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Homoeology of rye chromosome arms to wheat

T. Naranjo* and P. Fernández-Rueda

Departamento de Biología Funcional, Universidad de Oviedo, E-33071 Oviedo, Spain

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Summary. Cytological markers such as diagnostic C-bands, telocentrics, and translocations were used to identify the arms of rye chromosomes associated with wheat chromosomes at metaphase I in *ph1b* mutant wheat × rye hybrids. Arm homoeologies of rye chromosomes to wheat were established from the results of metaphase I pairing combined with available data on the chromosomal location of homoeoloci series in wheat and rye. Only arms 1RS, 1RL, 2RL, 3RS, and 5RS showed normal homoeologous relationships to wheat. The remaining arms of rye appeared to be involved in chromosome rearrangements that occurred during the evolution of the genus *Secale*. We conclude that a pericentric inversion in chromosome 4R, a reciprocal translocation between 3RL and 6RL, and a multiple translocation involving 4RL, 5RL, 6RS, and 7RS are present in rye relative to wheat.

Key words: Homoeologous pairing – Translocations – Rye evolution – C-banding

Introduction

The genomes of wheat and of the other species within the tribe Triticeae are assumed to be evolved from a common ancestral genome. The homoeologous relationships between the chromosomes of wheat and related species can be identified using three main approaches: substitution-compensation tests, analysis of homoeologous pairing at metaphase I, and genetic maps. Sears (1966) established the seven homoeologous groups of wheat using nullisomic-tetrasomic combinations. The analysis at metaphase I of induced homoeologous pairing in wheat × rye hybrids determined the homoeologous relationships between the arms of most wheat chromosomes, which were identified by means of C-banding (Naranjo et al. 1987, 1988a, b). The long arms of wheat chromosomes belonging to homoeologous groups 1, 3, 6, and 7 and of homoeologues 4B–4D and 5B–5D showed full pairing homoeology, as did the short arms of wheat chromosomes belonging to groups 1, 3, 5, and 6 and of homoeologues 4B–4D and 7A–7D. Chromosomes 2A, 2B, and 2D behaved as homoeologues, but the homoeologies of their arms could not be identified. A reduced homoeology of 4AL to 7AS and 7DS, of 5AL to 4BL and 4DL, and of 7BS to 5BL and 5DL was identified. The arms 4AL, 5AL, and 7BS are evidently involved in a double translocation that arose during the evolution of common wheat. Chromosome arm 4AS seldom paired; the existence of a pericentric inversion in chromosome 4A of hexaploid wheat was suggested as an explanation of such behavior. These structural modifications of chromosomes 4A, 5A, and 7B are also present in durum wheat (Naranjo 1990). On the basis of the location of 13 sets of homoeoloci, Sharp and Soltes-Rak (1988) concluded that group 2 chromosomes of hexaploid wheat have the following arm homoeology: 2AS, 2BS, and 2DS are homoeologous as are 2AL, 2BL, and 2DL. On the other hand, Chao et al. (1989) constructed genetic maps of wheat homoeologous group 7 chromosomes and confirmed that 4AL carries a translocated segment from 7BS.

On the basis of the ability of rye chromosomes to compensate when substituted for chromosomes of a single homoeologous wheat group, chromosomes 1R, 2R, 3R, 5R, and 6R were assigned to homoeologous groups 1, 2, 3, 5, and 6, respectively, while 4R and 7R showed partial and reciprocal homoeology to groups 4 and 7 (Sybenga 1983; Zeller and Hsam 1983; Miller 1984). The

* To whom correspondence should be addressed. Present address: Departamento de Genética, Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain

location of homoeoloci on the chromosomes of wheat and rye is in agreement with this group assignment, while at the same time indicating that most of the rye chromosomes can also show homoeology to more than one group of wheat (Zeller and Hsam 1983; Miller 1984).

In the wheat × rye hybrids analyzed by Naranjo et al. (1987, 1988a, b), chromosomes 1R, with an intercalary C-band adjacent to the nucleolar organizing region, and 5R, with both a proximal secondary constriction and a subterminal C-band in the long arm, were identified. The remaining rye chromosomes - metacentric chromosomes 2R, 3R, and 7R, and submetacentric chromosomes 4R and 6R – could not be identified. The frequency of association at metaphase I between wheat chromosomes and 1R or 5R indicated that 1RL is homoeologous to 1AL, 1BL, and 1DL, and 5RL is homoeologous to 5AL and, to some extent, to 4BL and 4DL. The existence of a translocation in rye involving 4RL and 5RL was demonstrated. Wheat-rye associations involving any of the unidentified rye chromosomes were less frequent than those involving 1RL and 5RL, except for an arm of a metacentric rye chromosome, probably 2R, that in some plants reached a level of pairing comparable to that of 1RL (Naranjo et al. 1988b). Differences in pairing shown by rye chromosomes in wheat × rye hybrids were suggested to be influenced by the following factors: the occurrence of a structural differentiation of rye chromosomes to wheat, the presence or absence of telomeric C-bands in rye chromosomes, and between groups variation for the frequency of competitive wheat-wheat pairing.

There are cytological markers in rye that enable the identification of metacentric chromosomes 2R, 3R, and 7R and submetacentric chromosomes 4R and 6R. These chromosome markers are intercalary or telomeric C-bands, telocentrics, and translocations giving rise to rearranged chromosomes that can be identified by their size. Some of these markers have been used in this work to identify the arms of rye chromosomes associated with wheat chromosomes at metaphase I in wheat × rye hybrids in order to establish the homoeology of the chromosome arms of rye to wheat.

