Theor Appl Genet (2009) 118:793–800
DOI 10.1007/s00122-008-0939-4

ORIGINAL PAPER

A consensus map of rye integrating mapping data from five mapping populations

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Received: 27 May 2008 / Accepted: 13 November 2008 / Published online: 9 December 2008
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Abstract A consensus map of rye (*Secale cereale* L.) was constructed using JoinMap 2.0 based on mapping data from five different mapping populations, including 'UC90' × 'E-line', 'P87' × 'P105', '$I_{0.1}$-line' × '$I_{0.1}$-line', 'E-line' × 'R-line', and 'Ds2' × 'RxL10'. The integration of the five mapping populations resulted in a 779-cM map containing 501 markers with the number of markers per chromosome ranging from 57 on 1R to 86 on 4R. The linkage sizes ranged from 71.5 cM on 2R to 148.7 cM on 4R. A comparison of the individual maps to the consensus map revealed that the linear locus order was generally in good agreement between the various populations, but the 4R orientations were not consistent among the five individual maps. The 4R short arm and long arm assignments were switched between the two population maps involving the 'E-line' parent and the other three individual maps. Map comparisons also indicated that marker order variations exist among the five individual maps. However, the chromosome 5R showed very little marker order variation among the five maps. The consensus map not only integrated the linkage data from different maps, but also greatly increased the map resolution, thus, facilitating molecular breeding activities involving rye and triticale.

Keywords Rye · *Secale cereale* · Consensus map · Linkage map

Communicated by Q. Zhang.

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Introduction

Rye (*Secale cereale* L.) is an important cereal crop in many parts of the world as it is the most adapted of the cereals for production in regions with adverse biotic and abiotic stresses. This adaptation to biotic and abiotic conditions has made rye an important source of gene complexes for utilization in wheat (*Triticum aestivum* L. em Thell.) improvement. Rye is one of the parents (the R genome donor) of the wheat–rye hybrid, triticale (X *Triticosecale* Wittmack), which is becoming an important cereal in many areas of the world, and is actively being used as a bridging species to introduce rye gene complexes into wheat.

The utilization of restriction fragment length polymorphisms (RFLPs) and various polymerase chain reaction-based marker systems have resulted in the creation of several genetic linkage maps in rye (Devos et al. 1993; Philipp et al. 1994; Senft and Wricke 1996; Loarce et al. 1996; Korzun et al. 1998, 2001; Saal and Wricke 1999, 2002; Ma et al. 2001; Masojć et al. 2001; Hackauf and Wehling 2001; Bednarek et al. 2003; Khlestkina et al. 2004; Milczarski et al. 2007). However, each of them contains only a small number of genetic loci; some maps even do not contain linkage maps of all seven rye chromosomes (Loarce et al. 1996); and one of the maps reported map distance as recombination unit rather than cM distance (Philipp et al. 1994).

Table 1 The five population maps used for construction of the consensus map

Parents	Population size	Number of markers	Number of linkage groups	Length of map (cM)	Reference
P87 × P105	275	183	7	1063.4	Korzun et al. (2001)
UC-90 × E-line	110	184	7	727.3	Ma et al. (2001)
Ds2 × RxL10	120	156	7	1068.0	Devos et al. (1993)
$I_{0.1}$-line × $I_{0.1}$-line	137	127	7	760.0	Senft and Wricke (1996)
E-line × R-line	54	89	6	339.7	Loarce et al. (1996)

