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Molecular linkage mapping in rye (*Secale cereale* L.)

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Abstract A rye linkage map containing clones from rye, wheat, barley, oat and rice genomic and cDNA libraries, known-function genes and microsatellite markers, was created using an F_2 population consisting of 110 F_2-derived F_3 families. Both co-dominant and dominant markers were added to the map. Of all probes screened, 30.8% were polymorphic, and of those polymorphic 79.3% were mapped. The current map contains 184 markers present in all seven linkage groups covering only 727.3 cM. This places a marker about every 3.96 cM on average throughout the map; however, large gaps are still present. The map contains 60 markers that have been integrated from previous rye maps. Surprisingly, no markers were placed between the centromere and C1–1RS in the short arm of 1R. The short arm of chromosome 4 also lacked an adequate number of polymorphic markers. The population showed a remarkable degree of segregation distortion (72.8%). In addition, the genetic distance observed in rye was found to be very different among the maps created by different mapping populations.

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Introduction

Rye (*Secale cereale* L.) is an important cereal crop in many countries around the world because of its good adaptation to adverse biotic and abiotic conditions. This adaptation has also made it a valuable source of alien genes for wheat (*Triticum aestivum* L.) improvement. In addition, rye is important as the R-genome donor to triticale (X *Triticosecale* Wittmack). These characteristics make the study of the genetics of rye of considerable interest and importance.

As with other species, molecular-marker technology has resulted in the creation of linkage maps in rye. Restriction fragment length polymorphisms (RFLPs) have been used to establish linkage maps because of their moderate level of polymorphism and simple Mendelian inheritance. In addition to RFLPs, PCR-based markers have also been used to improve mapping in cereals. Based on these two techniques, a series of rye genetic maps have been established (Wang et al. 1991; Wricke 1991; Devos et al. 1992, 1993a, 1993b; Rognli et al. 1992; Devos and Gale 1993; Plaschke et al. 1993, 1995; Philipp et al. 1994; Wanous and Gustafson 1995; Wanous et al. 1995; Korzun et al. 1996, 1997, 1998; Loarce et al. 1996; Senft and Wricke 1996; Börner and Korzun 1998; Voylokov et al. 1998). But many of the rye maps do not contain linkage maps of all seven chromosomes. The biggest map is that of Devos et al. (1993a), which consists of 156 loci spanning about 1000 cM and covers all seven rye chromosomes. This map gives the most-detailed description of rye chromosomes relative to their wheat homoeologues, but contains no rye genomic or cDNA markers. The Philipp et al. (1994) map consists of 60 loci, in which most of the markers are rye genomic clones. The Loarce et al. (1996) map consists of 89 loci spanning 339.7 cM on all the rye chromosomes, except for 2R. The Senft and Wricke (1996) map consists of

127 loci, of which 15 showed dominant segregation, spanning about 760 cM. The Korzun et al. (1998) map is a joint map derived from two reciprocal crosses, spanning 660 cM, consisting of 91 loci, of which 82 markers are integrated into previous rye, wheat, barley or oat maps, allowing for good comparisons between the different maps. The Wanous and Gustafson (1995) and Wanous et al. (1995) maps contain 68 markers covering about 702 cM on rye chromosomes 1R, 6R and 7R, and are the only maps to include cytological markers.

In general, all the rye mapping populations suffer from segregation distortion (Philipp et al. 1994; Wanous et al. 1995; Loarce et al. 1996; Senft and Wricke 1996; Korzun et al. 1998). Distorted segregation ratios may result from competition among gametes for preferential fertilization (Lyttle 1991). Rye is an outcrossing species, which possesses a self-incompatibility (SI) system (Lundqvist 1956). Inbreeding will cause selection among gametes, allowing the deviation of segregation from normal Mendelian ratios.

