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Chromosomal rearrangements in the rye genome relative to that of wheat

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Summary. An RFLP-based genetic map of *Secale cereale* has provided evidence for multiple evolutionary translocations in the rye genome relative to that of hexaploid wheat. DNA clones which have previously been mapped in wheat indicated that chromosome arms 2RS, 3RL, 4RL, 5RL, 6RS, 6RL, 7RS and 7RL have all been involved in at least one translocation. A possible evolutionary pathway, which accounts for the present day R genome relative to the A, B and D genomes of wheat, is presented. The relevance of these results for strategies designed to transfer useful genes from rye, and probably other related species, to wheat is discussed.

Key words: Translocations – Rye – RFLP – Genetic maps – Comparative mapping – Co-linearity

Introduction

Restriction fragment length polymorphism (RFLP) analysis has become a central technique in the development of dense genetic maps. Linkage maps are now being constructed in a variety of plant species mainly with the aim of localising genes of agronomic or adaptive significance, which can then be easily manipulated in breeding programmes. With the increasing interest in the use of alien germplasm as a source of useful genes for many crop species, it is also important to establish the degree of co-linearity of the genetic maps of the chromosomes of cultivated crops and those of related species. Indeed, a degree of synteny between the chromosomes of donor and recipient species is a prerequisite for the transfer of genetic material via homoeologous recombination. Chromosomal rearrangements, such as inversions, translocations or deletions in the donor relative to the recipient species are not only expected to restrict pairing, and thus the degree of homoeologous recombination possible, but may also result in deletion and duplication of genetic material in the recombinants produced.

Within the Triticeae, evolutionary translocations involving chromosome arms 4AL, 5AL and 7BS in wheat (Naranjo et al. 1987), and 4RL, 5RL and 7RS in rye (Koller and Zeller 1976; Naranjo et al. 1987; Naranjo and Fernández-Rueda 1991), deduced from patterns of allosyndetic chromosome pairing, have since been confirmed by RFLP analysis (Liu et al. 1992). However, the analysis of induced homoeologous pairing of wheat and rye chromosome arms in wheat × rye hybrids, combined with available data on homoeoallelic series of genes and RFLP loci in wheat and rye, have indicated the existence of further translocations in rye relative to wheat (Naranjo and Fernández-Rueda 1991). Other evidence, such as the location of *Xpsr167*, a wheat homoeologous group 6 short arm RFLP locus, on 4R (Sharp et al. 1989), and the location of *Ep-R1*, a marker for wheat homoeologous group 7 long arms, on 6R (Benito et al. 1991), has also indicated further differences in genome arrangement between rye and wheat.

In this paper, we present linkage maps of all seven rye chromosomes and provide evidence, based on the locations of molecular and biochemical markers, for the existence of multiple evolutionary translocations which differentiate the rye and wheat genomes.

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Materials and methods

Chromosomal locations

The chromosome arm locations in wheat of RFLP probes were determined by hybridization to DNA from nullisomic-tetrasomic (NT) (Sears 1954) and ditelosomic (DT) (Sears and Sears 1979) lines of the cultivar Chinese Spring (CS). The CS/*Secale cereale* cv 'Imperial' (Driscoll and Sears 1971) chromosome addition lines were used to assign chromosomal locations in rye. Genetic mapping was performed using a population of 120 F_2 plants, or their F_3 derivatives, from the cross between the inbred rye lines Ds2 × RxL10 (Masojć and Gale 1991).

RFLP markers

The clones numbered PSR100–PSR200 are cDNAs from the library described by Chao et al. (1989). The other PSR-probes are genomic DNA clones from *Pst*I and *Eag*I genomic libraries (PSR300–460, Harcourt 1992; PSR540–PSR700, PSR900–PSR999, Devos et al. 1992a), from a *Hpa*II library (PSR1000–PSR1199, Cheung et al. 1992), and from a PERT library (PSR1200–PSR1300, Clarke et al. 1992). The sources of the known function clones employed are described in the legend of Fig. 1.