The progress of linkage mapping in rye has been slow for several reasons. First, rye is an out-crossing species and suffers from severe inbreeding depression. Secondly, the high level of segregation distortion in rye significantly decreases the statistical power of mapping. Thirdly, the rye genome contains a large amount of repetitive sequences, which complicates genotyping. Therefore, it would be desirable to be able to efficiently use the mapping data from the current available mapping populations. In fact, most rye mapping populations have consistently been used for locus saturation, gene localization and quantitative trait loci (QTL) mapping. For example, the 'P87' × 'P105' population has been used for a series of mapping efforts from RFLP mapping with genomic and cDNA clones (Korzun et al. 1998) to mapping with simple sequence repeats (SSR) (Korzun et al. 2001), and from general linkage map development to locating genes and QTL (Börner et al. 2000; Korzun et al. 2001). Though several individual maps have been significantly extended, the relationship between the various population maps has not been well studied. It would certainly be beneficial to geneticists and breeders if the current rye mapping data were integrated. The mapping program JoinMap (Stam 1993) was designed to allow for the integration of data from individual maps into one consensus map using common markers. The JoinMap program has been used successfully to construct consensus maps by incorporating mapping data in other cereal species (Karakousis et al. 2003; Somers et al. 2004; Diab 2006; Varshney et al. 2007).

The present study constructed a rye consensus map using the mapping data from five rye mapping populations including 'UC90' × 'E-line' (Ma et al. 2001), 'P87' × 'P105' (Korzun et al. 2001), '$I_{0.1}$-line' × '$I_{0.1}$-line' (Senft and Wricke 1996), 'E-line' × 'R-line' (Loarce et al. 1996), and 'Ds2' × 'RxL10' (Devos et al. 1993). The five populations were selected because they have been extensively used for rye genetic mapping in the last decade. It is hoped that a rye consensus map will provide a high-density linkage frame for map-based genetic studies and further facilitate QTL localization and marker-assisted selection.

Materials and methods

Mapping data

Five sets of rye mapping data (Table 1) were included in consensus map construction. The five maps (Devos et al. 1993; Senft and Wricke 1996; Loarce et al. 1996; Ma et al. 2001; Korzun et al. 2001) contained over 700 loci including molecular markers developed from wheat, barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), rye, and rice (*Oryza sativa* L.). The QTL regions characterized by Korzun et al. (2001) were also covered in the present consensus map. All the investigators listed are gratefully acknowledged for making their published and unpublished mapping data sets available (Table 1). The major features of the five populations and the corresponding maps are described below.

'UC90' × 'E-line' Map

The mapping population 'UC90' × 'E-line' consists of 110 F_2-derived F_3 families (Wanous and Gustafson 1995; Wanous et al. 1995; Ma et al. 2001). It was initially used to establish the linkage map of only three rye chromosomes (Wanous and Gustafson 1995; Wanous et al. 1995) and then the map was extended to cover the entire rye genome involving 184 markers with 727.3 cM of coverage (Ma et al. 2001). This map was used as the core map for rye consensus mapping since it contains many common markers when compared to the other maps.

'Ds2' × 'RxL10' Map

The 'Ds2' × 'RxL10' map was constructed from 120 F_2 plants and 156 RFLP loci spanning about 1,000 cM (Devos et al. 1993). The map gives the most detailed description of rye chromosomes relative to their wheat homoeologues, but contains no rye genomic or cDNA markers. One notable observation regarding this population is that the loci on the individual chromosome maps were heavily clustered around the centromeres. This map was later significantly extended with random amplified polymorphic DNA (RAPD)

and amplified fragment length polymorphism (AFLP) markers (Masojć et al. 2001; Bednarek et al. 2003) and was also used as a reference for another recent rye map (Milczarski et al. 2007).

'E-line' × 'R-line' map

This map was built using 54 F_2 individuals from the cross of two inbred lines, 'E-line' and 'R-line' (Loarce et al. 1996). The map located 77 RFLP and RAPD markers spanning 339.7 cM and covered six rye chromosomes, the exception being 2R (Loarce et al. 1996).

'$I_{0.1}$-line' × '$I_{0.1}$-line' Map

This map was created from a F_2 mapping population of 137 individuals, which had been generated by crossing two $I_{0.1}$-lines from a synthetic rye population (Senft and Wricke 1996). The map also integrated the mapping data of Philipp et al. (1994), resulting in a map containing 127 RFLP and RAPD loci and covering 760 cM (Senft and Wricke 1996). The '$I_{0.1}$-line' × '$I_{0.1}$-line' map was later extended with SSR and AFLP markers (Saal and Wricke 1999, 2002).