Materials and methods

Plant material

The *ph1b* mutant line of *Triticum aestivum* cv "Chinese Spring" (Sears 1977) was crossed to the following plants of *Secale cereale*:

1) One plant heterozygous for both translocation T242W (2RL/6RL) (Sybenga et al. 1985) and an interstitial C-band on chromosome arm 2RL. From this cross, hybrids of three types (called *a, b* and *j*) were analyzed.

2) One plant of the double ditelocentric 3RS, 3RL line, which was provided by J. Sybenga, Agricultural University, Wageningen, The Netherlands. From this cross, hybrids of two types (called *c* and *d*) were analyzed.

3) One plant homozygous for a 2RL intercalary C-band marker and heterozygous for a prominent telomeric C-band that marked 3RS. Seeds carrying these two chromosome markers were obtained and provided by A. Lukaszewsky, University of Missouri, Columbia, Mo. USA From this cross, hybrids of the type (called *e*) were selected and analyzed.

4) One plant homozygous for both the intercalary C-band marker on 2RL and a prominent telomeric C-band marker on 3RL. The sample of seeds from which this plant was selected was also provided by A. Lukaszewski. From this cross, hybrids of the type called *f* were analyzed.

5) One plant homozygous for translocation T282W (5RL/7RS) (Sybenga et al. 1985). From this cross, hybrids of the type called *g* were analyzed.

6) One plant from cv La Raña homozygous for an intercalary C-band on 6RL, which was provided by J. Orellana, E.T.S.I. Agrónomos, Universidad Politécnica, Madrid, Spain. From this cross, hybrids of the type called *h* were analyzed.

7) One plant homozygous for translocation T501W (4RL/5RL) (Sybenga et al. 1985). From this cross, the hybrid of the type called *i* was analyzed.

All plants were grown in a controlled environment chamber at 16–18 °C after vernalization for 8 weeks at 6–8 °C.

Chromosome identification

Anthers at first metaphase of meiosis were fixed in 1:3 acetic-acid/alcohol, and stored at 0–4 °C for a minimum of 2 months. The fixed material was squashed and stained according to the C-banding technique of Giraldez et al. (1979).

Figure 1 shows a generalized C-banding pattern for the normal chromosomes of rye present in the hybrids analyzed as well as for telocentrics 3RS and 3RL of hybrids of types *c* and *d*, and the chromosomes involved in translocations T282W, T501W, and T242W present in hybrids of types *g, i,* and *j,* respectively. In each type of hybrid, rye chromosomes with a normal structure showed the following differences with respect to the C-banding pattern of Fig. 1. (1) The type *a* plant carried a thin telomeric C-band on 6RS and lacked the prominent intercalary C-band on 6RL(6RLi$^-$). (2) The type *b* plant was 6RLi$^-$ and carried a thin or medium-sized telomeric C-band on 3RS,

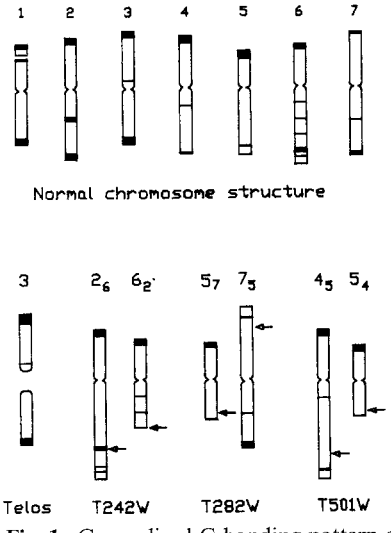

Fig. 1. Generalized C-banding pattern of the rye chromosomes with the normal structure present in the *ph1b* ABDR hybrids analyzed and structural modifications used as chromosome markers. *Arrows* indicate translocation points

4RS, and 6RS. (3) Hybrids of types *c* and *d* were 2RLi$^-$ (without the intercalary C-band on 2RL) and 6RLi$^-$; in addition, hybrids of the type *d* lacked telomeric heterochromatin on 2RL. (4) In types e and f hybrids, all chromosome arms except 3RS or 3RL, respectively, lacked prominent telomeric heterochromatin. These hybrids were 6RLi$^-$. (5) Type *g* hybrids were 2RLi$^-$ and 6RLi$^-$. (6) Type *h* hybrids were 2RLi$^-$; only the arms 7RS and 7RL showed a prominent telomeric C-band. (7) The type *i* plant was 2RLi$^-$ and 6RLi$^-$ and carried prominent telomeric C-bands on 7RS and 7RL. (8) The type *j* plant was 2RLi$^-$ and 6RLi$^-$ and showed a thin telomeric band on 4RS and a thick telomeric band on 7RL.

Chromosome identification was carried out in the following way. Wheat chromosomes and rye chromosomes 1R and 5R, and their arms, were identified according to Naranjo et al. (1987, 1988b) with the following modification. The arms of chromosomes 2A and 2D that paired with 2BS were considered to be 2AS and 2DS, respectively, and 2AL and 2DL, the arms that paired with 2BL. This was based on the homoeologous relationships of group 2 chromosome arms established by Sharp and Soltes-Rak (1988). In the hybrids carrying translocation T282W or T501W, the translocated chromosome 5R was the smallest one of the R genome. The chromosome nomenclature used here is that agreed to by the Seventh International Wheat Genetics Symposium, where the previous designations of 4A and 4B were reversed.

The identification of metacentric chromosomes 2R, 3R, and 7R was mainly based on the presence of the chromosome markers mentioned above. In addition, a proximal thin C-band on 3RS and an intermediate thin C-band on 7RL (Sybenga 1983), which were apparent in some pollen mother cells (PMCs), allowed the identification of 3R and 7R, respectively, in hybrids where such chromosomes carried no distinctive marker but showed a telomeric C-heterochromatin constitution different from that of the other metacentric chromosomes.