Protein markers

Segregation analysis of the grain esterase, *Est-5*, previously located on the long arms of the homoeologous group 3 chromosomes in wheat and on 6RL in rye, was carried out according to the method described by Ainsworth et al. (1984). An endopeptidase, *Ep-1*, was also mapped using the technique described by Koebner et al. (1988). *Ibf-1*, a locus for an iodine-binding factor, was mapped on 5RL according to the method described by Liu and Gale (1988).

RFLP and segregation analysis

All techniques of DNA extraction, restriction enzyme digestion, gel electrophoresis, Southern transfer, probe labelling and hybridization were as described by Devos et al. (1992a). The segregation data were analyzed by the software package, MAPMAKER Version 2.0 program, supplied by E. S. Lander, Whitehead Institute for Biomedical Research, Cambridge, Massachusetts. Recombination values were converted to genetic distances (cM) using the Kosambi function.

Results

Homoeologous locations of DNA and protein markers in wheat and rye

A comparison of the chromosomal locations of RFLP and biochemical loci in wheat and rye, obtained by NT, DT and CS/*S. cereale* cv Imperial single chromosome addition line analyses, revealed a number of intergenomic relationships other than simple homoeology between rye and wheat chromosomes. These loci and their locations in wheat and rye are presented in Table 1.

Intrachromosomal mapping

Linkage studies in the rye cross Ds2 × RxL10 provided evidence that the rye genome was extensively rearranged

Table 1. Chromosomal locations of RFLP and biochemical markers indicating the presence of translocations in the rye genome relative to that of wheat

Chromosomal location in rye	Chromosomal location in wheat			Loci
2R	6AS	6BS	6DS	*Gli-2[Sec2]*[a]
	7AS	4AL	7DS	*Xpsr160*
4R	6AS	2BS	6DS	*Xpsr899*[b]
	6AS	6BS	6DS	*XCxp3*[b], *XNra(1)*[b], *Xpsr167*[b]
	7AS	4AL	7DS	*XNra(2)*[b], *XNra(3)*[b], *XPer1*[b], *Xpsr119*[b], *Xpsr604*[b], *Per-4*
	7AS	7BS	7DS	*XSs1*[b], *Xpsr108, Xpsr150, Xpsr152*[b], *Xpsr662*[b], *Xpsr913*
5R	5AL	4BL	4DL	*Aco-2[Aco2], β-Amy-1 [β-Amy1], XCat*[b], *Xpsr164*[b]
6R	3AL	3BL	3DL	*Ndh-3, Est-5*[b], *XGlb33*[b], *XGlb35, Xpsr1205*[b]
	3AL	–	–	*Xpsr1203*[b]
	–	3BL	–	*Xpsr454*[b]
	7AL	7BL	7DL	*Ep-1*[b], *XGlb3*[b]–*Xpsr121*[c], *Xpsr148*[b], *Xpsr687*[b], *Xpsr965*[b]
7R	2AS	2BS	2DS	*Xpsr109, Xpsr150*[b]
	2AS	–	2DS	*Xpsr566*[b], *Xpsr928*[b], *Xpsr649*[b]
	4AS	4BL	4DL	*XFbp*[b], *Acph-1 [Acph], Xpsr59*[b], *Xpsr104*[b], *Xpsr157*[b], *Xpsr163*[b], *Xpsr1051*[b], *Xpsr1318*
	4AL	5BL	5DL	*Xpsr115*[b], *Xpsr580*[b]
	7BS	5BL	5DL	*Xpsr567*[b]

[a] The gene symbols are those of wheat; the rye equivalents, where known, are shown in [ ]
[b] Loci mapped in the Ds2 × RxL10 cross
[c] pLW2.1, which recognizes *XGlb3*, and PSR121 are synonymous clones