'P87' × 'P105' Map

The 'P87' × 'P105' map was based on a pooled mapping population generated by combining 275 F_2 individuals derived from a pair of reciprocal crosses of the two inbred parents (Korzun et al. 2001). The population has been used several times for rye mapping studies (Korzun et al. 1998, 2001; Börner et al. 2000). The map data incorporated in the present study is the Korzun et al. (2001) map spanning 1063.4 cM with 183 markers. In addition, this map also located 25 QTL and it is the only map containing QTL among the five maps to be integrated (Korzun et al. 2001).

Mapping strategy

The JoinMap 2.0 program (Stam 1993) was utilized to reproduce the five rye linkage maps and to generate a consensus map. The program used the individual population marker data to estimate all the pairwise recombination frequencies and the corresponding LOD values. Combining the pairwise recombination values and LOD scores was possible only by the utilization of 'common' markers that were shared by the individual linkage maps as the anchor around which the map was developed. The Kosambi mapping function was used to calculate map distances (Kosambi 1944).

The cutting value for recombination frequency was 0.4 for most of the maps, but various LOD scores were used for chromosome mapping. Several runs were performed to see how consistent the linkage mapping results were, especially between runs using different LOD scores, for a given set of markers.

Table 2 The numbers of loci those were common between the mapping populations in each chromosome

Mapping population	Chromosome							Total
	1	2	3	4	5	6	7	
UC90 × E-line and P87 × P105	3	0	0	2	0	1	3	9
UC90 × E-line and Ds2 × RxL10	8	3	1	3	2	1	6	24
UC90 × E-line and E-line × R-line	1	[a]	1	3	2	3	2	12
UC90 × E-line and $I_{0.1}$-line × $I_{0.1}$-line	0	1	2	2	1	1	1	8
P87 × P105 and Ds2 × RxL10	6	7	3	4	6	6	8	40
P87 × P105 and E-line × R-line	1	[a]	0	0	0	0	1	2
P87 × P105 and $I_{0.1}$-line × $I_{0.1}$-line	2	4	1	2	1	0	1	11
Ds2 × RxL10 and E-line × R-line	1	[a]	1	0	1	0	1	4
Ds2 × RxL10 and $I_{0.1}$-line × $I_{0.1}$-line	1	3	1	2	3	0	1	11
E-line × R-line and $I_{0.1}$-line × $I_{0.1}$-line	0	[a]	0	1	1	1	1	4
All five populations	0	[a]	0	0	0	0	1	1

[a] There was no 2R map for the 'E-line' × 'R-line' population

In addition, the consensus map was built upon a common core map as a base, which was the 'UC90' × 'E-line' map (Ma et al. 2001) since it contained the most diversified common RFLP markers when compared to the other maps. All consensus mapping was done using JoinMap with nonfixed orders. It was constructed with common pivotal marker loci (Table 2), such as *Xpsr162* and *Xpsr634* on chromosome 1R, with all other markers being added to the consensus map one at a time going in both directions from the pivotal marker. This allowed for the inspection of each marker placement as it was integrated into the consensus map. When a marker was placed into the consensus map and it did not noticeably increase the cM distance and did not greatly change the map order, the marker was assumed to be in its proper position. We proposed this is also the best way to map multi-loci markers in a consensus map because, even for the same probes, different loci could be involved when joining mapping data from several populations.

Results

The consensus map was established using mean pairwise recombination values and combined LOD scores, and covered all seven chromosomes of the rye genome (Fig. 1). Since four maps were originally built using MapMaker (Lander et al. 1987) and only one using JoinMap (Stam 1993), the pairwise recombination and LOD values were re-estimated and the maps were reproduced with JoinMap for the four populations that were initially created using

MapMaker (Devos et al. 1993; Senft and Wricke 1996; Loarce et al. 1996; Ma et al. 2001; Korzun et al. 2001). However, because the two mapping programs used different algorithms to calculate the map distances, this resulted in some marker order and cM distance changes. JoinMap uses all pairwise estimates, above the defined LOD threshold, to establish map length, whereas MapMaker establishes map length using only adjoining marker pairs to calculate the sum of adjacent distances. MapMaker assumes a lack of interference, thus recombination was simply translated into cM depending on the mapping function. However, JoinMap does take interference into account. So when the level of interference is high, the two mapping programs produced maps of varying lengths as observed in barley (Qi et al. 1996), even though they could have both used the Kosambi mapping function (Kosambi 1944).

