR1051*[b]
4BL 4DL	5U	*pTd78*[b]
5AL 4BL 4DL	5U	*PSR164*[b], *PSR567*[a], *pCat2.1c*[a]
5AS 5BS 5DS	5U	*PSR118*, *pTdubp3*[b]
5AL 5BL 5DL	5U	*PSR2*[a], *PSR109*[a,b], *PSR120*, *PSR145*[b], *PSR370*[b], *PSR637*[b], *PSR911*
4AL 5BL 5DL	4U	*PSR115*[b], *PSR580*, ABC310[a,b]
4AL 5BL	4U	*PSR1316*[b]
7BS 5BL 5DL	4U	*PSR567*[a,b]
6AS 6BS 6DS	6U	*PSR8*[b], PSR106[b], *pCat2.1c*[a,b], *pTtksuG48*[a]
6AS 6BS 6DS	*4U*	PSR141[a,b], PSR831[b]
6AS 6BS 6DS	7U	*PSR167*[a]
6AS 2BS 6DS	6U	*PSR899*[b]
6AL 6BL 6DL	4U	*PSR2*[a,b], *PSR149*[b], PSR154[b], *pTtksuD12*
6AL 6BL 6DL	2U	*pTtksuF37*
7AS 4AL 7DS	7U	*PSR119*, *PSR160*, *PSR604*[b], *pCSS22*[b], pST3[a,b]
7AS 7BS 7DS	7U	PSR65[b], *PSR103*, *PSR108*[a], *PSR152*, *pST8*[b], *pACP1*, *BCD98*[a]
7AL 7BL 7DL	7U	*PSR2*[a], *PSR56*[a], *PSR72*, *PSR129*[b], *PSR165*[b], *PSR547*[a,b], *PSR690*[b], *pFed*[b], pTdubp9[a,b]
7AL 7BL 7DL	6U	*PSR121*[a,b], PSR680[b], *PSR687*[a,b], *PSR1954*[b], *pTtksuD2*[b]

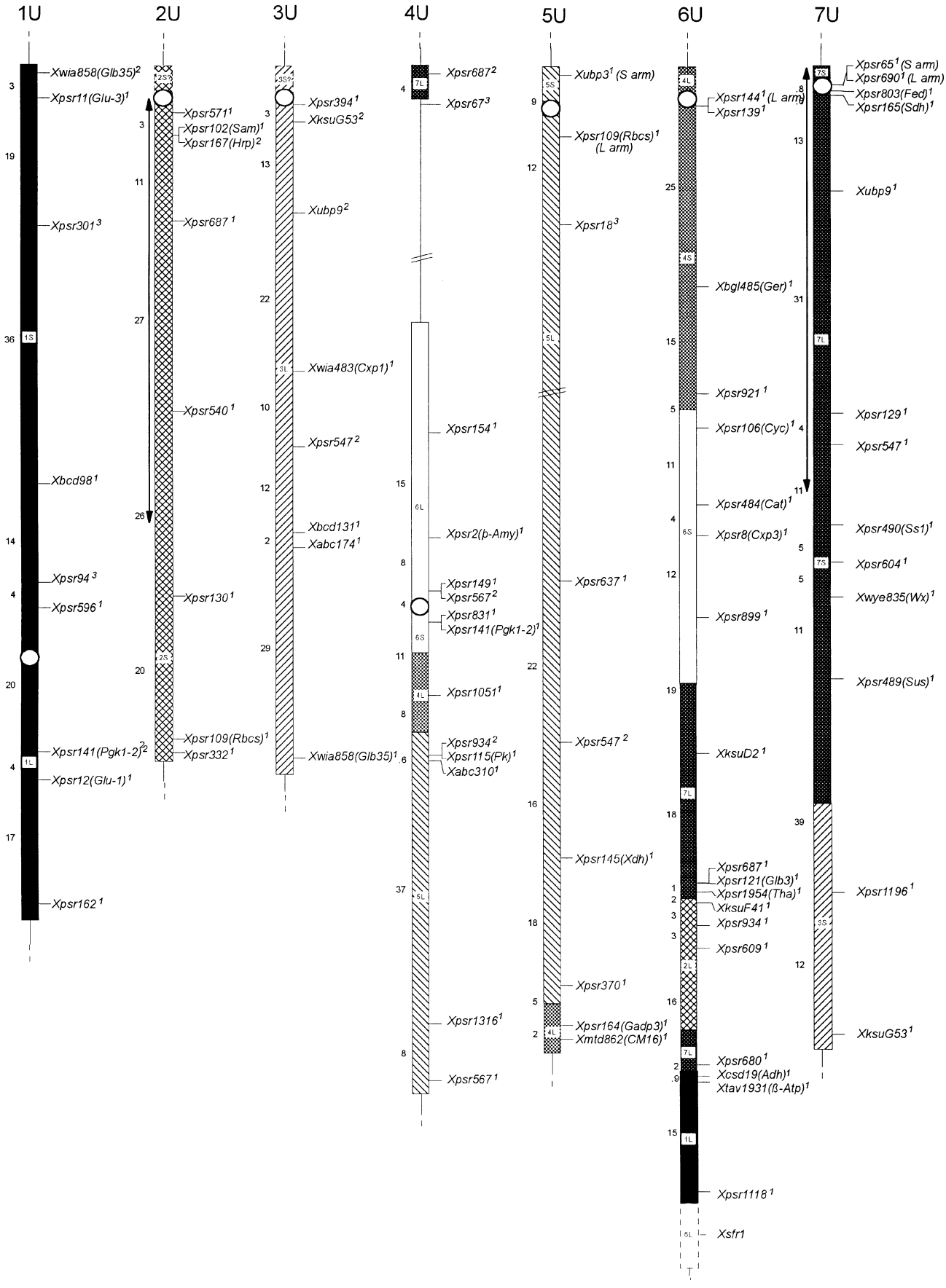
[a] These probes are not single copy and detect multiple loci in wheat and *Ae. umbellulata*
[b] Probes for which loci have been mapped in the *Ae. umbellulata* A × C cross
[c] Probes for which the chromosomal locations of loci have been identified using the CS/U addition lines are *in italics*