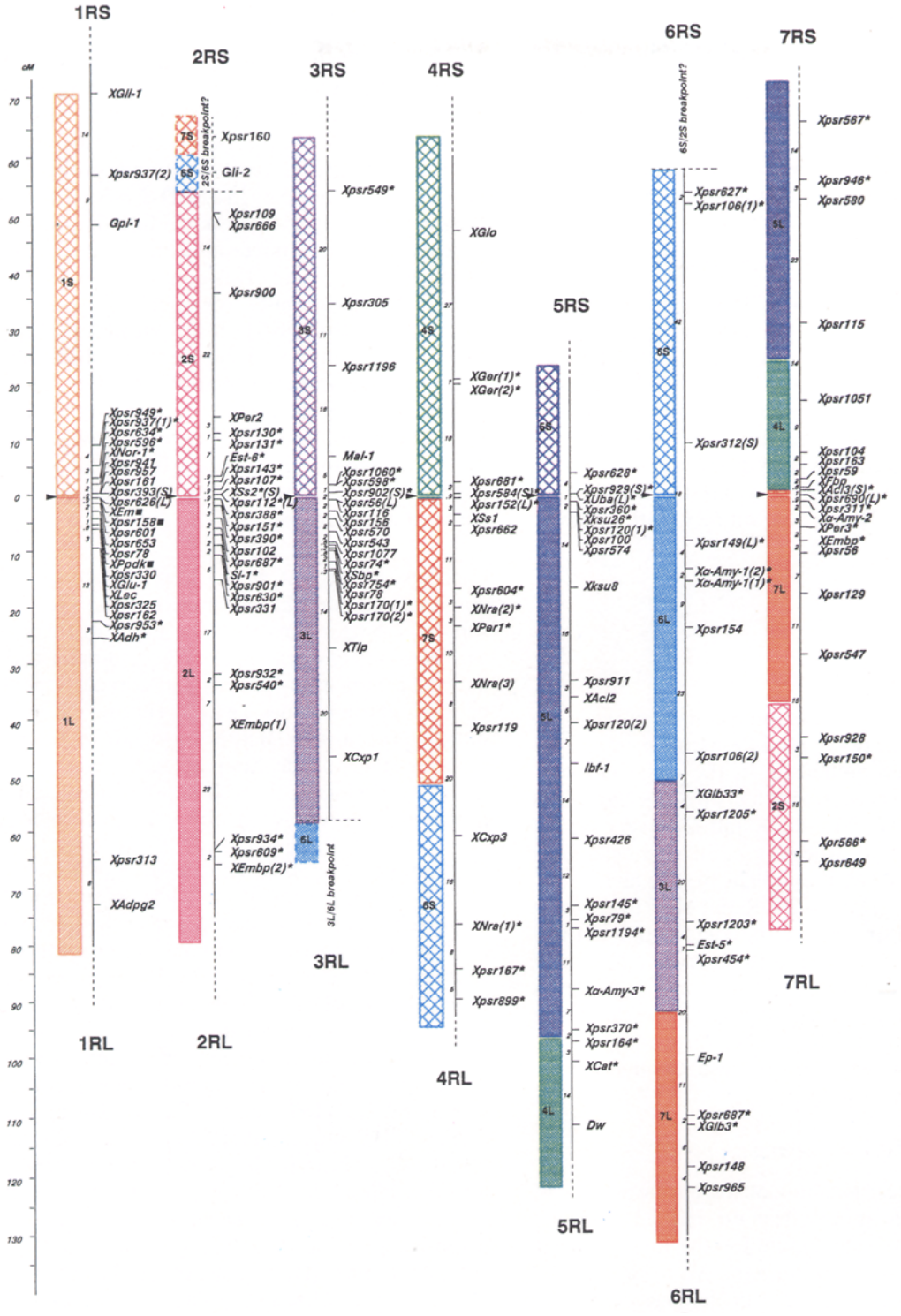

Fig. 1. Genetic maps of the *S. cereale* chromosomes and their relationships with the homoeologous wheat chromosomes. Sources of probes: *Xksu8* and *Xksu26*, B. Gill (Kam-Morgan et al. 1989); *XGlo* (PSP511), R. Quatrano (Quatrano et al. 1986); *XGer* (Germin cDNA), B. Lane (Dratewka-Kos et al. 1989); *XSs1* (pST8), P. Carbonero (Maraña et al. 1988); *XNra(1)*, *XNra(2)* and *XNra(3)* (bNRp 10), A. Kleinhofs (Cheng et al. 1986); *Xpsr899* (#7), M. Gulli (Personal communication); *XCxp3* (2437), D.C. Baulcombe (Baulcombe et al. 1987a); *XPer1* (BP1), S. K. Rasmussen (Rasmussen et al. 1991); *XAcl2* (pLH/ACPII/1.6), L. Hansen (Personal communication); *Xα-Amy-3* (33), D.C. Baulcombe (Baulcombe et al. 1987b); *Xα-Amy-1* (501), D.C. Baulcombe (Baulcombe and Buffard 1983); *XCat* (pCat2.1c), J.G. Scandalios (Bethards et al. 1987); *XGlb33* (p7E) and *XGlb35* (G5), G.B. Fincher (Personal communication); *XGlb3* (pLW2.1), G.B. Fincher (Loi et al. 1988); *XAdpg2* (pSh2.25), C.C. Ainsworth (Personal communication), *XUba* (UBA1), P.M. Hatfield (Hatfield et al. 1990). The sources of the other known function clones are listed elsewhere: 1R (Wang et al. 1991), 2R (Devos et al. 1992b), 3R (Devos et al. 1992a), 7R (Rognli et al. 1992).* indicates preferred map locations, obtained with a LOD < 2.5.■, indicates loci, mapped in a sub-population of 60 F_2 plants, for which the map position could not be determined unequivocally. ►, indicates the centromere