The maps also contain markers mostly generated from genomic libraries, which can show substantially higher levels of polymorphism (Hart 1990; Gill et al. 1991; Devos et al. 1992). However, problems associated with using genomic clones are that they can include the presence of a large number of repeat sequences which themselves can vary in number, leading to non-uniform hybridization. As the rye genome comprises about 92% repetitive sequences, rye genomic markers are capable of detecting multiple loci and, therefore, can appear non-syntenic in different populations (Gale 1990; Harcourt and Gale 1991; Devos et al. 1992).

RFLP-based linkage mapping has revealed a non-uniform distribution of mapped loci in plants. The presence of intra- and inter-chromosomal duplications has also been observed through rye RFLP mapping (Liu et al. 1992). In addition, most of the linkage maps show a clustering of markers near the centromeres. This clustering of markers results in inflated interval distances between distal loci, thus reducing overall map resolution and utility (Devos et al. 1993a).

Rogowsky et al. (1993) established the clustering of genetic loci on 1R utilizing chromosome deletion and recombination lines. Genetic linkage maps of 1R (Lawrence and Appels 1986; Benito et al. 1990; Baum and Appels 1991; Wang et al. 1991) revealed a clustering of loci around the centromeres and a non-linear relationship to physical distance. The physical mapping studies of Gustafson et al. (1990), Sybenga et al. (1990) and Rogowsky et al. (1993), comparing genetic linkage data for the 1RS arm, revealed a similar disparity. These studies agreed that genetic distances proximal to the NOR locus on 1RS were reduced, while those distal were expanded. C-banding data suggested that linkage maps are derived from recombination events occurring in the distal 20–30% of the arms (Lukaszewski 1992; Lukaszewski and Curtis 1993), and that a positive correlation exists between recombination and distance from the centromere (Curtis and Lukaszewski 1991; Gill et al. 1993; Lukaszewski and Curtis 1993). It is well known that the frequency and distribution of recombination along cereal chromosomes can also be influenced by the genetic background, which might explain some reduced recombination frequencies and divergent linkage estimates.

The relationship between genetic distance and physical distance in cereals has been estimated to be 1 cM every 440–1530 kb in the distal chromosome regions to 172000–234000 kb in regions adjacent to the centromere (Gill et al. 1993; Lukaszewski and Curtis 1993). However, these studies have not taken into account variations in chromatin structure (i.e., euchromatin vs heterochromatin) which exist along a chromosome, which affect recombination and, therefore, the accuracy of the above estimates.

The map we present here contains more markers (184 markers) than any other published rye linkage map. In addition, the present map contains 60 markers in common with the rye consensus maps of Börner and Korzun (1998) and Schlegel et al. (1998), thus allowing for the integration and comparison among different maps based on different mapping populations.

Materials and methods

Mapping populations, DNA extraction and Southern analysis

Two F_2 mapping populations were created. One consisted of 110 F_2-derived F_3 families from the cross 'UC-90 × E-line', which was used in the Wanous and Gustafson (1995) and Wanous et al. (1995) studies. The two parents were originally selected for two reasons. First, they were polymorphic for several of the telomeric C-bands. Second, each one of the parents had been inbred for more than seven generations before the population was created. Unfortunately, in the present study, none of the telomeric markers were linked as the cM distance between them and the nearest RFLP marker was too large to accurately place them on any linkage group. The second F_2 mapping population consisted of 58 F_2-derived F_3 families derived from the cross between 'King II' and 'Imperial' lines. The parents of this population had also been inbred for at least seven generations. In both populations, root tips were collected from each F_2 plant for C-banding at mitosis in order to look for the occurrence of any centric break and fusion translocations. Any plants showing translocations were removed from the population as they would effect the mapping. All normal (non-translocation) plants were grown in a glasshouse and were self-pollinated. At least 16 F_3 plants from each F_2 line were grown in the glasshouse and leaf tissue was harvested and bulked, thus re-creating the original F_2 genotype. All techniques involved in DNA extraction and Southern analysis were as described in the previous study by Wanous and Gustafson (1995).

