Theor Appl Genet (1992) 83:305–312

THEORETICAL AND APPLIED GENETICS

© Springer-Verlag 1992

Nonhomoeologous translocations between group 4, 5 and 7 chromosomes within wheat and rye

C. J. Liu, M. D. Atkinson, C. N. Chinoy, K. M. Devos, and M. D. Gale*
Cambridge Laboratory, Colney Lane, Norwich NR4 7UJ, UK

Received March 5, 1991; Accepted May 16, 1991
Communicated by J. W. Snape

Summary. Genetic maps of wheat chromosome 4A and rye chromosome arm 5RL, and the chromosomal locations of 70 sets of isozyme and molecular homoeoloci have been used to further define the structure of wheat chromosomes 4A, 5A and 7B, and rye chromosomes 4R, 5R and 7R. We provide evidence, for the first time, which is consistent with the presence of an interstitial segment on 4AL originating from 5AL, and of a segment originally from 5RL on 7RS. The evolutionary origins of the present chromosomes are discussed.

Key words: Wheat – Rye – RFLP – Isozymes – Evolutionary translocations

Introduction

Wheat (*Triticum aestivum*; 2n = 6x = 42, genomes AABBDD), barley (*Hordeum vulgare*, 2n = 2x = 14, genome HH) and rye (*Secale cereale*, 2n = 2x = 14, genome RR) are all part of the tribe Triticeae and, presumably, these now distinct genomes were all derived from a single common ancestor. Over the past two decades it has become increasingly clear that there remains much similarity between the various Triticeae genomes, even though they have long been isolated. Evidence for homoeology was first demonstrated by the ability of chromosomes to compensate for one another in nullisomic-tetrasomic combinations (Sears 1954, 1966). Later more evidence was assembled from both induced intergenomic pairing and recombination within hexaploid wheat (Riley and Chapman 1958) and between the wheat genomes and those of related species (Naranjo 1982; Koebner and Shepherd 1986), and from the concurrence of chromosomal and intrachromosomal locations of marker genes, particularly biochemical and molecular loci. These are often observed to be triplicated in wheat and have homoeoloci in one or more related species (see McIntosh et al. 1990). The most recent evidence derives from the detailed genetic maps that are beginning to emerge, such as for the homoeologous group 7 chromosomes of wheat (Chao et al. 1989), where the chromosomal location, order and genetic distances between markers is remarkably conserved over the A, B and D genomes.

The main disturbance to co-linearity of maps between genomes arises from intra- and interchromosomal translocations. Many intervarietal translocations have arisen since speciation, and an extensive, although probably not exhaustive list for wheat has been prepared by Schlegel and Schlegel (1989). Other evolutionary translocations (Gale et al. 1990) arose before the formation of species barriers and characterise the various Triticeae genomes.

In hexaploid wheat, evolutionary translocations involving chromosome arms 4AL (formerly 4BL), 5AL and 7BS were proposed by Naranjo et al. (1987) following a study of induced homoeologous chromosome pairing with the aid of differential chromosome staining. Some confirmatory evidence for the 4AL to 5AL translocation is also available from the nonhomoeologous locations of marker gene sets, e.g. *β-Amy-1* (Ainsworth et al. 1983) and for the 7BS to 4AL translocation from various isozyme and RFLP loci (Chao et al. 1989). In rye a similar situation exists involving chromosomes 4R, 5R and 7R. The translocation between chromosome arms 4RL and 7RS has long been recognised (Köller and Zeller 1976). It has also been speculated that, while largely homoeologous with group 5, chromosome 5R has a small amount of homoeology with group 4. Supporting evidence is summarized by Naranjo et al. (1987).

* To whom correspondence should be addressed

In the course of routine primary screening of DNA clones for utility as RFLP probes in this laboratory, two probes, PSR115, a wheat cDNA clone, and PSR580, a wheat genomic DNA clone, were identified which were located on chromosome 5H (chromosome 1) in barley, 7R in rye and 4AL, 5BL and 5DL in hexaploid wheat. These clones were potentially the first evidence of the reciprocal nature of the 4AL/5AL translocation. This finding led to the systematic analysis described below which enables the proposal of hypotheses to further describe the evolutionary translocations involving chromosomes 4A (formerly 4B), 5A and 7B in wheat and 4R, 5R and 7R in rye.

Materials and methods

Genetic stocks

The euploid and all the available nullisomic-tetrasomic (Sears 1954, 1966) and ditelosomic (Sears and Sears 1978) lines of Chinese Spring (CS) were used to determine the chromosomal location of random anonymous cDNA and genomic DNA clones in wheat. The locations of these clones in rye and barley were determined by hybridization to genomic DNA of the CS/*Secale cereale* cv 'Imperial' (Driscoll and Sears 1971) and CS/*Hordeum vulgare* vs 'Betzes' (Islam et al. 1981) individual chromosome addition lines, respectively. Fifty-one F_2 plants, or their F_4 progenies, from the cross between hexaploid wheat var ('Timgalen' and 'RL4137' (Chao et al. 1989) were used for mapping chromosome 4A. 60 F_2 plants, or their F_3 progenies, from the cross of 'Ds2' × 'RxL 10' (Wang et al. 1991) were used for mapping chromosome arm 5RL.