One of the challenges of integrating the map data was to deal with multi-locus markers. Even for the same probe, allele(s) mapped in one population could be the same or different from those mapped in other populations since multiple alleles or loci can be detected and mapped from many RFLP markers. For this reason, attempts were made at adding markers from other mapping populations to the 'UC90' × 'E-line' map one at a time. This also eliminated the use of common markers showing significant heterogeneity (i.e., potentially different loci) between different populations.

Interestingly, as the consensus map increased with the addition of more markers, the map generally condensed in cM length, which is what should happen as a map grows in marker number. For most markers, the liner order of the markers in the consensus map is in agreement with the individual maps, however, the consensus map did not always place markers in an identical order as on the original maps because JoinMap accommodated the marker positions if the original orders and/or distances were different between individual maps.

Chromosome 1R

The 1R consensus map is 134.3 cM in length and contains 57 markers from four of the five individual maps ('UC90' × 'E-line', 'Ds2' × 'RxL10', 'E-line' × 'R-line', and 'P87' × 'P105') (Fig. 1). No markers were integrated from the '$I_{0.1}$-line' × '$I_{0.1}$-line' map because of a lack of common markers. Two chromosomal landmark markers, the ribosomal nucleolar organizing region and the heterochromatic band on the distal end of the short arm, and at least five isozyme genes *adpg*, *Adh*, *Sec3*, *pgk*, and *Gpi-R1* were placed onto the consensus map. The locus (*Xiag186a*), associated with the QTL (*Gm.stp-1R.1*), was not integrated into the consensus map, but it is interesting to see that the QTL interval of *Gm.stp-1R.1* narrowed down

Fig. 1 The seven individual rye chromosome consensus maps. The chromosome orientation is always with the short arm at the top, and with all map distances in cM based on the Kosambi function (Kosambi 1944). The approximate centromere locations are filled in *black* on each chromosome ▶

to less than 2.0 cM between loci *Xpsr162* and *Xiag111* when compared to the original interval (Korzun et al. 2001). The 1R consensus map shows a good distribution of markers and contains only two large gaps (>10 cM), which were both located at the telomeric ends of the map. When compared to the individual maps, some marker orders were changed, but the changes were usually within a small local interval. There is one centromere to short arm inversion (~6 cM in the consensus map) involving some of the loci between *Xpsr601* and *XNor* when the 1R maps of 'UC90' × 'E-line', 'Ds2' × 'RxL10', 'E-line' × 'R-line' and 'P87' × 'P105' were compared to the 1R consensus linkage. This inconsistency may be caused by different mapping stringencies, especially in those regions containing segregation distortion.

Chromosome 2R

The 2R consensus map is 71.5 cM in length involving 68 markers from only four individual maps ('UC90' × 'E-line', 'Ds2' × 'RxL10', '$I_{0.1}$-line' × '$I_{0.1}$-line' and 'P87' × 'P105') (Fig. 1). The Loarce et al. (1996) map did not contain a linkage group for 2R. The 2R consensus map contains several isozyme genes including *Sod-R1*, *Est6*, and several alleles of *Embp*. The markers associated with the five QTL (*Flt.ipk-2R.1*, *Tgw.ipk-2R.1*, *Gm.ipk-2R.1*, *Eyd.ipk-2R.1*, and *Ean.stp-2R.1*) were all integrated into the map (Korzun et al. 2001). The markers from the 'UC90' × 'E-line' and 'Ds2' × 'RxL10' maps were placed in the consensus map in the expected order except for the two *Embp* alleles on the short arm, while the 'Ds2' × 'RxL10' map placed them on the long arm. The 'P87' × 'P105' 2R map was joined to the consensus map with more differences. The 2R map of '$I_{0.1}$-line' × '$I_{0.1}$-line' was also well integrated when compared to the original marker order, but all markers from the original top fragment were joined in the middle of the consensus map. This movement could be due to a potential wrong order assembly because the original 2R of '$I_{0.1}$-line' × '$I_{0.1}$-line' map contained three unlinked segments (Senft and Wricke 1996). If the top fragment of the '$I_{0.1}$-line' × '$I_{0.1}$-line' 2R map (Senft and Wricke 1996) were placed in the middle of the three genomic regions, then the marker order of the '$I_{0.1}$-line' × '$I_{0.1}$-line' 2R map would be in very good agreement with the 2R consensus map. The 2R consensus map contains no gaps of 10 cM or larger and the markers are well spread throughout the 71.5 cM map. The consensus

