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Detection of quantitative trait loci on chromosome 5R of rye (*Secale cereale* L.)

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Abstract Progenies of an F_2 mapping population were analyzed for quantitative traits to detect QTLs by using marker information from F_2 plants for chromosome 5R. The mapping population was segregating for the major dwarfing gene *Ddw1* and the gene *Hp1* for hairy peduncle. The only QTL determining plant height was located between HP1 and *Ddw1* on the distal part of chromosome 5RL. At the same position a QTL for peduncle length was found, and this trait was closely related to plant height ($r = 0.895$). Since *Hp1* and *Ddw1* are dominant marker loci, no dominance effect could be estimated. The QTLs for spike length and the number of florets were located near the centromere on 5RL. These two traits were correlated with $r = 0.824$ and showed partial dominance, but these traits were not correlated to plant height and peduncle length. Homoeologous relationships between the QTLs mapped for the first time in rye and those mapped in other Triticeae members are discussed.

Key words Quantitative trait loci · Genetic mapping · RFLP · Agronomic characters · *Secale cereale* L.

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Introduction

Molecular makers are widely used for tagging genes determining qualitative inherited characters. Examples in rye are the mapping of genes determining reduced plant height (Plaschke et al. 1993; Korzun et al. 1996) or self fertility (Voylokov et al. 1998). An even higher impact from applying molecular markers is expected by analyzing quantitative characters, as demonstrated in several crops including tomato (Paterson et al. 1988) and maize (Stuber et al. 1987). A prerequisite, however, is the availability of high-density linkage maps.

Within the Triticeae such maps have been published for wheat (Gale et al. 1995), barley (Langridge et al. 1995) and rye (Devos et al. 1993; Senft and Wricke 1996; Korzun et al. 1998). The identification of QTLs by using RFLP maps was demonstrated for barley (Backes et al. 1995; Bezant et al. 1996, 1997) and wheat (Anderson et al. 1993; Ben Amer et al. 1997), but not for rye. In the present paper, for the first time, we use rye for performing a QTL analysis considering one particular chromosome, 5R. Several morphological and yield parameters were analyzed using F_3 lines grown in the field.

Materials and methods

Plant material and marker analysis

A mapping population of 140 F_2 plants was produced from one single F_1 plant, by crossing the two self fertile lines 'R1620' and 'R347/1'. This population was segregating for two major genes determining dwarfness (*Ddw1*) and hairy peduncle (*Hp1*), both mapped on chromosome 5R by Korzun et al. (1996). The F_2 plants were grown in the greenhouse and the spikes were bagged just before flowering in order to produce selfed F_3 seeds. The F_2 population was already RFLP mapped and the details are described in Korzun et al. (1996).

In addition to the RFLP markers one wheat microsatellite marker (*Xgwm6*) and the two isozyme markers, β-amylase (*β-Amy-R1*) and

NADP-dependent aromatic alcohol dehydrogenase (*AadhNADP*), were also mapped. The procedures for the microsatellite investigation were as described by Röder et al. (1995). The isozyme studies were performed according to Davis (1964) and Liu (1991) for AadhNADP and β-amylase, respectively.

Field evaluation

Five single F_3 plants of each of the F_2 progenies were grown in a randomized design in the experimental fields of the St. Petersburg University, near St. Petersburg, in the 1996/1997 season. Only 107 progenies could be evaluated. The following nine traits were measured on each single plant: flowering time (days after sowing), number of tillers, plant height (main tiller without spike), number of internodes (main tiller), peduncle length (main tiller), spike length (main tiller), number of florets per spike (main tiller), number of grains per spike (main tiller) and number of grains per plant.

Statistical analysis

Mapping was done with MAPMAKER/EXP 3.0 (Lander et al. 1987) and QTL mapping for F_3 means with MAPMAKER/QTL 1.1 (Paterson et al. 1988). Since QTL analysis is possible only for the Haldane mapping function, the linkage map given by Korzun et al. (1996) for the Kosambi function was re-calculated.