DNA clones and isozyme systems

Two known-function clones, nitrate reductase (Cheng et al. 1986), provided by A. Kleinhofs, Washington State University, USA, and waxy (Rohde et al. 1988); three anonymous wheat cDNA clones (PSR81, PSR115 and PSR120); three anonymous wheat genomic clones (PSR360, PSR426 and PSR580); two anonymous barley genomic clones (KSU8 and KSU26 (Kam-Morgan and Gill 1989), provided by Dr. B. S. Gill, Kansas State University, USA); and four isozyme systems, *β-Amy-1*, *Ibf-1*, *Ndh-1* and *Per-4*, were used for intrachromosomal mapping.

RFLP and isozyme analysis

The methods used for DNA isolation and RFLP analysis were those described by Sharp et al. (1988), except that Hybond N Plus (Amersham) filters were used. The method used for the analysis of *β-Amy-1* is that described by Ainsworth et al. (1983); for *Ibf-1*, by Liu and Gale (1989); for *Ndh-1*, by Liu and Gale (1991); and for *Per-4*, by Liu et al. (1990).

Mapping analysis was carried out with the use of the software package MAPMAKER Version 2.0, supplied by E. S. Lander, Whitehead Institute for Biomedical Research, Cambridge, Mass., USA. The Kosambi transformation was used to convert recombination frequencies to centiMorgans (cM).

Results

1. Homoeologous groups 4, 5 and 7 marker gene locations

The chromosomal location of DNA probes was initially determined by hybridization to digested genomic DNA from the euploid, nullisomic-tetrasomic and ditelosomic lines of CS and the wheat/rye and wheat/barley chromosome addition lines. This analysis for PSR580 is shown in Fig. 1. This probe detected three major fragments in CS when hybridized with EcoRV-restricted genomic DNA. Nullisomic analysis showed clearly that these fragments were located on chromosomes 4A, 5B and 5D (Fig. 1 A). Ditelosomic analysis (not shown) subsequently showed the loci to be on the long arms of these chromosomes. Homologous sequences to this clone were located on 5H in barley and 7R in rye (Fig. 1 B). Chromosomal locations for the 70 sets of marker loci mapped to homoeologous group 4, 5 and 7 chromosomes in wheat and rye are summarized, and sources provided, in Table 1.

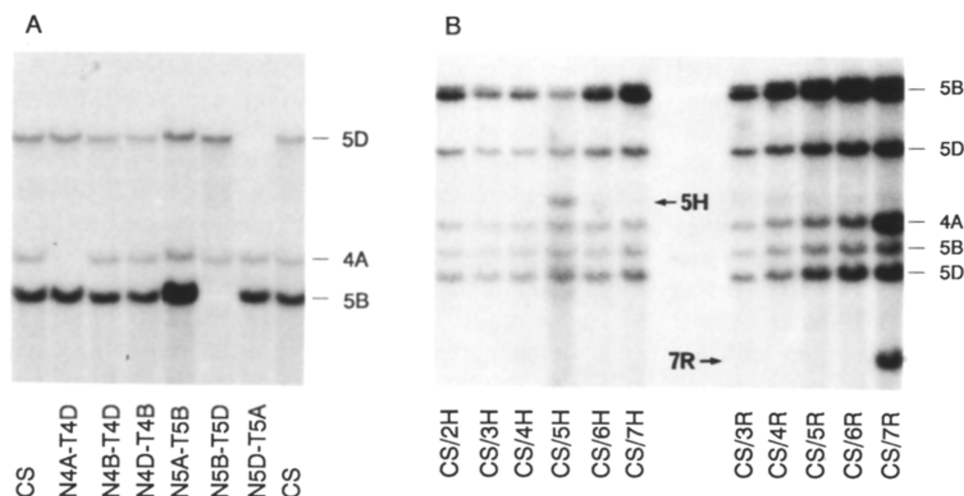

Fig. 1 A and B. Hybridization of PSR580 to (**A**) EcoRV-restricted genomic DNA of the homoeologous group 4 and 5 nullisomic-tetrasomic lines of CS and (**B**) HindIII-restricted genomic DNA of CS/*S. cereale* 'Imperial' and CS/*H. vulgare* cv 'Betzes' addition lines

Table 1. Molecular and biochemical marker loci on homoeologous group 4, 5 and 7 chromosomes of wheat and rye