7R

6R

5R

4R

3R

2R

1R

2R map is the densest among the seven rye chromosomes with an average resolution of about 1 cM.

Chromosome 3R

The 3R consensus map is 104.7 cM long and is comprised of 71 markers from all five individual maps (‘UC90’ × ‘E-line’, ‘Ds2’ × ‘RxL10’, ‘E-line’ × ‘R-line’, ‘$I_{0.1}$-line’ × ‘$I_{0.1}$-line’ and ‘P87’ × ‘P105’) (Fig. 1). The 3R consensus map contains at least four known-gene loci (*Fbp*, *Cxp*, *Mal*, and *Sbp*). Unfortunately, there was only one common marker (*Xpsr902*) between the core map (‘UC90’ × ‘E-line’) and the other two large maps (‘Ds2’ × ‘RxL10’ and ‘P87’ × ‘P105’). All of the markers from the Ma et al. (2001) map were in exactly the same order as in the consensus map. The other four 3R individual maps were combined with some order changes. About three to five markers around the centromere were inversely placed in the consensus map when compared to the four individual maps (Devos et al. 1993; Senft and Wricke 1996; Loarce et al. 1996; Korzun et al. 2001), which could be caused by lack of enough common markers between ‘UC90’ × ‘E-line’ and other maps.

Chromosome 4R

The 4R consensus map was built using markers from all five individual maps (Fig. 1). The map consists of 86 markers covering 148.7 cM. The 4R consensus map contains only one common locus (*Xpsr167*) that is present in more than two of the individual maps. The 4R consensus map contains six known-gene loci (*Nra*, *Glob*, *Ger*, *Ss1*, *Cxp*, and *Eper*). The markers *Xmwg539* and *Xpsr119* identifying the only QTL (*Ean.ipk4-R.1*) were joined in the consensus map from the ‘P87’ × ‘P105’ map (Korzun et al. 2001). The consensus map contains only one gap of 10 cM or larger at the telomeric end of the long arm, which is consistent with all previous published 4R linkage and physical maps (Miftahudin et al. 2004).

It should be noted that the entire 4R marker linkage set of ‘UC90’ × ‘E-line’ (Ma et al. 2001) and ‘E-line’ × ‘R-line’ (Loarce et al. 1996) were integrated into the 4R consensus map as an inversion when compared to the other three population maps, ‘$I_{0.1}$-line’ × ‘$I_{0.1}$-line’ (Senft and Wricke 1996), ‘Ds2’ × ‘RxL10’ (Devos et al. 1993), and ‘P87’ × ‘P105’ (Korzun et al. 2001), indicating that the original orientation and arm assignments of ‘UC90’ × ‘E-line’ and ‘E-line’ × ‘R-line’ maps were not compatible with the other three maps. Though different linkage orientations exist, the linear orders of markers are highly consistent among the five individual maps and the consensus map.