relative to that of wheat. Genetic maps for chromosomes 1R (Wang et al. 1991 and this paper), 2R and 3R (Devos et al. 1992a, b), 6R (Masojć and Gale 1991 and this paper), 7R (Rognli et al. 1992), and those of 4R and 5R, and their relationships with the homoeologous wheat chromosomes, are presented together in Fig. 1.

Abnormalities in wheat aneuploid stocks

During the routine screening of DNA clones a number of deletions and localised polymorphic regions have been observed in the CS aneuploid stocks. One such rearrangement has been found in the CS nullisomic-1A tetrasomic-1D stock maintained at the Cambridge Laboratory, and was used as a diagnostic for the present study. This line carries a deletion of the terminal region of 7DL which exactly, within the limits of the analysis, matches the segment on 6RL with homoeology to wheat 7L.

Discussion

The genetic map of Secale cereale

An important feature of the genetic maps of rye is the clustering of sequences around the centromere, due to localisation of recombination in the distal chromosome regions. The clustering of loci on the genetic maps of chromosomes 1R, 2R, 3R, 5R and 7R is very similar to that observed in wheat, e.g., in homoeologous groups 2 and 3 (Devos et al. 1992a, b). The lack of this feature in the linkage maps of 4R and 6R is likely to be due to a modified strategy for the construction of these later maps, where the previously observed co-linearity between the linkage maps of wheat and rye (Devos et al. 1992a, b) allowed the probes to be preselected on the basis of their location on the wheat maps (C. N. Chinoy, J. Z. Jia, unpublished results) in order to obtain more even coverage.