Homoeologous group	Probe or isozyme loci	Arm location wheat	Rye
4L	*Xpsr104*	4AS 4BL 4DL[b]	7R
	Xpsr157	4AS 4BL 4DL	7R
	Xpsr163	4AS 4BL 4DL[a]	7R
	XFbp	4AS 4BL 4DL[a]	–
	Acph-1	4AS 4BL 4DL[a]	7RS[a]
4L (4AL/5AL translocation)	*Xpsr164*	4BL 4DL 5AL	5R
	Aco-2	4BL 4DL 5AL[a]	5RL[a]
	β-Amy-1	4BL 4DL 5AL[a]	5RL[a]
4S	*Xpsr110*	4AL 4BS 4DS[a]	4R
	Xpsr139	4AL 4BS 4DS	4R
	Xpsr144	4AL 4BS 4DS[a]	–
	*Xpsr147**	4AL 4BS 4DS	4R
	Xpsr153	4AL 4BS 4DS	4R
	Xpsr166	4AL 4BS 4DS	4R
	Amp-2	4AL 4BS 4DS[a]	4RS[d]
	Adh-1	4AL 4BS 4DS[a]	4RS[a]
	Lpx-1	4AL 4BS 4DS[a]	–
	Ndh-1	4AL 4BS 4DS[a]	4RS
	Pgm-1	4AL – 4DS[a]	4RS[a]
5L	*Xpsr81*	5AL 5BL 5DL	5RL
	Xpsr120[a]	5AL 5BL 5DL	5RL
	Xpsr120[b]	5AL 5BL 5DL	5RL
	Xpsr120[c]	5AL 5BL 5DL	5RL
	Xpsr120[d]	– – –	5RL
	Xpsr128	5AL 5BL 5DL[a]	–
	Xpsr145	5AL 5BL 5DL	5R
	Xpsr360	5AL 5BL 5DL	5RL
	Xpsr426	5AL 5BL 5DL	5RL
	Xksu8	5AL 5BL 5DL[a]	5RL
	Xksu24[a]	5AL 5BL 5DL[a]	–
	Xksu24[b]	5AL 5BL 5DL[a]	–
	Xksu26	5AL 5BL 5DL[a]	5RL
	Xksu58	5AL 5BL 5DL[a]	–
	Adh-1	5AL 5BL 5DL[a]	5RL[a]
	Ibf-1	5AL 5BL 5DL[a]	5RL[a]
	Lpx-2	5AL 5BL 5DL[a]	–
	Ti-2	5AL 5BL 5DL[a]	5RL[a]
	Tpi-1	5AL 5BL 5DL[a]	5R[a]
5L (5AL/4AL translocation)	*Xpsr115*	5BL 5DL 4AL	7R
	Xpsr580	5BL 5DL 4AL	7R
5S	*Xpsr109*	5AS 5BS 5DS	5R
	Xpsr118	5AS 5BS 5DS[a]	5R
	Xα-Amy-3	5AS 5BS 5DS[a]	–
	Mdh-3	5AS 5BS 5DS[a]	–
	Nor-3	5AS – 5DS[a]	–
	Skdh-1	5AS 5BS 5DS[a]	5RS[a]
7L	*Xpsr72*	7AL 7BL 7DL[a]	–
	Xpsr105	7AL 7BL 7DL[a]	–
	*Xpsr117**	7AL 7BL 7DL[a]	7R
	*Xpsr121**	7AL 7BL 7DL[a]	–
	Xpsr129	7AL 7BL 7DL[a]	7R
	Xpsr165	7AL 7BL 7DL[a]	–
	Xpsr169	7AL 7BL 7DL[a]	7R
	XGapd2	7AL 7BL 7DL[a]	–
	XPepc	7AL 7BL 7DL[a]	7R[c]
	α-Amy-2	7AL 7BL 7DL[a]	7RL[a]
	Ep-1	7AL 7BL 7DL[a]	–
	Wsp-1	7AL 7BL 7DL[a]	–
7S	*Xpsr65*	7AS 7BS 7DS[a]	7R
	Xpsr103	7AS 7BS 7DS[a]	–
	*Xpsr108**	7AS 7BS 7DS[a]	4R
	*Xpsr150**	7AS 7BS 7DS	–
	Xpsr152	7AS 7BS 7DS[a]	4R
	XSs1	7AS 7BS 7DS[a]	–
	Est-3	– 7BS 7DS[a]	–
	Ndh-2	7A – 7DS[a]	7RS[a]
7S (7BS/4AL translocation)	*Xpsr119*	7AS 7DS 4AL[a]	4R
	Xpsr160	7AS 7DS 4AL[a]	–
	Per-4	7AS 7DS 4AL[a]	–
	*XNra**	7AS 7DS 4AL[a]	–
	XWx	7AS 7DS 4AL[a]	–

[a] Loci listed by McIntosh et al. (1990); [b] loci reported by Liu and Gale (1991); [c] loci reported by Chao et al. (1989); [d] the locus of *Amp-R2* was located on 4RS instead of on 4RL (R.M.D. Koebner, personal communication)
* Indicates that the probes used to identify these loci also detect homologous sequences elsewhere in the wheat genomes
–: Indicates that the arm location of the respective loci have not been determined or analyzed