Chromosome 2R had the long arm marked with the intercalary C-band in plant types *a, b, e,* and *f,* and with translocation T242W in the type *j* plant. In type *c* and *d* hybrids chromosome 2R could be identified since 3R was split into the telocentrics 3RS and 3RL, and 7R showed a different telomeric C-banding. In the type *c* plant 2RS and 2RL could not be distinguished cytologically from one another. In the two type *d* plants the arm of chromosome 2R without telomeric heterochromatin was identified as 2RL by virtue of pairing with 2AL, 2BL, and 2DL, In type *h* hybrids metacentric chromosomes 2R, 3R, and 7R showed a different C-banding pattern. The proximal thin C-band on 3RS and the intermediate thin C-band on 7RL, which were apparent in some PMCs, enabled the identification of 3R and 7R. The other metacentric chromosome was 2R. In this case, the 2RL arm was also identified by virtue of pairing with 2AL, 2BL, and 2DL. In type *g* hybrids chromosomes 2R and 3R could not be distinguished from one another. In type *i* hybrids none of the three metacentric chromosomes 2R, 3R, and 7R, could be identified. Types *c, g,* and *i* hybrids are not considered in the data on chromosome 2R.

The arms of chromosome 3R were identified in hybrids of types *b, c, d, e,* and *f.* Types *c* and *d* plants carried telos 3RS and 3RL substituted for the normal chromosome 3R; the two telos could be distinguished from one another by size. In types *e* and *f* plants 3R was marked with a telomeric C-heterochromatin block located on 3RS and 3RL, respectively. In the type *b* plant the marked chromosome was 2R; 3R and 7R, and their arms, with apparent differences in their telomeric C-heterochromatin constitution, could be identified since the diagnostic thin C-bands on 3RS and 7RL were observed in some PMCs. Chromosome 3R was identified in hybrids of types *a, h,* and *j,* but its arms could not be distinguished from one another in many PMCs. Hybrids of the types *a, g, h, i,* and *j* are not considered in the data on chromosome 3R.

Chromosome 7R was marked with translocation T282W, which involves its short arm, in type *g* hybrids. This chromosome and its arms could be identified by C-banding in plants of types *a, b, c, d, e, f,* and *j.* Although chromosome 7R was identified in type *h* plants, its arms, with similar telomeric C-heterochromatin blocks, could not be distinguished from one another in PMCs where the intercalary thin C-band on 7RL was not apparent. Types *h* and *i* plants are not considered in the data on chromosome 7R.

Submetacentric chromosomes 4R and 6R, with apparent differences in the length of their arms, could be identified in plants of types *a, h, i,* and *j.* In the type *a* plant 4RS carried much more telomeric C-heterochromatin than 6RS, and several intercalary thin C-bands that identify 6RL were apparent in PMCs with good quality C-banding. In type *h* hybrids chromosomes 4R and 6R could be identified since 6RL was marked with a prominent intercalary C-band. The type *i* plant carried translocation T501W that marked 4RL and 5RL; chromosome 6R differed in size from the translocated chromosomes 4R/5R and 5R/4R. The type *j* plant carried translocation T242W that marked 2RL and 6RL; chromosome 4R was longer than the translocated chromosome 6R/2R. Plants of types *b, c, d, e, f,* and *g* are not considered in the data on chromosomes 4R and 6R.

In each type of hybrids, one to three plants and generally more than 500 PMCs were analyzed.

Results and discussion

Pairing at metaphase I

In order to facilitate the identification of the homoeology of chromosome arms of rye to wheat, associations at metaphase I involving a given arm of rye and any of the arms or segments of wheat chromosomes that are homoeologous were pooled. The frequencies of association at metaphase I between rye chromosome arms with normal structure and arms of wheat chromosomes in the *ph1b* wheat × rye hybrids analyzed are given in Table 1. All associations observed between the chromosome arms of rye involved in translocations T242W (2RL/6RL), T501W (4RL/5RL), and T282W (4RL/7RS), and wheat chromosomes were distally located, which suggested that bonds occurred in the translocated (terminal) segment of the rye chromosomes. The frequencies of these wheat-rye associations are given in Table 2. Figure 2 shows examples of metaphase I configurations with chromosome arms of wheat and rye being bound.

Between-plants variation in the presence or absence of telomeric C-heterochromatin blocks of rye chromosomes and in their size was accompanied by a significant variation in the frequency of homoeologous wheat-rye pairing at metaphase I, confirming that telomeric C-heterochromatin of rye hinders wheat-rye pairing (Naranjo 1982). For chromosome arms 1RL and 2RL, which reached a relatively high level of pairing with wheat chromosomes, the presence of telomeric C-heterochromatin brought about a considerable decrease in the frequency of association with wheat chromosomes, but wheat-rye

Table 1. Frequency (%) of association between arms of rye and wheat chromosomes in *ph1b* wheat × rye hybrids with different C-banding pattern for the R genome