Homoeologous wheat-rye relationships

Homoeologous relationships of the chromosomes of rye to those of wheat have been established primarily by their ability to compensate for the loss of wheat chromosomes in substitution lines. More precise evidence has been accumulated over the past decade by the establishment of the chromosomal locations of an array of biochemical and molecular markers, listed in McIntosh (1988) and subsequent supplements. However, recently it has become clear that, for a growing number of biochemical and DNA markers, these locations do not fit a strict homoeologous wheat-rye relationship. When these loci are assembled, as listed in Table 1, the evidence for multiple chromosomal rearrangements between the wheat and rye genomes is very strong. The mapping of many of these loci (Fig. 1) confirms this hypothesis and, in many cases, defines the intergenomic translocation breakpoints very closely. The fact that identical translocations are indicated in cv Imperial and at least one, and probably both, parents of the mapping cross, Ds2 × RxL10, suggests that the rearrangements are evolutionary and define *S. cereale*, rather than reflecting intervarietal differences of more recent origin. This conclusion is further supported by the results obtained by Naranjo and Fernández-Rueda (1991) from pairing analyses in a range of different wheat/rye hybrids, which indicated that only rye chromosome arms 1RS, 1RL, 2RL, 3RS, 4RS and 5RS were homoeologous with their corresponding wheat arms. These chromosome pairing data are considered together with the linkage data presented in Fig. 1 in the discussion of the individual rye chromosomes that follows.

Chromosome 1R. All wheat homoeologous group 1 markers examined have homoeoloci on rye chromosome 1. Comparisons with the maps of the group 1 chromosomes of wheat (M. L. Wang, unpublished data) indicate complete co-linearity and arm correspondence between chromosomes 1A, 1B, 1D and 1R. Furthermore, neither arm of 1R appears to pair with any wheat chromosome outside homoeologous group 1. Thus there is no evidence that 1R is other than completely homoeologous with the group 1 wheat chromosomes.

Chromosome 2R. Sixteen probes, all of which detect loci on the long arms of the wheat group 2 chromosomes (2WL), map to the long arm of chromosome 2R. No homoeoloci have been found in wheat for *Si-R1*, a subtilisin inhibitor, or *XEmbp-2R*. Homoeology between 2RL and 2WL is further supported by their high level of chromosome pairing.

The linkage map of the short arm of chromosome 2R comprises ten loci with homoeologous locations in wheat and rye. However, the lack of pairing between 2RS and 2WS indicates that 2RS is structurally different from the short arms of the group 2 wheat chromosomes. RFLP studies have demonstrated that the distal ends of the short arms of the wheat group 2 chromosomes, comprising the loci *Xpsr109*, *Xpsr150*, *Xpsr928*, *Xpsr566*, and *Xpsr649* (Devos et al. 1992b), have homoeoloci located at the distal end of 7RL (Rognli et al. 1992). Furthermore, *Gli-2[Sec2]* is located on 6AS, 6BS and 6DS in wheat, 2RS in *S. cereale* and $6R^m$ in *S. montanum*. This has been presented as evidence for a translocation between part of the short arm of a group 2 chromosome and part of the short arm of a group 6 chromosome (2S/6S translocation) in the genome of *S. cereale* relative to those of wheat and *S. montanum* (Shewry et al. 1985). *Xpsr160*, the most distally mapped locus on 7AS, 4AL and 7DS in wheat (Harcourt 1992),