Results

All 18 polymorphic markers were mapped on a single linkage group. Sixteen markers had already been mapped in the same F_2 population by Korzun et al. (1996). The order was the same except for one exchange between markers *Xmwg042* and *Xpsr370* which changed places. Also the distances were similar. The total length of the map was increased by adding the two marker loci *Xgmw6* and *AadhNADP*. A further increase resulted from the change to the Haldane mapping function. But, in general, the changes were of minor importance. There is also good agreement with the map for chromosome 5R published by Korzun et al. (1988) for another F_2 population.

The QTL analysis showed that the QTL for plant height was located between *Hp1* and *Ddw1*. Peduncle length is very closely correlated with plant height ($r = 0.895$) and mapped at the same position (Fig. 1). Details on the QTLs are given in Table 1. Since *Hp1* and *Ddw1* are dominant markers, dominance could not be estimated. But, as seen from Table 2, all 25 F_3 progenies showing a recessive status for *Hp1* and *Ddw1* were homogeneous for tall plants, while all F_3 progenies showing a dominant status for *Hp1* and *Ddw1* were either short or segregating with a ratio of 48 short to 30 segregating progenies. Since only five plants were screened for each progeny, the probability of detecting a segregating one is only $1-0.75^5 = 76.3\%$. Therefore, the number of segregating progenies was systematically underestimated; the corrected numbers are 41.3 short : 40.7 segregating : 25 tall progenies which

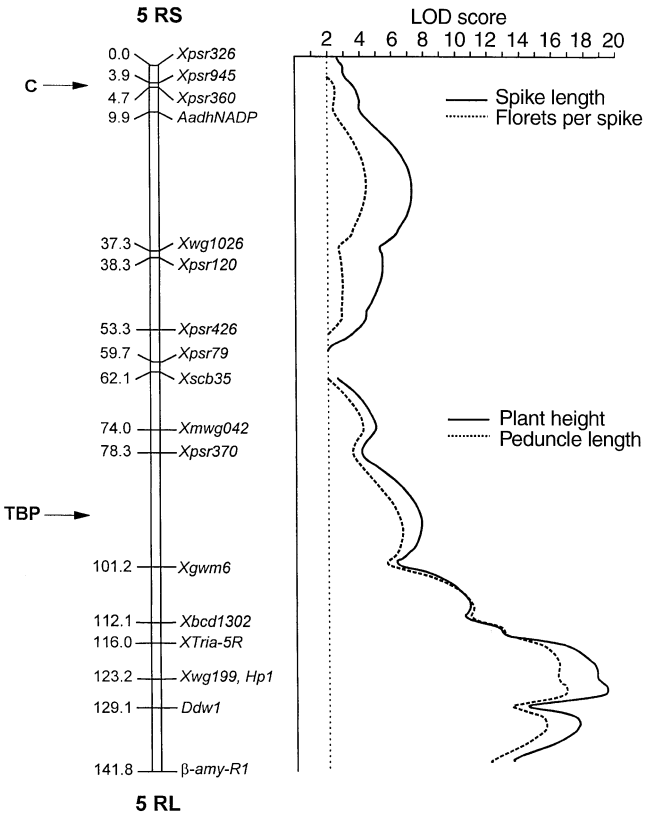

Fig. 1 Linkage map of chromosome 5 of rye together with LOD score plots showing the location of four QTLs. Genetic distances are given in centimorgans; c = centromere, TBP = 5L/4L translocation break point

still deviated from the expected 1 : 2 : 1 ratio. There were four progenies from F_2 plants showing recombination between *Hp1* and *Ddw1*, yielding a recombination rate of 0.036 between these loci.

QTLs for spike length and the number of florets per spike were found on 5R between *AadhNADP* and *Xwg1026* with a nearly equal distance to both markers. Since these two traits are closely correlated with each other ($r = 0.824$), the QTLs are located at nearly the same positions, as shown in Fig. 1. The details are given in Table 1. There was no correlation between these traits and plant height or peduncle length. Since *AadhNADP* and *Xwg1026* are co-dominant markers, a dominance model could be fitted, showing partial dominance for longer spikes and an increased number of florets per spike.