Rye-wheat association[a]	C-banding of the R telomere[b]			Rye-wheat association[a]	C-banding of the R telomere[b]		
	++ (plants)	+ (plants)	− (plants)		++ (plants)	+ (plants)	− (plants)
1RS-1WS	0.7		2.5	1RL-1WL	10.5		24.9
1RS-others (W)	0.1		0.0	1RL-others (W)	0.0		0.0
	(*a*+*b*+*c*+*d*+*g*+*i*+*j*)		(*e*+*f*+*h*)		(*a*+*b*+*c*+*d*+*g*+*i*+*j*)		(*e*+*f*+*h*)
2RS-2WS	0.0	0.2	0.3	2RL-2WL	1.8	9.1	25.6
2RS-others (W)	0.0	0.2	0.3	2RL-others (W)	0.1	0.1	0.2
	(*a*+*b*+*d*+*j*)	(*e*+*f*)	(*h*)		(*a*+*b*)	(*e*+*f*+*h*)	(*d*)
3RS-3WS	0.0	2.4	5.3	3RL-3WL	0.2		0.3
3RS-others (W)	0.4	0.2	0.2	3RL-6WL	0.1		2.0
	(*c*+*d*+*e*)	(*b*)	(*f*)	3RL-others (W)	0.1		0.0
					(*b*+*c*+*d*+*f*)		(*e*)
4RS-(4BS, 4DS)	0.1	5.3		4RL-(4BL, 4DL)		0.1	0.0
4RS-others (W)	0.0	0.0		4RL-6WS		1.8	1.7
	(*a*+*i*)	(*h*+*j*)		4RL-others (W)		0.2	0.1
						(*a*+*j*)	(*h*)
5RS-5WS	0.2	1.0		5RL-(5BL, 5DL)			0.3
5RS-others (W)	0.0	0.0		5RL-(5AL, 4BL, 4DL)			20.3
	(*a*+*b*+*c*+*d*+*g*+*i*+*j*)	(*e*+*f*+*h*)		5RL-others (W)			0.0
							(*a*+*b*+*c*+*d*+*e*+*f*+*h*+*j*)
6RS-6WS	0.1	0.0		6RL-6WL			0.2
6RS-others (W)	0.0	0.0		6RL-7WL			0.9
	(*i*+*j*)	(*a*+*h*)		6RL-3WL			0.2
				6RL-others (W)			0.2
							(*a*+*h*+*i*)
7RS-(7AS, 7DS)		0.0		7RL-7WL	0.0	0.1	
7RS-(5BL, 5DL, 7BS)		3.2		7RL-2WS	0.3	0.8	
7RS-others (W)		0.1		7RL-others (W)	0.2	0.2	
		(*a*+*b*+*c*+*d*+*e*+*f*+*j*)			(*g*+*j*)	(*a*+*b*+*c*+*d*+*e*+*f*)	

[a] W means any of the three wheat genomes

[b] ++, Presence of a prominent telomeric C-band; +, presence of a medium-sized or a thin C-band; −, absence of telomeric C-heterochromatin. The different types of hybrids analyzed in each case are indicated in parenthesis

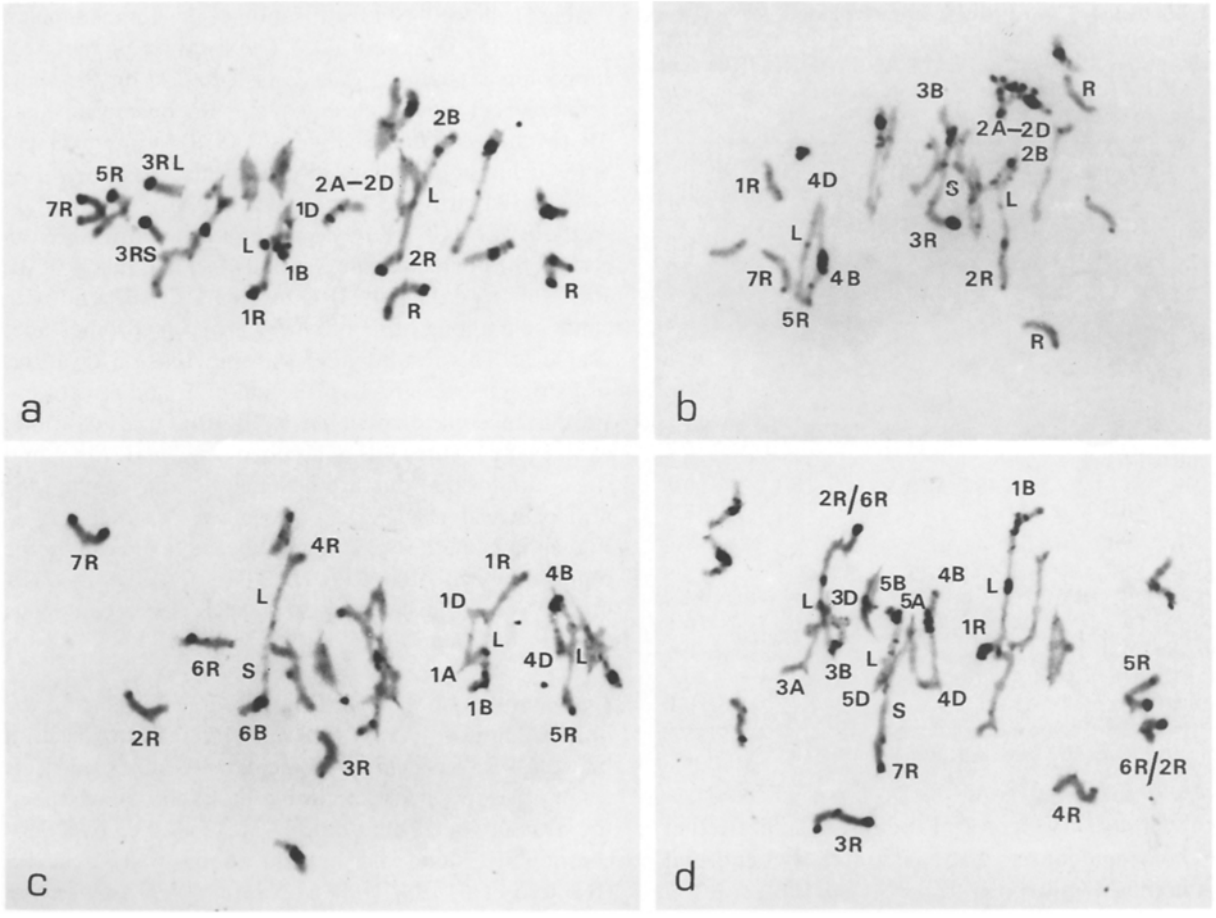

Fig. 2a–d. Association of rye and wheat chromosome arms in *ph1b* ABDR hybrids. **a** The arms 1RL-1BL-1DL are bound. In the chain quadrivalent formed by group 2 chromosomes, 2RL is bound with one of the arms 2AL or 2DL and 2BL with the other one. (Plant of type *d*). **b** The arm pairs 2RL-2BL, 3RS-3BS, and 5RL-4DL are bound. (Plant of type *f*). **c** The arm pairs 5RL-4BL and 4RL-6BS and the four arms 1RL-1DL-1AL-1BL are bound. (Plant of type *h*). **d** Association of the arms 1BL-1RL, 3BL-6RLt (the translocated segment of chromosome 2R/6R), and 5BL-5DL-7RS. (Plant of type *j*)