RFLP probes and C-banding markers

Several different sets of genomic and cDNA clones from rye, wheat, barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), rice (*Oryza sativa* L.), and *Triticum tauschii* were mapped. In addition, several functional genes were mapped (Table 1). The C-band marker C1–1RS was the only cytological marker from previous studies that was capable of being mapped (Wanous and Gustafson 1995). All loci identified on the map with DNA clones were designated by an ''X'' followed by either a laboratory code or by the name of the library, and by the number given to the clone. Those loci identified by a multiple-copy clone were identified in the same manner as above, except that following the clone number there is either a symbol or a letter identifying that particular locus.

Table 1 DNA clones used as RFLP markers

A. Individual clones

Locus	Clone	Function or laboratory	Reference
XNor	pScR4.T1	Rye ribosomal spacer DNA	Appels et al. 1986
XSec3 (XGlu)	pTag1290	Wheat HMW glutenin	Thompson et al. 1983
XPgk1	P7	Wheat chloroplast phosphoglycerate kinase	Longstaff et al. 1989
XAdh	p3NTR	3′ Untranslated wheat alcohol dehydrogenase	Mitchell et al. 1989
XAdpg2	pSh2.25	ADP glucose pyrophosphorylase	Devos et al. 1993a
XFbp	PSR39	Wheat chloroplast fructose-1,6-biphosphatase	Raines et al. 1988
XPepc	Pepco	Sorghum phosphoenolpyruvate carboxylase	Oswald et al. 1990
Xcsih69	IH69	P. Sharp, Australia	Baum and Appels 1991

B. Clone sets

Code	Laboratory	Type	Reference
SCG	P. Gustafson, U.S.A.	Rye gDNA	Wanous and Gustafson 1995
UAH	E. Ferrer, Spain	Rye gDNA	Loarce et al. 1996
IAG	P. Senft, Germany	Rye gDNA	Senft and Wricke 1996
PSR	M. Gale, U.K.	Wheat c and gDNA	Devos et al. 1993a
BCD	M. Sorrells, U.S.A.	Barley cDNA	Heun et al. 1991
CDO	M. Sorrells, U.S.A.	Oat cDNA	Heun et al. 1991
WG	M. Sorrells, U.S.A.	Wheat gDNA	Heun et al. 1991
RZ	M. Sorrells, U.S.A.	Rice cDNA	Causse et al. 1994
KSU	B. Gill, U.S.A.	Wheat gDNA	Gill et al. 1991
ABC	A. Kleinhofs, U.S.A:	Barley cDNA	Kleinhofs et al. 1993

PCR analysis

The primers selected were wheat and barley microsatellite primers from Röder et al. (1995) and Liu et al. (1996). Out of 23 primers tested, WMS6 and three loci involving HVM40 were mapped. Several others were polymorphic when the parents were screened, but were not mapped.

Genetic map

All mapping analyses were performed using the software package JoinMap version 2.0 (Stam 1993) at a LOD score of 3.0. Recombination values were converted to genetic distances (cM) using the Kosambi mapping function. Both co-dominant and dominant markers were added to the current map. Once a core map for each linkage group corresponding to a chromosome was created, additional markers were added one at a time. If the added marker did not significantly increase the size of the map or did not change the core marker order, then the added marker was left in place. The linkage groups were assigned to specific rye chromosomes based on the integrated markers from other published maps.