Discussion

The population investigated in the present study was known to segregate for the major dwarfing gene *Ddw1*. As expected, a QTL for plant height could be identified in exactly the same region in which *Ddw1* was mapped by Korzun et al. (1996). The presence of the major gene

Table 1 Description of QTLs on chromosome 5R

Item	Plant height	Peduncle length	Spike length	Number of florets per spike
Left marker	*Hp1*	*Hp1*	*AadhNADP*	*AadhNADP*
Right marker	*Ddw1*	*Ddw1*	*Xwg1026*	*Xwg1026*
Interval length (cM)	5.9	5.9	27.4	27.4
Position from left marker (cM)	2.4	2.2	16.4	14.5
Additive effect	18.7	5.7	0.6	4.0
Dominance effect	–	–	0.3	2.8
LOD score	24.3	19.2	7.5	5.0

Table 2 Frequencies of plant height classes in F_3 progenies of F_2 plants with defined marker types *Hp1* and *Ddw1*

Type of F_2 plant		Number of F_3 progenies			
Hp1	*Ddw1*	Short	Segregating	Tall	Sum
Dominant	Dominant	48	30	–	78
Dominant	Recessive	3	–	–	3
Recessive	Dominant	–	1	–	1
Recessive	Recessive	–	–	25	25
Sum		51	31	25	107

was the reason why the QTL for plant height explained a high percentage (61.1%) of the variation among the F_3 lines found in this study. *Ddw1* is a single major gene with dominance for reduced plant height. The residual variation in plant height could not be explained by a further QTL on chromosome 5R. Again no additional QTL could be detected on performing a separate analysis for the two homozygous allele classes at the *Ddw1* locus. The close correlation between plant height and peduncle length made it impossible to discriminate between closely linked loci as opposed and pleiotropy.

Robertson (1985) postulated that many, if not all, loci for which qualitative mutants have been found also have quantitative alleles. If this relationship is true, qualitative mutants like *Ddw1* could be used to detect quantitative loci in plant material lacking the major gene. Furthermore, if it should be possible to isolate the mutant DNA, it can also be used to isolate the DNA of quantitative alleles.

To study homoeologous relationships it should be mentioned that *Ddw1* is known to be located on that part of chromosome 5R which has been shown to be homoeologous to the group-4L chromosomes of the other Triticeae species. In barley, QTLs for plant height were identified in several mapping populations including some located on chromosome 4HL (Hayes et al. 1993; Backes et al. 1995). These QTLs, however, were shown to reside on that part of chromosome 4HL which is not included in the translocation present in rye and, therefore, were not comparable to that described on 5RL.

For the two QTLs determining spike length and the number of florets per spike, located in the centromere region on chromosome 5RL, pleiotropic determination of only one locus may again be postulated since the traits are also closely correlated. Considering other Triticeae it should be mentioned that a QTL for ear grain number in barley was detected on the long arm of chromosome 5H by Bezant et al. (1997). The QTL found in rye seems to be located more proximally than that localized in barley which was described to map in the region of *Xwg644* known to be closely linked to *Xpsr426* of our map (Galiba et al. 1995).

No QTL for flowering time was detected in our material. Chromosome 5R is known to carry a major gene for vernalization response (*Sp1*) which was shown to have homoeoloci on wheat chromosomes 5A, 5B and 5D (*Vrn*-genes) and on barley 5H (*Sh2*) as demonstrated by Börner et al. (1998). The two parents were winter ryes and, therefore, seem to contain identical alleles at the *Sp1* locus. Additional flowering time gene loci, comparable to those known to be mapped on chromosome 5H or the distal end of chromosome 4HL (Laurie et al. 1995; Bezant et al. 1996), were also not detectable in rye.

Finally, it should be stated that, as in many other crops, we were able to detect QTLs in rye two of which mapped close to a major gene region. To carry out further homoeologous comparisons to already mapped loci in other cereals the whole rye genome should be considered in further studies.

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