2. Intrachromosomal mapping

The DNA probes were hybridized to genomic DNAs from 'Timgalen', 'RL4137', 'Ds2' and 'RxL 10' digested with eight (wheat) or four (rye) restriction enzymes. Informative probe × restriction enzyme combinations were identified and used to map PSR115, Wx and Nra on wheat chromosome 4A, PSR81, PSR120, PSR360, PSR426, KSU8 and KSU26 on rye chromosome arm 5RL, and PSR115 and PSR580 on 7R. The *Per-B4* locus on 4AL was scored for allelic variation in the 'Timgalen' × 'RL4137' progenies. Similarly *Ibf-R1* and *β-Amy-R1* loci on 5RL displayed allelic variation and were scored in six individual F_3 grains of each of the 'Ds2' × 'RxL 10' progenies.

a) Wheat chromosome 4A. The results for *Xpsr115-4A*, *XNra-4A*, *XWx-4A* and *Per-B4* were combined with those already obtained for *Xpsr104-4A*, *Xpsr110-4A* and *Ndh-A1* (Liu and Gale 1991) to produce the map shown in Fig. 2, which consists of two linkage blocks. The orientation of the four marker loci in the distal linkage block on 4AL has not been experimentally determined. None of the loci in this group was linked with *Ndh-A1*, the most distally located marker on 4AL in the proximal linkage block. However, the orientation shown in Fig. 2 is that considered most likely from the hypotheses surrounding the evolution of the compound chromosome (see below).

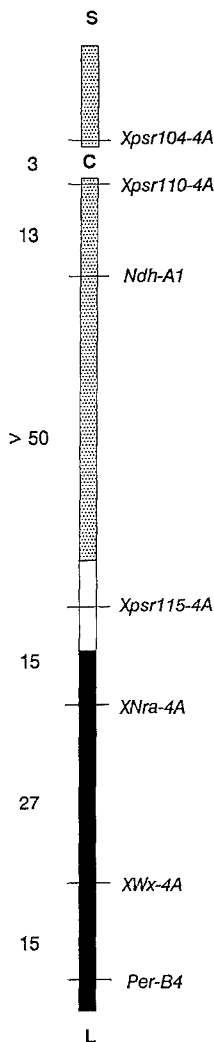

Fig. 2. Genetic map of chromosome 4A. *Dotted, solid* and *unfilled rectangles* represent three different chromosome segments of the original 4A, 7B and 5A chromosomes, respectively (see also Fig. 4). Genetic distances in cM are shown on the *left-hand side*

b) Rye chromosome 5R. Four of the six DNA probes analyzed for linkage on 5RL, i.e., PSR81, PSR360, PSR426 and KSU26, each detected a single fragment. The other two probes, i.e., PSR120 and KSU8, each detected five fragments in each parent, and the segregations were initially treated as being from different loci. All five "loci" detected by KSU8 co-segregated, and thus *Xksu8* appears on the map as a single locus. Four of the five "loci" detected by PSR120 mapped to different locations along the chromosome arm, spanning a genetic distance of almost 60 cM. The best-fit map comprising 11 loci is shown in Fig. 3. This map contains no locus on the short arm of 5R, and thus the orientation relative to the centromere could not be determined experimentally. Again, from the evolutionary arguments, the location of the segment containing *β-Amy-R1* is most likely to be distal.

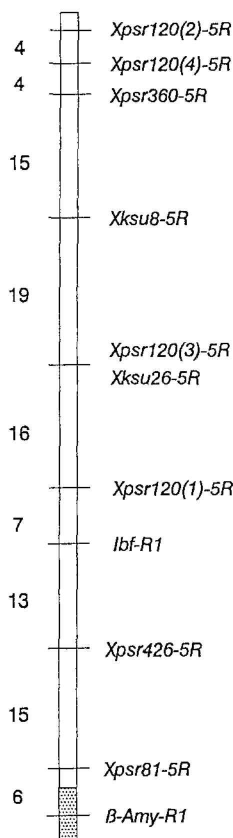

Fig. 3. Genetic map of chromosome arm 5RL. Key: the *dotted region* represents the segment transferred from the original 4RL (see also Fig. 5). Genetic distances in cM are shown on the *left-hand side*

c) Rye chromosome 7R. Segregational analysis between *Xpsr580-7R* and *Xpsr115-7R* indicated that these two loci were linked by 24.6 ± 3.8 cM.