associations occurred in the presence of prominent telomeric C-bands. For arms 1RS, 3RS, 3RL, 4RS, and 5RS, which showed lower wheat-rye pairing levels, the presence of prominent telomeric C-bands almost totally suppressed their association with wheat chromosomes.

Naranjo et al. (1989) demonstrated that most, if not all, of the associations at metaphase I between the long arms of group I chromosomes in wheat × rye hybrids are the result of chiasmata formed at pachytene. They concluded that the frequency of wheat-rye associations at metaphase I can be used as an estimate of wheat-rye recombination. On the basis of this conclusion, the frequencies of rye-wheat associations in the absence of telomeric C-heterochromatin, which are listed in Table 2, may concern breeders interested in transferring useful agronomic characters from rye to wheat.

Homoeologous relationships

The frequencies of the rye-wheat associations that are listed in Tables 1 and 2, especially those of plants without telomeric C-bands, in combination with the chromosomal location of different genetic markers in wheat and rye allowed us to identify the following homoeologous relationships of rye chromosome arms to wheat.

Chromosome 1R. The short arm paired with 1AS, 1BS, and 1DS, and the long arm paired with 1AL, 1BL, and 1DL, which is in agreement with earlier reports (Naranjo et al. 1987, 1988a, b). The *Nor-1, Gpi-1, Per-1,* and *Gli-1* sets of loci are located on the short arm of wheat and rye group 1 chromosomes, and the *Mdh-1, Glu-1* and *Pur-1* sets of loci are located on the long arm of these chromo-

Table 2. Frequency (%) of pairing at metaphase I between the translocated segment of the chromosome arms of rye involved in translocations T242W (2RL/6RL), T501W (4RL/5RL), and T282W (4RL/7RS) and arms of wheat chromosomes in *ph1b* wheat × rye hybrids

Rye-wheat association[a]	Translocation	Type of hybrids	%
2RLt-2WL	2RL/6RL	*j*	0.0
2RLt-others (W)			0.0
6RLt-6WL	2RL/6RL	*j*	0.8
6RLt-7WL			0.8
6RLt-3WL			0.8
6RLt-others (W)			0.5
4RLt-(4BL, 4DL)	4RL/5RL	*i*	0.2
4RLt-6WS			0.5
4RLt-others (W)			0.2
5RLt-(5BL, 5DL)	4RL/5RL	*i*	0.7
5RLt-(5AL, 4BL, 4DL)			17.5
5RLt-others (W)			0.7
5RLt-(5BL, 5DL)	5RL/7RS	*g*	1.1
5RLt-(5AL, 4BL, 4DL)			26.6
5RLt-others (W)			0.1
7RSt-(7AS, 7DS)	5RL/7RS	*g*	0.0
7RSt-(5BL, 5DL, 7BS)			0.8
7RSt-others (W)			0.1

[a] W means any of the three wheat genomes

somes (McIntosh 1988). All of these data indicate that 1RS is homoeologous to 1AS, 1BS, and 1DS and that 1RL is homoeologous to 1AL, 1BL, and 1DL.

Chromosome 2R. The 2RS arm seldom paired (Table 1). The location on 2RS, 2BS, and 2DS of the *Per-2* set of loci (McIntosh 1988) and the location of the two sets *Xβ-amy-2* and *Xpsr135* of RFLP loci on the short arm of wheat group 2 chromosomes and on chromosome 2R (Sharp et al. 1988, 1989) indicate some homoeology of 2RS to 2AS, 2BS, and 2DS. The lack of rye-wheat associations between these arms suggests that 2RS is structurally different from 2AS, 2BS, and 2DS. Homoeoloci *Gli-2* were found to be located on arms 2RS, 6AS, 6BS, and 6DS (McIntosh 1988). Shewry et al. (1985) located *Gli-2* genes on chromosome $6R^m$ of *S. montanum* and concluded the presence of a translocation between 2R and 6R in *S. cereale* relative to *S. montanum* and probably to wheat.

The result that pairing of 2RL with wheat chromosomes occurred (Table 1) indicated that 2RL is homoeologous to 2AL, 2BL, and 2DL. This conclusion is supported by the location of *Sod-1, Xpsr101,* and *Est-7* on chromosome 2R and on the long arm of wheat group 2 chromosomes (McIntosh 1988; Sharp et al. 1989; Liu and Gale 1990).

Chromosome 3R. The frequency of association at metaphase I between 3RS and wheat chromosomes (Table 1) allowed the identification of the homoeology of 3RS to 3AS, 3BS, and 3DS. The location of the three homeoloci sets *Est-1, Tpi-1,* and *Xpsr-123* on the short arm of wheat group 3 chromosomes and on chromosome 3R (McIntosh 1988; Sharp et al. 1989) is in agreement with such a homoeologous relationship.