extensive rearrangements that have taken place in the *Ae. umbellulata* genome relative to wheat, it was not always possible to unambiguously correlate the arms of the genetic maps with the cytologically assigned short and long arms.

Chromosome 1 U. Chromosome 1 U is homoeologous and co-linear with most, but not all, of wheat chromosome 1D. The distal segment of the long arm of wheat 1D is homoeologous to a distal segment of 6UL. This is consistent with the results of Yang et al. (1996) which suggested that 1 U has undergone a reciprocal translocation relative to wheat. Although it is likely that 1 U carries a, presumably small, segment with homoeology to a wheat chromosome other than 1D, no RFLP evidence is available as to the existence of this *Ae. umbellulata* segment on 1 U.

Koebner (1987) demonstrated that the trypsin inhibitor locus, *Ti-2*, which is located on the long arm of the homoeologous group-5 chromosomes of wheat, is located on *Ae. umbellulata* chromosome 1 U. Furthermore, substitutions of 1D for 1 U appear to be meiotically unstable at low temperatures, a character which is reminiscent of the effect of the removal of chromosome 5D (Riley 1966). These results would suggest that 1 U carries a segment of the original 5 U; however, our study provided no evidence for a rearrangement involving chromosomes 1 U and 5 U.

Chromosome 2 U. Chromosome 2 U is homoeologous with most, but not all, of wheat chromosome 2D. As the distal part of 2DL is co-linear with part of chromosome 6 U, 2 U appears also to have been involved in a reciprocal translocation. No mapping evidence is available for the presence on 2 U of a segment with homoeology to part of the long arm of 6D. However, one probe, pTtksuF37, was identified that mapped to the long arms of the wheat group-6 chromosomes and identified a hybridizing fragment on the 2 U disomic addition. Chromosome 2 U has also undergone an inversion, which spans at least part of the long arm and most likely includes part of the short arm. Kimber (1967) observed that centromeres are generally located at sub-median positions throughout the *Triticum* and *Aegilops* genera and suggested that sub-terminal centromere positions were the result of structural