Discussion

Evolution of translocations in wheat and rye

Consideration of the maps of wheat chromosome 4A and rye chromosome arm 5RL, the chromosomal locations of other marker loci (Table 1), and published evidence for homoeologous chromosomal pairing allows the development of hypotheses for the evolution of the wheat and rye genomes with regard to chromosomes of homoeologous groups 4, 5 and 7. The proposed hypotheses are represented schematically in Figs. 4 and 5. Below, we first review the evidence for the constitution of the present 4A, 5A and 7B chromosomes in wheat and the present 4R, 5R and 7R chromosomes in rye; secondly we describe the means by which the translocated chromosomes may have arisen. The arguments proposed are based on genetic maps and numbers of marker loci and, thus, may

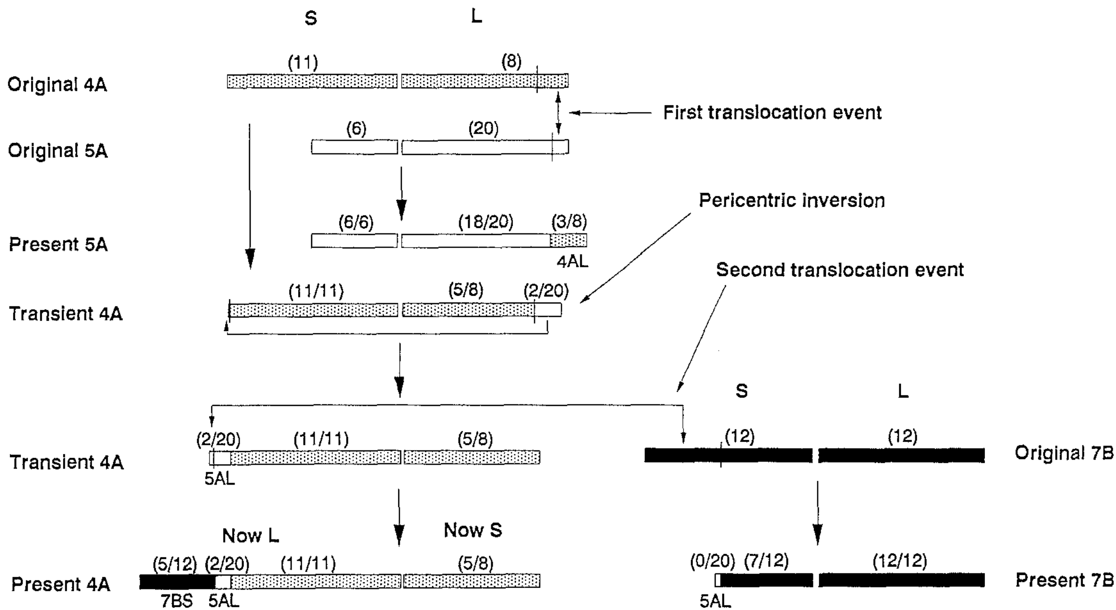

Fig. 4. The present structures of chromosomes 4A, 5A and 7B and their origins. The numbers of known marker loci on the "original" chromosomes are shown in *parentheses*. The proportions, based only on numbers of genetic markers, remaining and transferred during the translocation events, are shown for "transient" and "present" chromosomes. *S* and *L* are the arm designations of the "original" chromosomes. In the case of chromosome 4A the designations are reversed, i.e. the original short arm becomes the present long arm and the original long arm becomes the present short arm. See text for detailed description

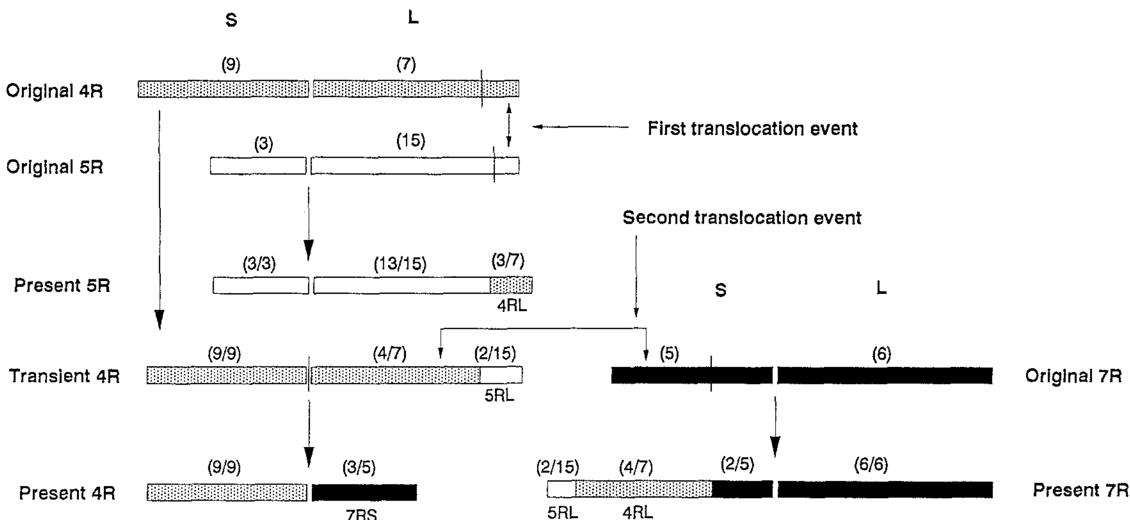

Fig. 5. The present structures of chromosomes 4R, 5R and 7R and their origins. Explanation as for Fig. 4

not reflect actual physical chromosome length, because the genetic maps are likely to be distorted relative to the physical maps in Triticeae species, as described by Wang et al. (1991).