Chromosome 5R

The chromosome 5R consensus map spans 118.1 cM with 79 markers from all five individual maps (Fig. 1). The 5R consensus map contains many known genic loci (*β-amy-R1*, *Cat*, *Ddw1*, *Hp1*, *Dw*, *α-amy-3*, *Ph-2*, and several copies of *Est*). The two major QTL regions from the ‘P87’ × ‘P105’ map (Korzun et al. 2001) were incorporated to the consensus map, covering all 14 QTL (*Eal.stp-5R.1*, *Fln.stp-5R.1*, *Flt.ipk-5R.1*, *Flt.stp-5R.1*, *Gm.ipk-5R.1*, *Tgw.ipk-5R.1*, *Eyd.ipk-5R.2*, *Syd.ipk-5R.1*, *Ht.ipk-5R.1*, *Ht.ipk-5R.2*, *Ht.ipk-5R.3*, *Ht.stp-5R.1*, *Pdl.ipk-5R.1*, and *Pdl.stp-5R.1*) detected by Korzun et al. (2001). The 5R consensus map was the easiest one of all the rye chromosome maps to build as the data from all of the individual population maps were placed into a consensus map without any significant locus location change, except for three loci at the very end of the ‘P87’ × ‘P105’ map, indicating that the chromosome structure of 5R is highly conserved among the parents used in creating the mapping populations. The short arm of the 5R consensus map ended with the placement of locus *Xpsr945*. The ‘P87’ × ‘P105’ 5R map placed three loci (*Xhvsut2*, *Xmwg502*, and *Xmwg2225*) distal to *Xpsr945* while the consensus map moved the three loci to the middle of the linkage group. This inconsistency could be caused by the weak linkage (39.5 cM) between the three distal markers and other 5R markers of the original map (Korzun et al. 2001). The 5R consensus map contains only one large gap (13.4 cM) at the distal end of the long arm.

Chromosome 6R

The 6R consensus map consists of 67 markers, representing 113.2 cM, from all the five individual maps (Fig. 1). The 6R consensus map contains a few genic loci (*α-amy-1.1* and *1.2*, *Glb33*, *Gal*, *Ep*, *Dia*, *Wsp*, *Opt,* and several copies of *Est*) and the three QTL (*fln.stp-6R.1*, *Ean.ipk-6R.1*, and *Syd.stp-6R.1*) intervals reported by Korzun et al. (2001). The 6R consensus map contains only one recombination gap larger than 10 cM, which is an interstitial gap of 11.0 cM located in the middle of the short arm. The marker order of the 6R consensus map is identical to the marker order of the ‘UC90’ × ‘E-line’ 6R map (Ma et al. 2001). Good marker order consistency was also observed between the other four 6R individual maps and the consensus map, but all markers that located on the long arm terminal region from *Xpsr965* to *Xbcd385* (32.4 cM) were inverted in order on the consensus map when compared to the other four population maps, ‘E-line’ × ‘R-line’ (Loarce et al. 1996), ‘$I_{0.1}$-line’ × ‘$I_{0.1}$-line’ (Senft and Wricke 1996), ‘Ds2’ × ‘RxL10’ (Devos et al. 1993) and ‘P87’ × ‘P105’ (Korzun et al. 2001).

Chromosome 7R

The 7R consensus map is 88.5 cM long and comprised of 73 loci from the five individual maps (Fig. 1). The 7R consensus map contains several genic loci (*α-amy-2*, *Embp*, *Per*, *Adpg*, *pepco*, and *Fbp*). It also covers the only QTL (*Flt.psr-7R.1*) mapped by Korzun et al. (2001). Rye chromosome 7R is the only chromosome where all five individual maps contain a common locus (*Xpsr129*). However, the markers that can be joined on the consensus map are mainly from only three maps, 'UC90' × 'E-line', 'Ds2' × 'RxL10', and 'P87' × 'P105'. The other two maps, 'E-line' × 'R-line' and '$I_{0.1}$-line' × '$I_{0.1}$-line', added only one locus (*Xuah6*) besides the common locus (*Xpsr129*). The resulting consensus map is relatively small and contains no recombination gaps of more than 10 cM. The 'UC90' × 'E-line' map order is, in general, in agreement with the consensus map except for the presence of a few locus order changes. The other two 7R population maps, 'Ds2' × 'RxL10' and 'P87' × 'P105', were integrated into the consensus 7R with a similar change by moving two to five markers on the terminal end of the long arm to the middle, around the locus *Xpsr566*, of the consensus 7R map.