The 3RL arm seldom paired with 3AL, 3BL, or 3DL. In the few PMCs where such arm associations were observed, the bonds were interstitially located. In 2% of the PMCs of type *e* plants 3RL formed a distal bond with some of the long arms of wheat group 6 chromosomes (Table 1). This result agrees with previous observations of pairing between 6AL, 6BL, and 6DL and a metacentric chromosome of rye in *ph1b* ABDR hybrids (Naranjo et al. 1988 b). Three sets of homoeoloci, *Got-3, Est-2,* and *Xpsr-156,* located on chromosome 3R and on the long arm of wheat group 3 chromosomes (McIntosh 1988; Figueiras et al. 1989; Sharp et al. 1989) indicate some homoeology of 3RL to 3AL, 3BL, and 3DL. Consequently, only a distal segment of 3RL is homoeologous to 6AL, 6BL, and 6DL.

Chromosome 4R. Pairing results (Table 1) indicate the homoeology of 4RS to 4BS and 4DS. No association between 4RS and chromosome 4A was observed. This result was expected since, during the evolution of wheat, the structure of chromosome 4A was modified by a pericentric inversion and translocations 5AL/4AL/7BS (Naranjo et al. 1987, 1988 a; Naranjo 1990). Nevertheless, 4RS is to some extent homoeologous to 4AL as can be deduced from the location of the homoeoloci sets *Adh-1* and *Pgm-1* on arms 4RS, 4AL, 4BS, and 4DS (McIntosh 1988). It is worth mentioning that on chromosomes 4A, 4B, and 4D, all three loci *Adh-1, Pgm-1, and Amp-2* are located on the same arm (4AL, 4BS, and 4DS, respectively), whereas in chromosome 4R, *Adh-1* and *Pgm-1* are located on the short arm and *Amp-2* on the long arm (Koebner et al. 1987; McIntosh 1988). This change in the position of these loci with respect to the centromere indicates the existence of a pericentric inversion in chromosome 4R of rye relative to wheat. Furthermore, the segment inverted in chromosome 4R is shorter than the one inverted in chromosome 4A.

The 4RL arm paired with the short arm of wheat group 6 chromosomes in 1.7% of the PMCs of type *h* hybrids and 1.8% of the PMCs of types *a* and *j* hybrids (Table 1). In the type *i* plant the frequency of 4RL–6AS, 4RL–6BS, or 4RL–6DS associations (Table 2) was lower owing to the fact that this plant carried a translocation (T501W) between 4RL and 5RL. Associations between the short arm of wheat group 6 chromosomes and the long arm of a submetacentric chromosome of rye were also observed by Naranjo et al. (1988b). These results indicate some homoeology of 4RL to 6AS, 6BS, and 6DS. The asociations of 4RL with other wheat chromo-

somes showed very low frequencies (Tables 1 and 2). On the basis of the location of the *Xpsr167* RFLP marker on chromosome 4R of rye and on arms 6AS, 6BS, and 6DS of wheat, Sharp et al. (1989) concluded that chromosome 4R contains genetic material from homoeologous group 6 short arm. Since metaphase I bonds between 4RL and 6AS, 6BS, or 6DS were distally located, the segment of 4RL that is homoeologous to 6AS, 6BS, and 6DS should be distal and include *Xpsr167* as well as the *Got-1* gene located on chromosome 4R (Tang and Hart 1975; Rebordinos and Pérez de la Vega 1988). In wheat, *Got-1* genes were located on arms 6AS, 6BS, and 6DS (Tang and Hart 1975). The other segment of 4RL is homoeologous to the short arm of wheat group 7 chromosomes, as deduced from the chromosomal location of the following sets of loci: *Pc* on 4RL and 7BS (Miller 1984), *Rc* on 4RL, 7A, 7BS, and 7DS (Miller 1984; McIntosh 1988), *Xpsr152* on 4R, 7AS, 7BS, and 7DS (Sharp et al. 1989), and LMWP genes on 4RL, 7AS, 4A, and 7DS (Gómez et al. 1988). This conclusion is in agreement with the translocation 4RL/7RS detected by Koller and Zeller (1976). Associations at metaphase I did not reflect the existence of this translocation. Since bonds at metaphase I were mostly located in the distal region of the chromosomes, the segment of 4RL containing genetic material from group 7 should be located between the centromere and the segment containing information from group 6. On the other hand, the LMWP genes found on chromosome 4A should be included in the segment of 7BS translocated to 4AL, which suggests that their homoeologous genes on 7AS and 7DS occupy a more distal position than *Rc* and *Xpsr152*. This order may be retained on the 4RL arm.

Chromosome 5R. The frequency of wheat-rye associations involving 5RS (Table 1) was rather low, probably because this arm always carried telomeric C-heterochromatin. The fact that such associations occurred between 5RS and 5AS, 5BS, or 5DS, in addition to the fact that the *Skdh-1* and *Xpsr118* sets of loci are located on the 5RS arm and on chromosome 5R, respectively, as well as on the short arm of wheat group 5 chromosomes (McIntosh 1988; Sharp et al. 1989) indicate that 5RS is homoeologous to 5AS, 5BS, and 5DS.

The 5RL arm paired with 5AL and with a terminal segment of 4BL or 4DL at a relatively high frequency, and with an interstitial segment of 5BL and 5DL at a much lower frequency (Tables 1, 2). This pairing pattern does not differ from that reported by Naranjo et al. (1987, 1988 b) and confirms that 5RL carries a translocated segment from 4RL. Six sets of homoeoloci, *Aadh-1, Aco-2, Ti-2, Ibf-1, Tpi-2,* and *Xpsr128,* located on the long arm of wheat group 5 chromosomes and on the 5RL arm or on chromosome 5R (McIntosh 1988; Liu and Gale 1989; Sharp et al. 1989), indicate that a segment of 5RL between the centromere and the translocation point is homoeologous to 5AL, 5BL, and 5DL. The location of the *β-Amy-1* homoeoloci set on arms 5RL, 4AL, 4BL, and 4DL (McIntosh 1988) is the result of the translocations 5AL/4AL and 5RL/4RL that occurred during the evolution of wheat and rye, respectively. In the genetic maps of 5RL and 5AL, *β-Amy-1* should be located more distant to the centromere than the other six loci mentioned above.