Results and discussion

Segregation distortion

Segregation significantly different from the expected Mendelian ratios, 1:2:1 for co-dominant alleles, and 3:1 for dominant alleles is defined as segregation distortion. In previous studies involving rye, six (1R, 2R, 4R, 5R, 6R and 7R) out of the seven rye chromosomes showed certain degrees of segregation distortion (Philipp et al. 1994; Wanous et al. 1995; Loarce et al. 1996; Senft and Wricke 1996; Korzun et al. 1998). In the present study, all seven chromosomes showed considerable segregation distortion. Among the 184 mapped markers, 134 (72.8%) demonstrated significant segregation distortion at the $P < 0.01$ level with two directions of skewness. Eighty nine loci were skewed in favor of the E-line allele, 41 loci in favor of the UC-90 allele, and four loci in favor of heterozygosity. As an outbreeding species, rye is well known to suffer a strong reduction in viability when inbred. Selection for segregation distortion operating at any stage of development from zygote to seedling may have introduced a bias into the progeny (Loarce et al. 1996). Segregation distortion can result from many genetic and environmental factors (Xu et al. 1997). It is not clear why such a higher number of the alleles deviated from normal segregation in this mapping population as compared to other rye mapping populations (Philipp et al. 1994; Loarce et al. 1996; Senft and Wricke 1996; Korzun et al. 1998). The most probable answer is that the distortion was due to the biology of the parents used in creating the mapping population.

Genetic distance relative to the mapping population

In order to investigate whether different mapping populations give different relative genetic distances for common intervals, we created a second mapping population involving ‘Imperial × King II’ and mapped the same probes to that population as those mapped onto 1R in the ‘UC-90 × E-line’ population. The results, comparing only chromosome 1R between the two mapping populations, clearly showed differences between the two populations using the mapping program JoinMap (Fig. 1). The genetic distance between the two terminal markers in the ‘Imperial × King II’ mapping population was

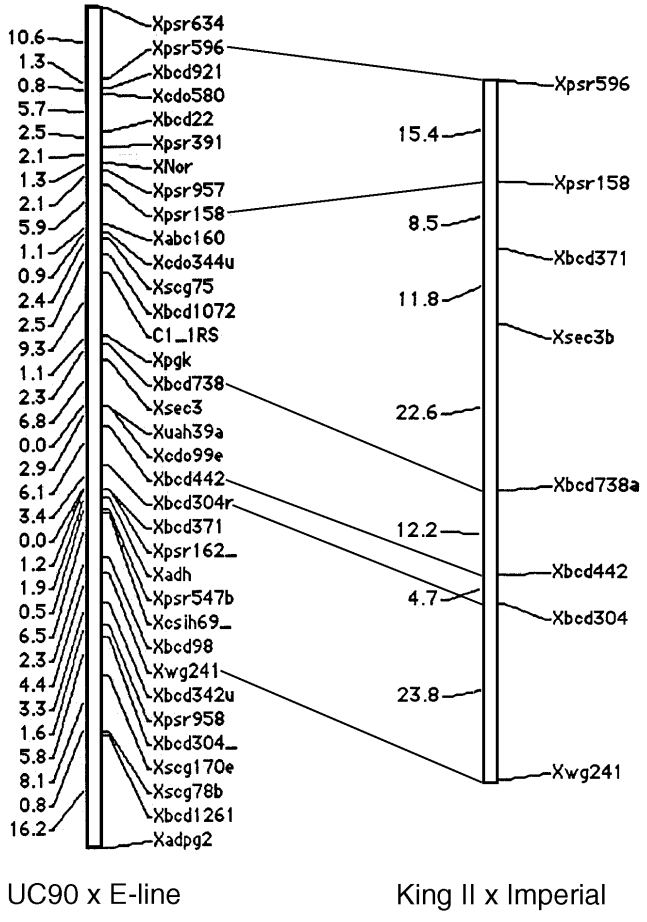

Fig. 1 The comparison of the linkage map of rye chromosome 1R between two populations, 'UC-90 × E-line' and 'King II × Imperial, using the mapping program JoinMap

99 cM, while in the 'UC-90 × E-line' population the genetic distance of the same interval was 82.3 cM. Similar differences were found comparing common intervals (from *Xpsr104* to *Xpsr928* on 7R) between the 'UC-90 × E-line' (Wanous et al. 1995) and 'Ds2 × RxL10' (Devos et al. 1993a) mapping populations, which were both created by the mapping program MAPMAKER. Variation in genetic distance for common intervals in rye was also reported by Melz et al. (1992). Environmental differences, such as temperature, or genetic differences between parents selected for mapping populations, may account for the variation in recombination observed between different studies (Tulsieram et al. 1992; Fatmi et al. 1993). In addition, different population sizes and mapping algorithms can also cause differences.