1U
2U
3U
4U
5U
6U
7U
Xwia858(Glb35)2
Xpsr11(Glu-3)1
Xpsr3013
Xbcd981
Xpsr943
Xpsr5961
Xpsr141(Pgk1-2)2
Xpsr12(Glu-1)1
Xpsr1621
Xpsr5711
Xpsr102(Sam)1
Xpsr167(Hrp)2
Xpsr6871
Xpsr5401
Xpsr1301
Xpsr109(Rbcs)1
Xpsr3321
Xpsr3941
XksuG532
Xubp92
Xwia483(Cxp1)1
Xpsr5472
Xbcd1311
Xabc1741
Xwia858(Glb35)1
Xpsr6872
Xpsr673
Xpsr1541
Xpsr2(ß-Amy)1
Xpsr1491
Xpsr5672
Xpsr8311
Xpsr141(Pgk1-2)1
Xpsr10511
Xpsr9342
Xpsr115(Pk)1
Xabc3101
Xpsr13161
Xpsr5671
Xubp31 (S arm)
Xpsr109(Rbcs)1 (L arm)
Xpsr183
Xpsr6371
Xpsr5472
Xpsr145(Xdh)1
Xpsr3701
Xpsr164(Gadp3)1
Xmtd862(CM16)1
Xpsr1441 (L arm)
Xpsr1391
Xbgl485(Ger)1
Xpsr9211
Xpsr106(Cyc)1
Xpsr484(Cat)1
Xpsr8(Cxp3)1
Xpsr8991
XksuD21
Xpsr6871
Xpsr121(Glb3)1
Xpsr1954(Tha)1
XksuF411
Xpsr9341
Xpsr6091
Xpsr6801
Xcsd19(Adh)1
Xtav1931(ß-Atp)1
Xpsr11181
Xsfr1
Xpsr651(S arm)
Xpsr6901 (L arm)
Xpsr803(Fed)1
Xpsr165(Sdh)1
Xubp91
Xpsr1291
Xpsr5471
Xpsr490(Ss1)1
Xpsr6041
Xwye835(Wx)1
Xpsr489(Sus)1
Xpsr11961
XksuG531

alterations. A large inversion, including the centromere, would explain the sub-terminal centromere position on 2 U (arm ratio L : S = 1 : 3.3; Friebe et al. 1995).

Chromosome 3 U. Yang et al. (1996) suggested that a translocation may exist between *Ae. umbellulata* chromosomes 3 U and 7 U. This is confirmed by our study which shows that most or all of the short arm of the original chromosome 3 U has been translocated to 7 U. No evidence was found for the presence of a part of the original 7 U onto 3 U, indicating that an exchanged segment, if present at all, is small. However, no 3 U addition-line data were available to confirm this. This rearrangement is however consistent with the sub-terminal centromere position on chromosome 3 U (arm ratio L : S = 1 : 2.3; Friebe et al. 1995).

Chromosome 4 U. This chromosome is probably homoeologous with the distal part of the long arm of wheat 7D, the long arm and the proximal part of the short arm of 6D, a segment of 4DL and the distal segment of 5DL. The centromeric region of 4 U is homoeologous with the centromeric region of the wheat group-6 chromosomes, as was previously reported by Yang et al. (1996). Evidence for homoeology between 4 U and 7D is based on the locus *Xpsr687-4U*. In rye, the probe PSR687 was shown to detect one locus on 2RL and two loci about 25-cM apart on a segment of 6RL with homoeology to the wheat group-7 chromosomes (Devos et al. 1993 and unpublished results). Homoeoloci in *Ae. umbellulata* are located on 2 U, 4 U and 6 U. The 4UL/5UL translocation noted by King et al. (1994) has, within the limits of our analysis, an identical breakpoint to the 4AL/5AL and 4RL/5RL translocations in wheat and rye.

Chromosome 5 U. Chromosome 5 U is homoeologous with the short arm and most of the long arm of 5D, and a distal segment of 4DL. However, 5 U appears to be completely co-linear with wheat chromosome 5A, including the reciprocal 4L/5L translocation common to other Triticeae genomes. Chromosome 5 U also carries a distal 18S–25S and a more proximal 5S rRNA site similar to the rDNA sites on wheat chromosome 5D (Castilho and Heslop-Harrison 1995). The location of *Ti-2* loci on the long arms of the wheat homoeologous group-5 chromosomes and on chromosome 1 U of *Ae. umbellulata* (Koebner 1987) may indicate that this chromosome has been rearranged relative to wheat; however, no further evidence was found in this study.

Chromosome 6 U. The study by Yang et al. (1996) indicated that this chromosome had been involved in a multiple translocation with 1 U and 4 U, and that the 6 U centromere was homoeologous to the wheat group-4 centromeres. However, our results show that the structure of 6 U is even more complex. Chromosome 6 U carries segments with homoeology to the short arms of wheat 4D (orientated centromere to telomere), wheat 6DS, and distal segments of wheat 7DL, 2DL (intercalated in the 7L segment) and 1DL. Chromosome 6 U may also carry a segment with homoeology to the distal part of 6DL. The reasoning for this unconfirmed hypothesis is that two loci, *XksuD27* and *Xsfr1*, were shown to be tightly linked to the *Lr9* resistance gene (Schachermayr et al. 1994; Autrique et al. 1995). No chromosomal location was obtained in *Ae. umbellulata* for the locus detected by probe pTtksuD27, which maps distally on 6DL in wheat and *T. tauschii* (Gill et al. 1991; Marino et al. 1996). Primer pairs J13/1 and J13/2, however, clearly detect a *Xsfr1* locus on the CS/6 U addition line. This highly rearranged structure of chromosome 6 U is consistent with the extreme acrocentric nature of 6 U, with a long-to- short arm ratio of 5 : 1 (Friebe et al. 1995).