Chromosome 6R. The loci *co* and *amp-1* are located on 6RS and on chromosome 6R, respectively, and on the short arm of wheat group 6 chromosomes (Miller 1984; McIntosh 1988). This indicates the homoeology of 6RS to 6AS, 6BS, and 6DS. However, the 6RS arm seldom paired (Table 1). This result and the fact that 4RL carries a translocated segment from 6RS indicate that the 6RS arm was involved in some chromosome rearrangement that occurred during the evolution of rye. As a result of this structural change, 6RS should contain genetic material from an other homoeologous group or groups.

The 6RL arm paired with wheat chromosomes of different groups, such as 6, 3, and 7. In all cases, the frequency was rather low (Tables 1, 2). This behavior may be explained in terms of 6RL containing information from different groups. Genetic markers *Aadh-2, Aco-1, α-Amy-1, Got-2,* and *Xpsr154* were found to be located on the 6RL arm or on chromosome 6R (*Xpsr154*), and on arms 6AL, 6BL, and 6DL (McIntosh 1988; Sharp et al. 1989). This chromosomal location indicates the homoeology of 6RL to 6AL, 6BL and 6DL. Likewise, some homoeology of 6RL to 3AL, 3BL, and 3DL is deduced from the location of the genetic markers: *R* on 6RL, 3AL, 3B, and 3DL (Miller 1984; McIntosh 1988); *s* on 6RL and 3D (Miller 1984); *Est-5* on 6RL, 3AL, 3BL, and 3DL (McIntosh 1988). Since a reduced homoeology of 3RL to 6AL, 6BL, and 6DL was identified, a reciprocal translocation involving 3RL and 6RL is present in rye relative to wheat. Pairing between 6RL and the long arm of wheat group 7 chromosomes suggests that an additional rearrangement involving 6RL and 7RL could occur in the evolution of rye.

Chromosome 7R. The short arm of chromosome 7R did not pair with 7AS or 7DS, but paired instead with 5BL, 5DL, and 7BS. Such bonds are very distally located and, in the 7BS arm, they are most likely formed in the segment translocated from 5AL. The frequency of associations between 7RS and 7BS, 5BL, or 5DL (Tables 1, 2) indicates that a terminal segment of 7RS is homoeologous to the long arm of group 5 chromosomes, that is to say a 7RS/5RL translocation is present in rye relative to wheat. The gene *Acph-R1,* which controls acid phosphatase production in rye, is located on 7RS. In wheat, similar genes are located on 4AS, 4BL, and 4DL (McIntosh 1988). This chromosomal location of the homoe-

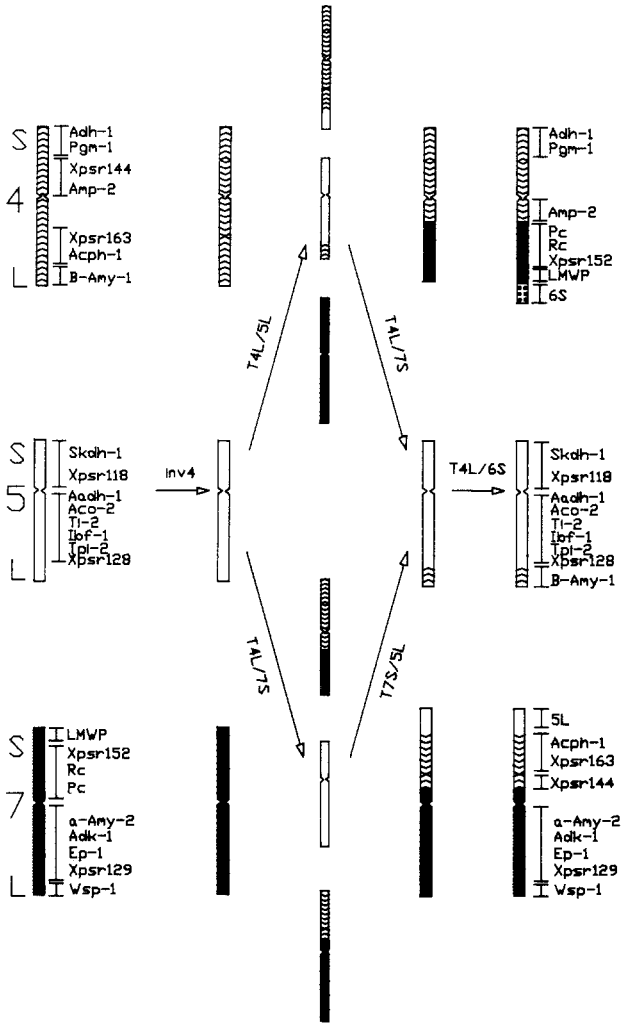

Fig. 3. Sequence of chromosome rearrangements that occurred in the evolution of the genus *Secale* as inferred from the genetic architecture of chromosomes 4R, 5R, and 7R of *S. cereale* relative to wheat. From left to right: chromosomes 4, 5, and 7 of the ancestral genome; pericentric inversion of chromosome 4; translocation between 4L and 5L or between 4L and 7S; double translocation involving 4L, 5L, and 7S; translocation of a segment 6S to the modified 4L arm–whether this segment came from chromosome 6 or from other chromosomes previously translocated with 6S remains to be determined. The order of different chromosome segments is discussed in the text, and the order of the loci within a given segment is arbitrary