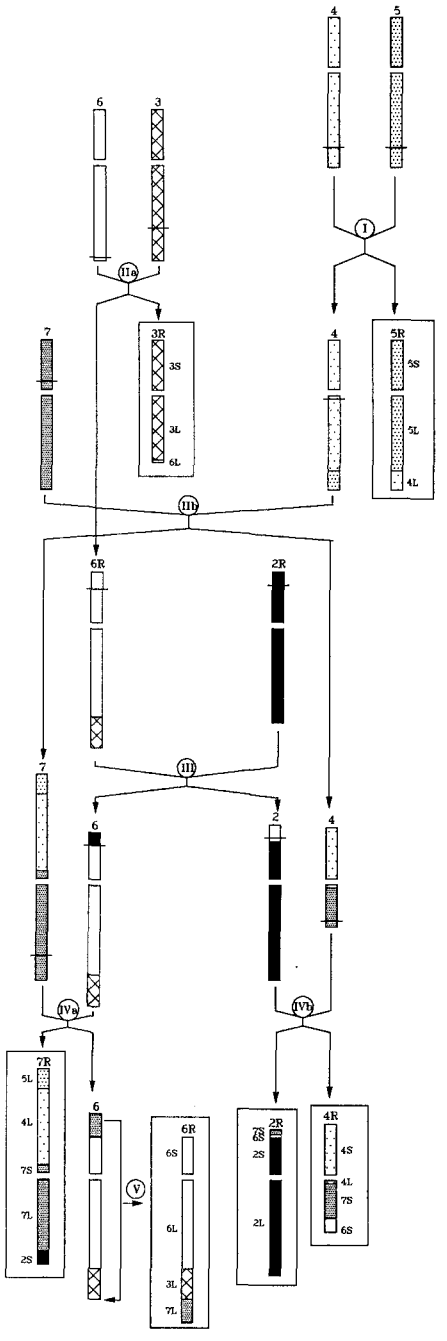

Fig. 2. A model for the evolution of the *S. cereale* genome from a basic Triticeae genome. The proposed order of events is indicated in roman numerals.

is also present on chromosome 2R of Imperial rye. Unfortunately, polymorphism could not be detected for either *Xpsr160* or *Gli-2* in the Ds2 × RxL10 cross, and hence we were unable to obtain evidence for their location on 2RS by linkage. The positions of *Xpsr160* and *Gli-2* on 2RS shown in Fig. 1 are inferred from their relative positions on the wheat map and the likely consequence of the various rearrangements in the rye genome as described below in the discussion of Fig. 2.

Chromosome 3R. The 3R map comprises only markers with homoeologous locations in wheat and rye, with the exception of *Xpsr549* which has non-homoeologous 1AL, 2BS and 3AL locations in wheat that provide no prediction for rye locations. The map location of *Mal-1* on 3RS (Devos et al. 1992a) relative to the 3RL location obtained with DT analysis (Liu and Gale 1988) remains unexplained.

The involvement of 3R in an interchromosomal translocation is, however, indicated by the homoeologous locations of *XGlb33*, *XGlb35*, *Xpsr1205*, *Xpsr1203*, *Est-5*, and *Xpsr454* on 3AL, 3BL and 3DL in wheat and on 6R in rye. The phenotype of 6R wheat/rye addition lines also indicates that this translocation may carry the genes controlling red seed colour and sphaerococcum-like grain shape, both of which are controlled, in wheat, by genes carried on the long arms of the group 3 chromosomes (Miller 1984).

No biochemical or molecular evidence is available for the presence of a reciprocally translocated rye segment to 3RL. However, the observation of pairing of the distal end of 3RL with 6WL, with the relatively high frequency of 2%, is indicative of the existence of the 3L/6L translocation shown in Fig. 1.

Chromosome 4R. The genetic map of 4R suggests that this chromosome has been involved in multiple translocations. RFLP and pairing data show that the short arm of chromosome 4R is homoeologous with wheat chromosome arms 4BS and 4DS and partially homoeologous with chromosome arm 4AL, which has itself been involved in evolutionary translocations between chromosome arms 4AL, 5AL, and 7BS (Naranjo et al. 1987; Liu et al. 1992).

The long arm of 4R comprises a proximal segment with homoeology to most of the short arms of wheat group 7 chromosomes, as deduced from the locations of biochemical and molecular loci, listed in Table 1, and *Pc*, the gene controlling purple culm (Miller 1984). The distal end of 4RL shows, both in pairing and RFLP analyses, homoeology with the distal ends of the short arms of the wheat group 6 chromosomes.

The fact that *Xpsr920*, which is located on the long arms of the wheat homoeologous group 4 chromosomes (4AS 4BL 4DL), is located on 4R rather than 7R indicates that a small portion of 4L remains on 4R and hence that the 4L/7S breakpoint is not centromeric. Unfortunately, PSR920 revealed no polymorphism between the two mapping parents with the restriction digests tested.

Chromosome 5R. The short arm and most of the long arm of 5R show homoeology with wheat chromosomes 5B and 5D. However, the distal end of 5RL carries two loci, *Xpsr164* and *XCat*, with homoeoloci on 5AL, 4BL and 4DL. The involvement of 4AL and 5AL in a

reciprocal translocation has previously been reported (Naranjo et al. 1987; Liu et al. 1992), and the available evidence does not exclude the possibility that both the wheat and rye 4L/5L translocations derive from the same event. The predicted homoeology of 5RS with 5WS and the distal end of 5RL with a terminal segment of 5AL, 4BL and 4DL is supported by chromosome pairing data.