Chromosome 7U. This chromosome is composed of segments with homoeology to a small proximal segment of 7DS, the proximal region of 7DL, most of 7DS, and the short arm of 3D. The interspersed 7DS/7DL structure is the result of a pericentric inversion spanned by *Xpsr65* and *Xpsr547*.

In *Ae. umbellulata*, chromosomal rearrangements have been extensive and have involved all seven chromosomes. Assuming that the D genome of wheat has the more ancestral configuration, the *Ae. umbellulata* chromosomes must have undergone a minimum of 11 reciprocal translocations and inversions to arrive at their current structure (data not shown). Major homoeologous relationships between wheat and *Ae. umbellulata* were confirmed for chromosomes 1 U, 2 U, 3 U, 5 U and 7 U. Although 4 U and 6 U are partly homoeologous with wheat groups 4 and 6, it is clear that the centromeres of 4 U and 6 U are homoeologous to the centromeres of the wheat group-6 and -4 chromosomes, respectively. Therefore, it may be pertinent, as was suggested by Yang et al. (1996), to re-name the current 4 U to 6 U, and *vice versa*, to reflect the existing homoeology across the centromeres.

Fig. 1 Relationship between the genomes of *Ae. umbellulata* and wheat. Arm designations *within rectangular blocks* indicate homoeology of the *Ae. umbellulata* chromosome segments to wheat. *Double-headed arrows* indicate inversions. *Circles* indicate predicted centromere positions. [1]indicates loci for which homoeoloci were identified in wheat; [2]indicates loci detected in addition to the homoeoloci presented in Table 1; [3]indicates loci for which no homoeoloci have, as yet, been mapped in wheat

Sears' wheat – *Ae. umbellulata* translocation lines

In 1956, Sears produced a number of irradiation-induced translocation lines between wheat and *Ae.*

umbellulata chromosome 6 U to transfer the leaf rust resistance gene, *Lr9*, to wheat. Five of these lines have been maintained and have been characterised by C-banding and GISH analysis (Friebe et al. 1995). They identified line T40 as T6BL.6BS-6UL, T41 as T4BL.4BS-6UL, T44 as T2DS.2DL-6UL, T47 as T6BS.6BL-6UL, and T52 as T7BL.7BS-6UL. The size of the introgressed *Ae. umbellulata* segment varied considerably and amounted to 79%, 86%, 28%, 7% and 48% of the total *Ae. umbellulata* chromosome 6UL arm in lines T40, T41, T44, T47, and T52 respectively. Mapping of *Lr9* in material derived from T47 ('Transfer'), the line which carries the smallest *Ae. umbellulata* segment, showed that the gene was introgressed in the distal region of chromosome arm 6BL and was tightly linked to the loci *XksuD27* and *Xsfr1* (Schachermayr et al. 1994; Autrique et al. 1995). Although we were not able to map loci from that region of the long arm of homoeologous wheat group 6 in *Ae. umbellulata*, *Xsfr1* was shown to be located on the 6 U addition. The 6 U segment, carrying *Lr9* and homoeologous to the distal part of the long arms of the wheat group-6 chromosomes, is likely to be located distally on chromosome arm 6UL.

Although it would appear that most of Sears' radiation-induced transfers involved non-homoeologous chromosomes, they may in fact represent homoeologous exchanges between wheat chromosomes and different segments of the highly rearranged 6 U. The exception is line T52, where radiation treatment gave rise to a translocation between a segment of wheat chromosome arm 7BS and *Ae. umbellulata* chromosome 6 U. As no segment was found on 6 U with homoeology to the short arms of the wheat group-7 chromosomes, T52 must have been the result of a non-homoeologous exchange. For lines T40, T41, T44 and T47, the size of the introgressed fragments corresponds well with a homoeologous exchange model, with lines T6BS.6BL-6UL and T4BL.4BS-6UL carrying the smallest and largest *Ae. umbellulata* segment respectively (Fig. 1). Only translocations between 6BL and 6UL would be fully compensating. Exchanges of 4BS, 6BS and 2DL with 6 U would result in most of the wheat genes being replaced with homoeologous *Ae. umbellulata* genes; however, these lines would carry an extra *Ae. umbellulata* copy in addition to the three wheat copies for some genes. Most other rearrangements would result in deletions. So, although radiation-induced transfers are not normally considered to be homoeologous exchanges, it may be that such exchanges give rise to pollen with a competitive advantage compared to random rearrangements.