Genetic linkage map

A total of 753 markers were screened; 232 markers (30.8%) showed polymorphism. Of the polymorphic markers, 184 (79.3%) were mapped. The individual linkage groups ranged from 35 markers on chromosome 1R to 22 markers on 6R (Fig. 2). The remaining 48 polymorphic markers could not be mapped to any of the current seven chromosome linkage groups.

The linkage map generated from the 'UC-90 × E-line' F_2 population contains 172 genomic and cDNA clones from rye, wheat, barley, oat, rice and *T. tauschii* genomic and cDNA libraries, seven functional genes, four microsatellite markers from wheat and barley, and one cytological marker from rye. The markers appeared to be evenly distributed throughout the seven homoeologous groups. The genetic distance covered by the current map is relatively small, but covers 727.3 cM, ranging from 123.4 cM on 1R to 74.3 cM on 2R (Fig. 2). This makes for an average of 3.96 cM between markers on the map. However, there were still some rather-large interstitial gaps that occurred in the map. One located on the distal portion of the long arm of 1R, and one located on the distal portion of the short arm of 1R in the previously published rye maps of Devos et al. (1993a) and Senft and Wricke (1996), were both present in the 'UC-90 × E-line' population. This indicates that these genetic gaps are not unique to just one mapping population, but might be common throughout the species.

Of other major importance was the fact that no RFLP marker had been mapped to the region between the cytological marker C1–1RS and the centromere. This indicates that a very large portion of the short arm of rye chromosome 1 (1RS) contains no polymorphic markers in the mapping population. Lukaszewski (1992) also noted this region when he studied the frequency and distribution of recombination utilizing cytological markers. This leads to the interesting question, what is present in this region of 1RS? It has been shown, by C-banding, that this region contains little heterochromatin. Also, none of the microsatellites so far mapped have gone to this region. In addition, no noticeable C-band variation in the size of this region has been observed in any rye analyzed. No ideas have been presented to-date that even venture a guess as to what is contained in this large region of the short arm of rye chromosome 1R. The results indicate that it may be extremely difficult to fill in the regions of a genome where large gaps exist, as these gaps seem to be present regardless of the parents involved.

Big gaps can also be seen in the distal regions of the long arms of 6R and 7R (Fig. 2). Interstitial gaps were also observed on the short arm of 3R, the long arm of 4R, the short arm of 5R and both the short and long arms of 6R, and two were noted on the long arm of 7R. Only rye chromosome 2R was fairly uniform and showed no significant gaps or clusters of markers. Loarce et al. (1996) and Philipp et al. (1994) noted that 2R contained the fewest number of markers of all the chromosomes. The Senft and Wricke (1996) map contained three unlinked groups for chromosome 2R. The present study contains an adequate number of markers compared to the other linkage groups, but clearly 2R was the shortest (74.3 cM) of all the linkage groups (Fig. 2).