A single partially recessive dwarfing gene was observed to segregate in the mapping population. This gene, which causes a height reduction of about 60 cm in RxL10 was found to be located distally on 5RL in the 4L segment. This gene has been assigned the temporary symbol *Dw* since tests of allelism with *dw1* and *Ddw6*, two dwarfing genes with loci on 5R (listed in Melz and Schlegel 1990), have not been carried out.

Chromosome 6R. Pairing and linkage analyses indicate that chromosome 6R has been involved in multiple interchromosomal rearrangements. Although all 6RS loci examined have homoeoloci on wheat chromosome arms 6AS, 6BS and 6DS, pairing between 6RS and 6WS was seldom observed. This is likely to be due to the effective deletion of the terminal segment of 6RS, now present on 4RL, which may preclude pairing initiated at the ends of the chromosome arms. The genetic map of 6RL comprises a proximal region with homoeology to the wheat group 6 chromosomes, an interstitial region with homoeology to the long arms of the wheat group 3 chromosomes, and a distal region with homoeology to the long arms of the wheat group 7 chromosomes.

Chromosome 7R. The genetic map of chromosome 7R shows regions with homoeology to wheat groups 2, 4, 5 and 7 and has been discussed in detail by Rognli et al. (1992). It is of interest that, as with all other rye chromosomes, 7R carries the centromeric region of the original group 7 chromosome. *XAcl3* and *Xpsr65*, which were not mapped in the Ds2 × RxL10 population, are both present on 7R and on 7S in wheat.

Evolution of the S. cereale *genome*

The evolutionary route by which the *S. cereale* genome arose from the basic Triticeae genome can be rationalised, to some extent, by drawing on evidence for similar translocations in other related genomes, and information indicating the presence of some translocations in the more primitive rye species *S. montanum.* One such hypothesis is shown in Fig. 2. This model employs a minimum number of successive chromosomal rearrangements starting from the basic genome, assumed to be exemplified by the D genome of hexaploid wheat. The choice of the D genome is, of course, arguable, but the present day arrangement of the A and B genomes of wheat can be most easily rationalised as deriving from the D genome conformation (Liu et al. 1992). Moreover, as far as the authors are aware, the D genome has the same conformation as the H genome of barley.

The 4L/5L translocation (event I in Fig. 2) is placed first in the model since its presence in various Triticeae species suggests that this translocation is probably extremely primitive. The breakpoints, on the original 4L between *Xpsr1051* and *Xpsr164* and on the original 5L between *Xpsr370* and *Xpsr115*, are identical, within the limits of the analysis, to those defining the 4A/5A translocation in wheat. Evidence for the 4A/5A and 4R/5R translocations representing the same event is strengthened by the presence of similar translocations in *Aegilops umbellulata* and *Thinopyrum bessarabicum* (I. P. King, personal communication).

The pericentric inversion seen in chromosome 4A, whereby the 5L segment became attached to 4A at a distal position on the short arm, has not taken place in the rye genome. The key diagnostics, shown in Fig. 1 on 7RS, are that the 5L segment is attached to the 4L segment at the original 4L/5L breakpoint and that the gene order and orientation of the 4L chromosome arm, dispersed between 5R and 7R, is identical to that of 4DL (unpublished results).

The 4L/7S and 3L/6L translocations (events II in Fig. 2) are placed next in the model because both are probably present in the *S. montanum* genome. The evidence concerning 4L/7S derives from the similar plant morphology of the CS/4R and CS/4R^m disomic addition lines, including the presence of the purple culm gene in both additions (Miller 1984), which in wheat is carried on 7S (Law 1966). The evidence for the 3L/6L translocation in both rye species relies on the presence of the grain esterase gene, *Est-5*, carried on the long arms of the wheat group 3 chromosomes and both 6R and 6R^m (Ainsworth et al. 1986).