a) Nonhomoeologous translocations between chromosome 4A, 5A and 7B

Evidence for the presence of a segment of the original 4AL on the present 5AL. Results from chromosome pairing demonstrated that the terminal segment of 5AL is homoeologous to 4BL and 4DL (Naranjo et al. 1987). This is supported by the locations of *Aco-2*, *β-Amy-1* and *Xpsr-164* on 4BL, 4DL and 5AL (Table 1).

Evidence for the presence of a segment of the original 5AL on the present 4AL. Two RFLP loci, *Xpsr115* and *Xpsr580*, have been shown to be located on 4AL, 5BL and 5DL, suggesting that the group 4 location has arisen by translocation from 5AL. Furthermore, *Xpsr115* has

been shown to be linked with several other markers also translocated to 4AL, but from 7BS. However, no chromosome pairing evidence is available to support these findings. Of all the 20 sets of loci presently placed on the long arms of 5BL and 5DL (Table 1), only these 2 were located on the present 4AL, indicating that the segment translocated from 5AL and remaining on the present 4AL may represent a relatively small part of the original 5AL arm. Moreover, this segment is inferred to be interstitially located (see below), which may explain why chromosome pairing analysis has not yet been able to detect its existence.

Evidence for the presence of a segment of the original 7BS on the present 4AL. Much evidence is available to demonstrate the existence of this segment. Initially, a set of isozyme loci, *Per-4*, were located on 7AS, 7DS and 4AL (Kobrehel and Feillet 1975; Benito and Perez de la Vega 1979), and this was followed by the same chromosomal location of another four sets of RFLP loci, *Xpsr119*, *Xpsr160*, *XNra* and *XWx* (Table 1). In addition, analysis of chromosome pairing has also demonstrated that the terminal segment of 4AL is homoeologous to 7AS and 7DS (Naranjo et al. 1987).

Evidence for the presence of a segment of the original 5AL on the present 7BS. The only supporting evidence derives from chromosome pairing analysis, which demonstrated that the terminal segment of 7BS is homoeologous to 5BL and 5DL (Naranjo et al. 1987). However, none of the 20 marker loci on the original 5AL is found on 7BS, indicating that the segment of 5AL on 7BS is likely to be small.

Combining all the above observations, a hypothesis involving two translocation events is proposed, as shown in Fig. 4. Basically this is an extension of that proposed by Naranjo et al. (1987), but incorporates the new data concerning the structure of chromosome 4A.

Existing evidence from chromosome pairing and marker gene location indicates that the present 4AL is at least partly homoeologous to 4BS and 4DS, while 4AS is homoeologous to 4BL and 4DL. Naranjo et al. (1987) also observed that in some pollen mother cells (PMCs) of 5B-deficient plants, 4AS was seen to be weakly bound to the end of 4BS and 4DS and that in other PMCs it appeared interstitially associated with 4DL, although the numbers of these PMCs were small. Thus Naranjo et al. (1987) and Naranjo (1990) suggested the existence of a pericentric inversion involving a substantial portion of this chromosome during the evolution of hexaploid wheat. The evidence available to date shows that the inversion contains all 19 of the group 4 marker loci listed in Table 1, because none is located on the three long or the three short arms of the present homoeologous group 4 chromosomes. The possibility remains that a telomeric segment of the original 4AS is located on the present 4AS, which is consistent with the pairing evidence of Naranjo et al. (1987).

Thus, the most likely course of events is: (1) a reciprocal interchromosomal translocation of the original 4AL and 5AL; (2) the transposition of the translocated 5AL segment from the original 4AL to 4AS, i.e., a pericentric inversion. This event resulted in the reversal of the arm ratio of 4A with the result that the present short and long arms are homoeologous with the long and short arms, respectively, of chromosome 4B and 4D. The present evidence is unable to show whether the breakpoints in the inter- and intrachromosomal events on 4A differ; and (3) a reciprocal translocation between 4AL, distal to the 4AL/5AL breakpoint, and part of 7BS. It should be noted that the order of events (2) and (3) above may be interchanged and still be consistent with the present data. The orientation of the segment translocated from 7BS (Fig. 1) is also at variance with published data unless the segment was inverted during the chromosomal rearrangements. Liu et al. (1990), while mapping *Per-A4* on 7AS, assumed, based on the result of Chao et al. (1989), that *Per-A4* was the most proximal of the three loci. It appears now, however, from the map of 4AL, that the order of these loci on chromosome arms 7AS and 7DS is most likely to be, from the centromere, *XNra-7* – *XWx-7* – *Per-4*.

b) Nonhomoeologous translocations between chromosomes 4R, 5R and 7R

Evidence for the presence of a segment of the original 4RL on the present 7RS. The first evidence for this came from the findings of Köller and Zeller (1976), which was confirmed by the study of Naranjo et al. (1987). Supporting evidence includes the locations of *Acph-R1*, *Xpsr104*, *Xpsr157* and *Xpsr163* (Table 1). In fact, none of the seven marker loci on the original 4RL (as deduced from the location of their homoeoloci in wheat) is retained on the present 4RL, suggesting that a substantial part, at least, of this chromosome arm was translocated to 7RS.