All of the integrated markers from other publications mapped to the chromosomes as expected, except for four

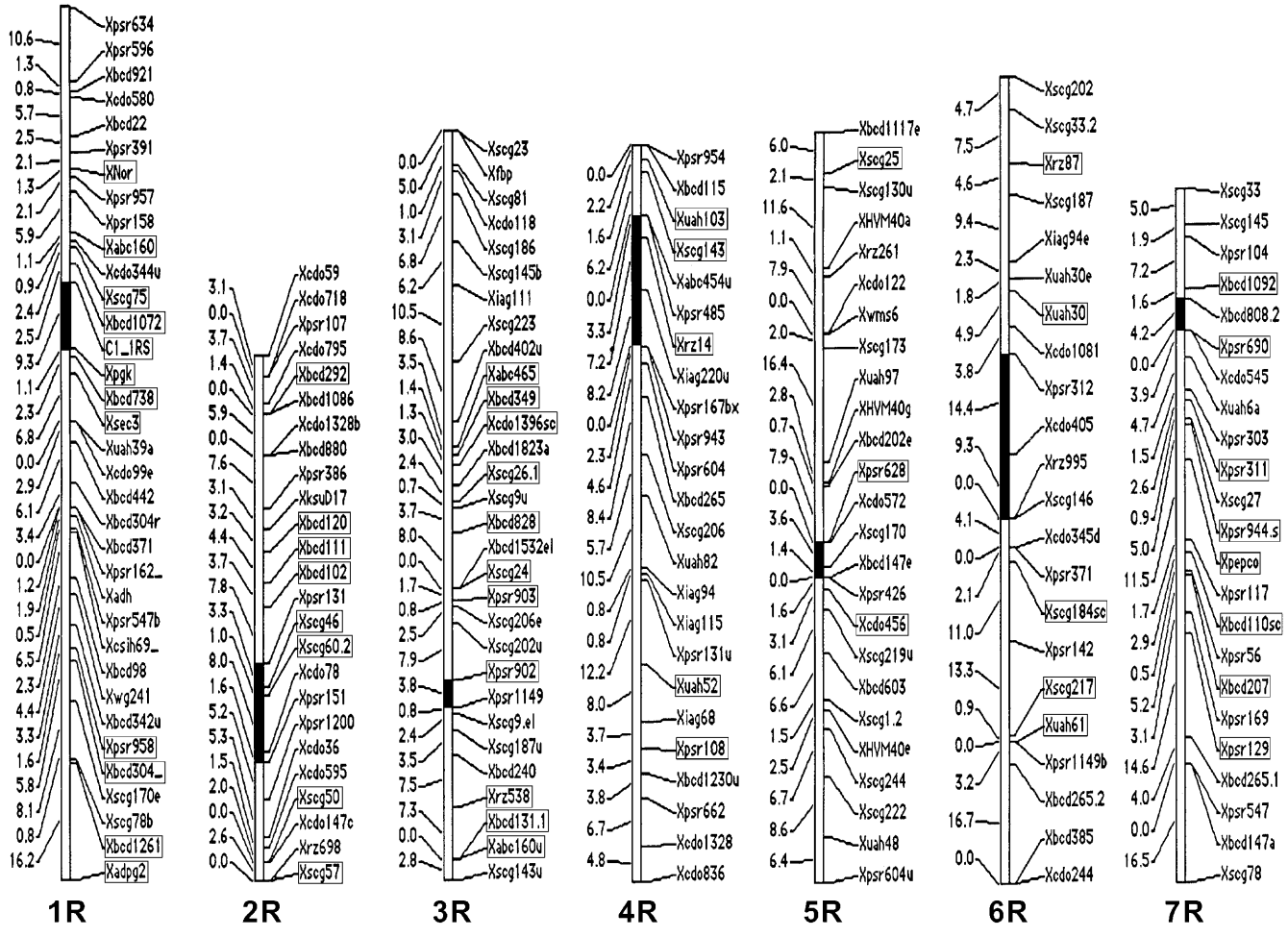

Fig. 2 Genetic linkage map of rye. The solid bars show the approximate positions of the centromeres deduced from Gale et al. (1995), Börner and Korzun (1998) and Schlegel et al. (1998). The short arms of each chromosome are located above the centromere bars, while the long arms are located below the centromere bars. Markers which are labeled with a *rectangle* showed normal segregation, all other markers showed segregation distortion at the $P < 0.01$ level. Individual chromosome cM distances are 1R (123.4 cM), 2R (74.3 cM), 3R (106.3 cM), 4R (104.2 cM), 5R (106.6 cM), 6R 113.8 cM), and 7R (98.7 cM)

