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Molecular mapping of the intermedium spike-c (*int-c*) and non-brittle rachis 1 (*btr1*) loci in barley (*Hordeum vulgare* L.)

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Abstract Lateral spikelet fertility and a non-brittle rachis are key characters in studying the evolution of barley. The fertility of lateral spikelets is controlled predominantly by the alleles at the *vrs1* locus on chromosome 2HL and is modified by the alleles at the *int-c* locus on chromosome 4HS. The non-brittle rachis is controlled by alleles at two tightly linked loci, *btr1* and *btr2*, on chromosome 3HS. This paper presents the integration of the *int-c* and *btr1* loci in molecular linkage maps of barley. The *int-c* locus was mapped to the end of chromosome 4HS, 8.2 cM distal from the *MWG2033* locus. The analysis was followed by a composite interval mapping of quantitative trait loci, which verified the position of the *int-c* locus. Linkage analysis using recombinant inbred lines showed that the *btr1* locus is flanked between two AFLP loci, *e14m27.4.1* and *e15m19.7*, with map distances of 3.1 cM and 4.2 cM, respectively. The molecular markers will expedite further high-density mapping of the *int-c* and *btr1* loci.

Keywords Morphological marker loci · Domestication · Amplified-fragment-length polymorphism (AFLP) · Recombinant inbred lines (RILs) · Quantitative trait loci (QTLs)

Introduction

Lateral spikelet fertility and a non-brittle rachis were key characters in the evolution of cultivated barley, *Hordeum vulgare* ssp. *vulgare* (Takahashi 1955; Harlan 1968; Bothmer and Jacobsen 1985). Perhaps the first step in the domestication of wild barley (*H. vulgare* ssp. *spontaneum*) would have been the development of a tough or non-brittle rachis. The brittle rachis is formed by complementary genes at two tightly linked loci, *btr1* and *btr2* (formerly *bt* and *bt2*), located on chromosome 3HS (Takahashi and Hayashi 1964; Franckowiak and Konishi 1997a, b). Wild barley has the sequence *Btr1Btr1Btr2Btr2*. Cultivated barley has a mutation in one of these loci: most Occidental cultivars are recessive at the *btr1* locus (*btr1btr1Btr2Btr2*), whereas most Oriental cultivars are recessive at the *btr2* locus (*Btr1Btr1btr2btr2*) (Takahashi 1955, 1963; Takahashi et al. 1983).

Spikes of barley possess three 1-flowered spikelets (triplet) at each rachis node. In cultivated barley, the central spikelet is fertile and able to develop into grain. The lateral spikelets are either fertile or sterile, as controlled by two gene loci: recessive homozygosity at the *vrs1* (formerly *v*) locus gives a 6-rowed barley, whereas dominant homozygosity gives a 2-rowed type (Ubisch 1916; Franckowiak and Lundqvist 1997). When a plant is heterozygous at the *vrs1* locus, alleles at the *int-c* (formerly *i*) locus modify the degree of fertility in lateral spikelets: the *int-c.b* (formerly *i*) allele prevents anther development in lateral spikelets, whereas the *Int-c.h* (formerly I^h) allele allows the development of anthers and promotes occasional seed set in lateral spikelets (Leonard 1942; Woodward 1947; Lundqvist and Lundqvist 1987). The *vrs1* locus is located on chromosome 2HL, and the *int-c* locus is located on chromosome 4HS (Lundqvist and Franckowiak 1997).

To study the differentiation of barley, we constructed a high-resolution map of the *vrs1* locus (Komatsuda et al. 1997, 1999). Restriction analysis and DNA sequencing of a marker linked to the *vrs1* locus indicated the multiple origin of 6-rowed barley (Tanno et al. 1999, 2002). To progress the molecular study of the *int-c* and *btr1* loci, this paper presents the results of molecular mapping of the loci.