These data suggest that the numerous rearrangements that distinguish the *Ae. umbellulata* and wheat genomes not only affect gene introgression by homoeologous recombination, but also influence gene transfer following pre-meiotic irradiation treatment.

Translocation breakpoints

Comparisons of the structural changes that have taken place within Triticeae species, such as the 4/5/7 translocations in wheat (Devos et al. 1995) and the numerous rearrangements that characterise the rye (Devos et al. 1993) and *Ae. umbellulata* genomes, indicate that the translocation involving chromosome arms 4L and 5L has, within the limits of analysis, identical breakpoints in wheat, rye and *Ae. umbellulata*. In addition, some chromosomes were identified that appeared to break preferentially in a specific region. An example is the distal segment of 7L that has been translocated, although to different chromosomes, in rye (Devos et al. 1993) and *Ae. umbellulata*, and has been deleted from 7AL in our Chinese Spring (CS) nullisomic 1A-tetrasomic 1D (N1AT1D) stocks and from 7DL in our CS ditelosomic 1BS stocks (unpublished results). Similarly, most of the genetical short arm of chromosome 3 was translocated in *Ae. umbellulata* and the same region has been deleted in the JIC CS ditelosomic 2AS stock (unpublished results).

A FISH study in Chinese hamster cell lines has revealed that in the presence of the enzyme responsible for the synthesis of telomere repeats, telomerase, 93% of the breakpoints of spontaneously occurring terminal deletions and 25–46% of radiation-induced breaks are located in chromosome regions containing interstitial telomere repeats (ITR) (Slijepcevic et al. 1996) and most likely within the telomeric sequences themselves (Alvarez et al. 1993). This may be explained by the fact that double-stranded breaks that generate 3′-end overhangs in ITR sequences provide a good template for the *de novo* synthesis of telomeres, thereby stabilizing the broken chromosomes. The study by Slijepcevic et al. (1996) also implied that a subclass of DNA breaks within ITRs were not healed, and were likely to be rejoined or misjoined, giving rise, for example, to chromosomal translocations. In wheat, a number of telomere repeats have been mapped at interstitial sites (Mao et al. 1997) and interstitial sites can also be observed by *in situ* hybridization (T. Schwarzacher, personal communication). So far, no studies have been carried out in *Ae. umbellulata*. However, if ITRs are indeed the remnants of ancestral fusion sites (Meyne et al. 1990), one would expect them to be present at homoeologous locations across Triticeae species. None of the translocation breakpoints in wheat appeared to co-map with any of the limited number of ITRs mapped to-date, and confirmation of the hypothesis that preferential breakage sites within Triticeae chromosomes may lie within ITRs clearly needs to await further experimental data.

Implications for wheat-alien gene introgression and evolutionary considerations

Structural rearrangements between genomes of related species have important implications for the development

of strategies for gene transfer (Devos et al. 1993). The introgression of donor genes from a translocated genome into a receptor background using induced homoeologous recombination between, what are thought to be, homoeologous chromosomes may result in progeny with non-balanced genomes. The presence of chromosomal deletions and duplications, although not necessarily lethal in a hexaploid background such as wheat, will almost certainly affect the agricultural performance of the generated lines.

Interestingly, there appears to be no correlation between the number of chromosomal rearrangements that distinguish species and their degree of relatedness. Phylogenetic studies of Triticeae species indicate that *Hordeum*, *Secale* and the *Aegilops*/*Triticum* group diverged, in that order, from a common Triticeae ancestor (Kellogg et al. 1996). With increasing time of divergence, one might expect a deterioration in genome relationships. However, the minimum number of rearrangements that differentiate the D genome of wheat from that of *Ae. umbellulata*, the closer relative, rye, and the more distant relative, barley, is 11, seven (Devos et al. 1993), and none (Laurie et al. 1993) respectively. This clearly indicates that the number of structural rearrangements cannot be taken as a measure of evolutionary divergence. A wider comparative analysis within the grass family has demonstrated that some chromosomal rearrangements characterise taxonomic groups, while others were likely to have accumulated at differential rates during, or following, speciation (Devos and Gale 1997).

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