Discussion

Comparisons of the consensus chromosome maps with the five individual rye maps provided useful insights concerning the reliability and usefulness of consensus maps. Since the consensus map was built using the 'UC90' × 'E-line' linkage (Ma et al. 2001) as the core map, the marker orders in the consensus map are highly consistent with the 'UC90' × 'E-line' map, though 4R is in an opposite orientation. Of the other four individual population maps (Devos et al. 1993; Senft and Wricke 1996; Loarce et al. 1996; Korzun et al. 2001), most markers were also mapped to the consensus map in their original orders, but a small number of markers were joined with order changes, which could be caused by computational variation resulting from (1) recombination heterogeneity between different populations; (2) weak linkages existing in the various maps; (3) missing or poor quality data; (4) different mapping programs being used for constructing the individual and the consensus maps; and (5) different thresholds statistics being applied for creating the consensus maps and the original maps.

A linkage group is correctly constructed only when the genotyping data are of high quality and the proper LOD scores and recombination frequencies are used. For consensus mapping, it is sometimes hard to adjust the thresholds statistics especially when a linkage group contains many segregation-distorted markers and the population sizes are very different between populations. In order to maximize the number of markers to be integrated in the rye consensus map in their original orders, different LOD values have been attempted. However, in many cases, a given set of thresholds statistics are good for one chromosome arm (or region), but not for another arm (or region) even for the same linkage groupings.

Map comparisons showed that, of the five original maps, the 'Ds2' × 'RxL10' and 'P87' × 'P105' maps (Devos et al. 1993; Korzun et al. 2001) were more closely correlated in terms of the marker linear orders within the maps, indicating that the parental chromosome structures of the two populations are very similar. The 'UC90' × 'E-line' and 'E-line' × 'R-line' maps also demonstrated good correspondence, because of the common parent, 'E-line', used in the both populations (Loarce et al. 1996; Ma et al. 2001). More variation was observed between the 'UC90' × 'E-line' map and the 'Ds2' × 'RxL10' and 'P87' × 'P105' maps, but the differences were usually restricted to small regions, which often involved the terminal ends, such as 6R and 7R. Terminal ends often contain large recombination gaps, suggesting that the disagreement between different maps in such regions could be caused by weak linkage (large cM gaps).

The consensus map did not place all markers from the individual maps, but only about 75% of the total available data, mainly due to very weak linkages between markers, a lack of common markers, and high recombination heterogeneity of common markers in different populations. The analysis was also clear in that it was easier to place loci on the consensus map if they were located in a marker cluster. It was challenging, because of the weak linkages, to place any locus on the consensus map that spanned a large recombination gap or where there was a very large distance between markers.

Building a consensus map is not possible without common or pivotal loci present on each chromosome arm. It was clear that not all common probes were useful because they could actually represent different loci of a multi-locus marker. Therefore, one should use common loci with care, and compile a consensus map using a single pair of linked loci at a time only when they give similar recombination frequencies between individual populations. The consensus map was constructed based on many selected thresholds statistics, such as LOD score, jump value, recombination frequency (Stam 1993). Therefore, the result is only as good as the values for the selected parameters. The JoinMap program provides a 'fixed order' option, which is very useful for map extension if the linear order of the selected markers is verified. However, to come up with a large set of fixed orders is not easy for rye consensus mapping because there is very limited rye genomics information available to verify if a chosen marker order is certainly correct. None of

the consensus linkages in this study were built using the 'fixed order' option.

Though inconsistencies exist, there is a relatively good agreement of the consensus loci order when compared to the five original population maps. Overall, there are 501 loci mapped in the consensus map covering 779 cM, resulting in an average resolution of about 1.6 cM, which is certainly hard to achieve based on a single mapping population. It is hoped that the integrated map can provide valuable information for the molecular breeding programs of rye and triticale.

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