Evidence for the presence of a segment of the original 7RS on the present 4RL. This was also first demonstrated by the work of Köller and Zeller (1976). Other marker gene locations (Table 1) provide supporting evidence. Three out of the five loci on the original 7RS were found to be located on the present 4RL. The other two loci, *Xpsr65* and *Ndh-2*, are retained on the present 7RS (Table 1), which provides the first evidence that the breakpoint is in 7RS and not at the centromere. All the nine loci on the original 4RS were found on the present 4RS. Similarly, all the six loci on the original 7RL were found on the present 7RL (Table 1). These results are consistent with the hypothesis that the present 4RS is the original 4RS

while the present 4RL is part of the original 7RS. Similarly, the present 7RL is the original 7RL while the present 7RS contains a segment of the original 4RL.

Evidence for the presence of a segment of the original 4RL on the present 5RL. This is supported by results from both chromosome pairing (Naranjo et al. 1987) and marker gene locations. Three of the seven loci on the original 4RL, *Aco-2*, *β-Amy-1* and *Xpsr164*, were detected on the present 5RL (Table 1).

Evidence for the presence of a segment of the original 5RL on the present 7R. The chromosome locations of *Xpsr115* and *Xpsr580* provide the only evidence to date. No chromosome pairing evidence has been obtained in support of this, although the segment is inferred to be terminally located on 7RS. A corollary is that both *Xpsr115* and *Xpsr580* are expected to map in the terminal region of 5BL and 5DL in wheat and 5HL in barley.

All the above observations can be explained by reciprocal translocation events between chromosome arms 4RL/5RL and 4RL/7RS, as shown in Fig. 5. It should be noted that the first event was not necessarily between 4RL and 5RL. It is equally possible that the first event was between 4RL and 7RS.

The involvement of homoeologous group 4, 5 and 7 chromosomes in translocations in the evolution of both wheat and rye is remarkable and all the more so because the breakpoints on 5AL and 5RL seem to be located, within the limits of the analysis described here and assuming co-linearity of the maps, in the same region. However, the breakpoints in 7BS and 7RS are quite different. The breakpoint on 7RS is more proximal than that on 7BS. This can be seen from the locations of *Xpsr108* and *Xpsr152*. Homoeoloci to both of these are located on all the three short arms of wheat homoeologous group 7 chromosomes, indicating that they were not involved in the translocation in wheat. However, they are both located on 4R in rye. Thus, it can be reasonably expected that these two loci will map proximally to all those markers having 7AS, 7DS and 4AL locations, but map distally to others having 7AS, 7BS and 7DS locations.

These results also confirm that the group 4/7 translocations in wheat and rye represent two independent events. However, it is not clear whether the group 4/5 translocations are coincident. The results available to date can not rule out the possibility that a single group 4/5 translocation occurred before the differentiation of genomes A and R. If this is the case then it would follow that the A genome is more closely related to the R genome than to the B and D genomes, although the intergenomic relationships may have become less distinct if species evolution and differentiation have occurred at different rates as suggested by Dvořák (1988). The available evidence from pairing studies, chromosome substitution and compensation, and from the hybridization of DNA probes is not adequate to confirm or disprove this hypothesis. Clearly, however, the putative pericentric inversion (or intrachromosomal translocation) must have occurred after the group 4/5 translocation in wheat. The association of the original 5RL segment (containing *Xpsr115* and *Xpsr580*) along with the original 4RL segment (containing *Xpsr104*, *Xpsr157*, *Xpsr163* and *Acph-1*) on the present 7RS (Table 1 and Fig. 5) provides evidence that chromosome 4R has never suffered a large pericentric inversion.

Conclusions

The present study demonstrates that genetic markers, when available in adequate numbers, can detect translocations which may be too small to be identified by cytological studies. Apart from the rearrangements discussed above, there are other possible non-homoeologous translocations in the Triticeae. For example, the chromosomal location of *Est-5* (Ainsworth et al. 1984) and *Ndh-3* (Liu and Gale 1991) in wheat and rye suggest the existence of another, as yet cytologically unidentified, translocation between 3R and 6R, relative to wheat. A detailed description of these intergenomic translocations will emerge from the development of dense RFLP-based genetic maps that are being produced in several laboratories. It is important that they are well understood for increasing the efficiency and precision of future chromosome engineering and introgression of chromosome segments containing useful genes to cultivated crops.