Van Heemert and Sybenga (1972) reported that the genomes of *S. cereale* and *S. montanum* differed by at least two interchanges involving chromosomes 2R, 6R and 7R. Therefore, the remaining three translocations may characterize *S. cereale* alone. It remains an open question, however, of whether the rearrangements involved an interchange between chromosome arms 2S and 6S (event III in Fig. 2), followed by a 6S/7L and a 2S/4L translocation (events IV in Fig. 2), or interchanges between 2S/7L and 6S/4L followed by a 2S/6S rearrangement. The chromosomal location of the *Got-1* genes on the short arms of the homoeologous group 6 chromosomes in wheat (Hart 1975), and on the long arms of both chromosomes 4R and 7R in rye (Wehling 1991), favours the first model (Fig. 2), assuming that during the evolution from *S. montanum* to *S. cereale* the *Got-1* gene underwent duplication, followed by translocation of one gene copy to 7RL, while the second copy was translocated first to 2RS and subse-

quently to 4RL. The 6S/7L translocation will have been followed by a pericentric inversion in chromosome 6R (event V in Fig. 2), comparable to the events leading to the present-day arrangement of 4A in wheat (Liu et al. 1991), in order to obtain its present conformation as shown in Fig. 1.

Implications for breeding

Strategies for the introgression of genes through meiotic exchange from related species to wheat are predicated on homoeology between the donor and recipient chromosomes. In general, these strategies involve the induction of pairing between the alien and cultivated crop species chromosomes, if necessary under conditions of relaxed pairing control, followed by selection of the desired phenotype through a backcross programme. These methods assume that the translocations induced will involve substitution of wheat alleles with homoeoalleles from the donor species.

The results presented here indicate that, although the assumption concerning co-linearity in the region of the target gene is likely to be correct, homoeologous transfer will often not provide the required genotype. The important point is that homoeologous recombination must be induced between a wheat chromosome with homoeology to the chromosome segment on which the target gene is carried. Furthermore, if the target gene is on an interstitial segment (e.g., the 3L segment on 6RL), either a double cross-over event or a further round of homoeologous recombination will be required to return to a balanced genomic state. In order to achieve such transfers, some knowledge of the chromosomal and map location of the target gene is required.

A further complication arises from the reduction in pairing between wheat and rye chromosomes when the distal chromosome regions are not homoeologous. An examination of the rye-wheat pairing data presented by Naranjo and Fernández-Rueda (1991) shows that substantial pairing occurs only between wheat and rye chromosome arms where the homoeology extends to the telomeres, i.e., 1RS/1WS, 1RL/1WL, 2RL/2WL, 3RS/3WS, 3RL/6WL, 4RS/4WS, 4RL/6WS, 5RS/5WS, 5RL/4WL, 6RL/7WL, 7RS/5WL, and 7RL/2WS. Interstitial homoeologous chromosome regions pair infrequently, e.g., 3RL/3WL, 5RL/5WL, 6RL/6WL, as do chromosome arms where homoeology is not complete in the distal region, such as 6RS/6WS. Thus, transfers in which recombination occurs in interstitial regions may be relatively rare.

To date, successful wheat-rye transfers with a positive impact on wheat production have been limited to substitutions and translocations involving chromosome 1R, evidently the only non-translocated rye chromosome. Similarly, studies investigating the recovery rate of rye chromosomes in F_4 progenies from a hexaploid triticale (AABBRR) × bread wheat (AABBDD) cross revealed that chromosome 1R was recovered most frequently, while chromosomes 4R, 5R and 7R were always transmitted together (Gustafson et al. 1985; Takita et al. 1988). These preferential substitutions of D genome for R genome chromosomes are likely to be correlated with the rearrangements in the rye genome, and clearly have a bearing on attempts to construct substituted hexaploid triticales where almost all will result in an unbalanced and, to a greater or lesser extent, aneuploid genome.

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