PSR, two IAG and two UAH markers. PSR547b mapped onto 1RL whereas Devos et al. (1993a) mapped it to 7RL. PSR131u mapped onto 4RL whereas Devos et al. (1993a) mapped it onto 2RS. PSR604 mapped onto 5RL whereas Devos et al. (1993a) mapped it to 4RL. PSR1149b mapped to 6RL when Devos et al. (1993a) mapped it to 3RL. The rye markers IAG220 and IAG68 were mapped onto 1R and 2R, respectively, by Senft and Wricke (1996), whereas in the current map they were mapped to 4R. UAH30 and UAH48 were mapped to rye chromosome 1R and 7R, respectively, by Loarce et al. (1996), but the present map has them on 6RS and 5RL, respectively. One explanation for these differences is that the clones in question show multiple banding patterns when hybridized to rye and that the segregating band mapped in the present study most likely was not the one mapped in the earlier studies. Both the Loarce et al. (1996) and Senft and Wricke (1996) maps contained probes that showed multiple bands and mapped to different loci on one, or more than one, chromosome. In addition, Fbp was mapped to 3RS, while it was located to 7RS by Devos et al. (1993a).

The markers located on rye chromosomes by Devos et al. (1993a) and wheat chromosomes by Gale et al. (1995) were placed one to their arm locations by utilizing the nullisomic-tetrasomic and ditelosomic aneuploid stocks of wheat. Our results showed that markers PSR391, PSR957 and PSR158 were located on the short arm of 1R spanning the nucleolus organizing region (NOR) locus; whereas the Gale et al. (1995) wheat map had all three markers mapped on the long arm. In the Devos et al. (1993a) rye map, PSR158 was placed on the long arm, but PSR957 was on the short arm. The PSR391 marker was not located on the Devos et al. (1993a) rye map. The differences in the results could actually be due to a translocation occurring within one of the parents used in creating the various mapping populations, or due to the markers being multilocus in nature and capable of being mapped to a different locus depending on the parents used in creating the mapping population.

Röder et al. (1995) located wheat microsatellite marker WMS6 to two sites within hexaploid wheat, on chro-

mosome arms 4DL and 4BL. However, in the present study, WMS6 was located to a site on 5RS. The reason for this difference is not known.

We were also surprised at the relatively low rate of rye genomic probes (21.5%) being mapped as compared to wheat genomic probes (28.9%), barley genomic probes (33.3%), barley (44.8%) and oat (34.4%) cDNA probes. The low rate of rye genomic probes being mapped could be due to the fact that we only mapped single- or low-copy probes and a large number of the rye probes obtained were relatively high in copy number, making them extremely difficult to map. In addition, as observed by Loarce et al. (1996), a majority of the rye probes used showed polymorphism with more than one restriction enzyme, thus indicating that they probably originated from insertions and deletions rather than point mutations.

The locus order in the present map showed some minor differences from the Wanous and Gustafson (1995) and Wanous et al. (1995) maps on chromosomes 1R, 6R and 7R derived from the same mapping population. The reason may be that we added more markers to the map, especially more dominant markers. In addition, the mapping program JoinMap, used in the present study, may give slight differences as compared to the mapping program MAPMAKER used by Wanous and Gustafson (1995) and Wanous et al. (1995).

The current map contained 184 markers and increased the rye mapping resolution to 3.96 cM. This will provide more information for future efforts in marker-assisted selection and map-based cloning. Further, more than 60 markers in the present map have been mapped to other rye mapping populations (reviewed by Börner and Korzun 1998; Schlegel et al. 1998), and 128 markers on the present map were derived from plants other than rye, allowing good integration with other linkage maps of rye, as well as various cereal species.

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