Acknowledgements. C.J. Liu is grateful to the Agricultural Genetics Company for the financial support during the tenure of his Ph.D. studentship. We would also like to thank T.E. Miller, R.M.D. Koebner and I.P. King for helpful discussion and critical reading of the manuscript.

References

Ainsworth CC, Gale MD, Baird S (1983) The genetics of β-amylase isozymes in wheat. 1. Allelic variation among hexaploid wheat varieties and intrachromosomal gene locations. Theor Appl Genet 66:39–49

Ainsworth CC, Gale MD, Baird S (1984) The genetic control of grain esterases in hexaploid wheat. 1. Allelic variation. Theor Appl Genet 68:219–226

Benito C, Perez de la Vega M (1979) The chromosomal location of peroxidase isozymes of the wheat kernel. Theor Appl Genet 55:73–76

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. Theor Appl Genet 78:495–504

Cheng C-L, Dewdney J, Kleinhofs A, Goodman HM (1986) Cloning and nitrate induction of nitrate reductase mRNA. Proc Natl Acad Sci USA 83:6825–6828

Driscoll CJ, Sears ER (1971) Individual addition of the chromosomes of "Imperial" rye to wheat. Agron Abstr 1971:6

Dvořák J (1988) Cytogenetical and molecular inferences about the evolution of wheat. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp. Institute of Plant Science Research, Cambridge, pp 187–192

Gale MD, Chao S, Sharp PJ (1990) RFLP mapping in wheat – progress and problems. In: Gustafson JP (ed) Gene manipulation in plant improvement II. Plenum, New York, pp 353–364

Islam AKMR, Shepherd KW, Sparrow DHB (1981) Isolation and characterization of euplasmic wheat-barley chromosome addition lines. Heredity 46:161–174

Kam-Morgan LNM, Gill BS (1989) DNA restriction fragment length polymorphisms: a strategy for genetic mapping of D genome of wheat. Genome 32:724–732

Kobrehel K, Feillet P (1975) Identification of genomes and chromosomes involved in peroxidase synthesis of wheat seeds. Can J Bot 53:2336–2344

Koebner RMD, Shepherd KW (1986) Controlled introgression to wheat of genes from rye chromosome arm 1RS by induction of allosynthesis. 1. Isolation of recombinants. Theor Appl Genet 73:197–208

Köller OL, Zeller FJ (1976) The homoeologous relationship of rye chromosome 4R and 7R with wheat chromosomes. Genet Res 28:117–188

Liu CJ, Gale MD (1989) *Ibf-1* (Iodine binding factor), a highly variable marker system in the *Triticeae*. Theor Appl Genet 77:233–240

Liu CJ, Gale MD (1991) The chromosomal location of genes encoding NADH dehydrogenase isozymes in hexaploid wheat and related species. Genome 34:44–51

Liu CJ, Chao S, Gale MD (1990) The genetic control of tissue-specific peroxidases, *Per-1*, *Per-2*, *Per-3*, *Per-4* and *Per-5* in wheat. Theor Appl Genet 79:305–313

McIntosh RA, Hart GE, Gale MD (1990) Catalogue of gene symbols for wheat: Cereal Res Commun [Suppl] 18:141–157

Naranjo T (1982) Preferential occurrence of wheat-rye meiotic pairing between chromosomes of homoeologous group 1. Theor Appl Genet 63:219–225

Naranjo T (1990) Chromosome structure of durum wheat. Theor Appl Genet 79:397–400

Naranjo T, Roca A, Goicoecha PG, Giraldz R (1987) Arm homoeology of wheat and rye chromosomes. Genome 29:873–882

Rohde W, Becker D, Salamini F (1988) Structural analysis of the *waxy* locus from *Hordeum vulgare*. Nucleic Acids Res 16:7185–7186

Riley R, Chapman C (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Schlegel G, Schlegel R (1989) A compendium of reciprocal intervarietal translocations in hexaploid wheat. Kulturpflanz 37:163–176

Sears ER (1954) The aneuploids of common wheat. Agric Exp Stn Res Bull, University of Missouri 572:1–58

Sears ER (1966) Nullisomic-tetrasomic combinations in hexaploid wheat. In: Riley R, Lewis KR (eds) Chromosome manipulation and plant genetics. Oliver and Boyd, London, pp 29–45

Sears ER, Sears LMS (1978) The telocentric chromosomes of common wheat. In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp. Indian Society of Genetics and Plant Breeding, New Delhi, pp 389–407

Sharp PJ, Kries M, Shewry PR, Gale MD (1988) Location of β-amylase sequences in wheat and its relatives. Theor Appl Genet 75:286–290

Wang ML, Atkinson MD, Chinoy CN, Devos KM, Harcourt RL, Liu CJ, Rogers WJ, Gale MD (1991) RFLP-based genetic map of rye (*Secale cereale* L.) chromosome 1R. Theor Appl Genet 82:174–178