oloci *Acph-1* is in agreement with the translocation 4RL/7RS of rye detected by Koller and Zeller (1976). The two sets of RFLP loci *Xpsr163* and *Xpsr144* are located on chromosome 7R in rye. In wheat, *Xpsr163* and *Xpsr144* are located at both sides of the centromere of group 4 chromosomes: *Xpsr163* on arms 4AS, 4BL, and 4DL and *Xpsr144* on arms 4AL, 4BS, and 4DS (Sharp et al. 1989). Assuming that the ancestral arm location of *Xpsr163* and *Xpsr144* is retained in wheat chromosomes 4B and 4D, a minimum of two chromosome rearrangements had to occur in the evolution of rye to change the location of these two loci from chromosome 4 to chromosome 7. Chromosome 4R suffered a pericentric inversion and its long arm was involved in translocations with 7RS and other arms. The pericentric inversion of chromosome 4R could change the position of *Xpsr144* relative to the centromere and situate this locus between the centromere and *Xpsr163*. Later, the occurrence of the interchange 4RL/7RS, that overlapped the pericentric inversion, translocated both *Xpsr144* and *Xpsr163*, as well as *Acph-1*, from the long arm of chromosome 4 to the short arm of chromosome 7 (Fig. 3). Thus, *Xpsr144* and *Xpsr163* are expected to be located on the 7RS arm in the order centromere-*Xpsr144*–*Xpsr163*. The segment of 7RS containing genetic material from group 4 should be intercalary since the distal part of 7RS is homoeologous to group 5 chromosomes. Whether 7RS carries or does not carry information of the group 7 short arm can not be established in the light of available data.

The homoeology of the 7RL arm to 7AL, 7BL, and 7DL is deduced from the location of genetic markers *Ep-1*, *α-Amy-2*, and *Adk-1* on these arms (Koebner et al. 1987; McIntosh 1988; Benito et al. 1990). In addition, RFLP homoeoloci *Xpsr129* were found to be located on chromosome 7R and on arms 7AL, 7BL, and 7DL (Sharp et al. 1989). However, the 7RL arm seldom paired with wheat chromosomes (Table 1). Associations of 7RL and the short arm of chromosomes 2A, 2B, and 2D were the most frequent ones, reaching a frequency of 0.8%. The 7RL arm should carry information from other groups arising from translocations. One structural change involving 7RL and 6RL was suggested above to be present in rye. Moreover, pairing results suggest that 7RL may also contain some segment homoeologous to 2AS, 2BS, and 2DS.

Evolution of the chromosome structure of rye

Translocations are thought to have played an important role in the evolution of the genus *Secale* (Stutz 1972). Evidence supporting this is provided by the results showed in the present work. Only the arms 1RS, 1RL, 2RL, 3RS, and 5RS show normal homoeologous relationships to wheat. The remaining arms of rye appear to be involved in translocations, or even in inversions, as 4RS and 4RL. A reciprocal translocation between 3RL and 6RL and a multiple translocation involving the arms 4RL, 5RL, 6RS, and 7RS have been detected. Other translocations that most likely exist in *S. cereale* remain to be identified.

Evidently, the complete sequence of chromosome rearrangements that have occurred during the evolution of rye will not be established until all of the rearrangements and the species in which they are present are well defined. However, available data concerning the structure of chromosomes 4R, 5R, and 7R suggest, at least in part,

how these chromosome evolved. This partial view of the evolution of rye is illustrated in Fig. 3. Chromosomes 4, 5, and 7 of the ancestral genome, from which the A, B, D, and R genomes diverged, are assumed to present a structure comparable to the one of chromosomes 4D, 5D, and 7D. This is based on the fact that chromosomes of the D genome are not involved in the structural changes detected in hexaploid wheat. In the evolution of the R genome, chromosome 4 suffered a pericentric inversion followed by two interchanges. These two interchanges could occur either of two orders: (1) the first trranslocation between 4L and 5L and the second translocation between 4L and 7S; (2) the first translocation between 4L and 7S and the second translocation between 7S and 5L. In any case, the inversion and translocation 4L/7S overlapped. Subsequently, a segment from 6S was translocated to 4L. Whether this segment came from chromosome 6 or from some other chromosome previously translocated with 6S can not be established. Naranjo et al. (1987) concluded that the double translocation 5AL/4AL/7BS occurred in the evolution of wheat and that the double translocation 5L/4L/7S of rye arose independently. The fact that the segment from 7BS translocated to 4AL did not include the loci *Xpsr152, Pc,* and *Rc* supports the argument that interchanges of wheat and rye had different origins.

The four chromosome rearrangements of Fig. 3 do not explain the chromosomal location of all of the genetic markers of groups 4, 5, and 7 in wheat and rye. The loci *Wsp-1* are located on the long arm of wheat group 7 chromosomes (Liu et al. 1989). In the genetic map of 7BL, *Wsp-1* occupies a distal position. Since no structural change involving 7BL has been detected, the *Wsp-1* locus would be distally located on ancestral chromosome arm 7L. In rye, *Wsp-1* was found on chromosome 4R (Liu et al. 1989). This location was attributed to translocation 4RL/7RS detected by Koller and Zeller (1976). This translocation, which corresponds to translocation 4L/7S of Fig. 3, did not modify the position of any marker located on the long arm of chromosome 7. It is possible that other rearrangements involving the long arm of chromosome 7 and chromosome 4 would occur in the evolution of rye. Such chromosome rearrangements could also affect the *Got-1* genes, which are duplicated in rye and were located on chromosome 4R and on the arm 7RL, whereas in wheat, *Got-1* genes were found on 6AS, 6BS, and 6DS (Tang and Hart 1975; Rebordinos and Pérez de la Vega 1988).

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