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Materials and methods

Nomenclature

We follow the new system for descriptions of barley genes recommended by Franckowiak et al. (1997) and Lundqvist et al. (1997). Barley chromosome designation follows the nomenclature recommended by Linde-Laursen et al. (1997).

Plant materials

'Azumamugi' has 6-rowed spikes, with all rows similar in both awn length and seed fertility. 'Kanto Nakate Gold' has 2-rowed spikes, with all the lateral spikelets having large anthers and fertile pollen, but they are female-sterile. The known genotype of 'Azumamugi' is *vrs1*, *Int-c.h*, *Btr1* and *btr2*, and that of 'Kanto Nakate Gold' is *Vrs1*, *int-c.b*, *btr1* and *Btr2* (Komatsuda et al. 1993, 1999; this study). Ninety nine F_8-derived recombinant inbred lines (RILs) of 'Azumamugi' × 'Kanto Nakate Gold' have been developed by single-seed descent.

Fertility of lateral spikelets

A tester having *vrs1vrs1* and *int-c.bint-c.b* was isolated as follows. Among F_6-derived RILs, we found a line segregating 6-rowed and "non-6-rowed" plants. All the non-6-rowed plants were completely sterile in the lateral spikelets, indicating that this line had *int-c.bint-c.b*. Therefore, a single 6-rowed plant from this line was self-pollinated for two generations and isolated as a 6-rowed tester (RIL#73) (*vrs1*, *int-c.b*). 'Kanto Nakate Gold' was used as a 2-rowed tester.

To determine the genotypes of RILs, a single plant (F_9) from each 6-rowed RIL as female was pollinated with 'Kanto Nakate Gold' as male, and a single plant from each 2-rowed RIL as female was pollinated with RIL#73 as male, to make all the F_1 families heterozygous (*Vrs1vrs1*), thus allowing us to detect the genotypes for the *int-c* locus. The test cross generated a total of 85 F_1 families, which were grown in the field. At maturity, the percentage of fertile lateral spikelets was evaluated for 5 to 20 F_1 individuals from each F_1 family, two spikes from each F_1 individual, and 46 to 70 lateral spikelets from each spike.

Rachis brittleness

The genotype of RIL#73 was determined by crossing the line with known genotypes: 'Hayakiso 2' and 'Mokusekko 3' (*Btr1Btr1btr2btr2*), and 'Kanto Nakate Gold', 'Chevalier' and 'Hanna' (*btr1btr1Btr2Btr2*). The genotypes of the five cultivars had already been determined by the Barley Germplasm Center, Research Institute for Bioresources, Okayama University, Kurashiki, and the data were either published (Takahashi et al. 1983) or kindly provided by Professor K. Takeda (unpublished data). The results showed RIL#73 to have the genotype *Btr1Btr1btr2btr2*. 'Azumamugi' was shown to have the same genotype from crosses with 'Kanto Nakate Gold', 'Chevalier', 'Hayakiso 2' and RIL#73. Rachis brittleness was observed at 2–4 weeks after maturation in 5–20 F_1 individuals from each F_1 family.

Gene mapping

We constructed a linkage map for the RILs (F_9) with 272 loci, which provided an average density of 6.5 cM/locus with considerable marker clustering in certain regions (Mano et al. 2001). We selected a subset of 101 markers to provide a density of 5- to 10-cM intervals without the clustering markers, and reconstructed a "base map" with these markers by using MAPMAKER 3.0 (Lander et al. 1987; Lincoln et al. 1992). Map distances were estimated by using Kosambi's map function (Kosambi 1944). QTL mapping for lateral spikelet fertility (arcsin √p transformed) was performed by composite interval mapping using the computer program QTL Cartographer version 1.14 (Basten et al. 2000). The mapping was run with the default setting for model 6 (five background markers and a window size of 10 cM). The inclusion of background markers makes the analysis more precise and permits efficient mapping of QTLs. A log-likelihood (LOD) score threshold of 3.0 was used to identify regions containing putative loci associated with a trait.

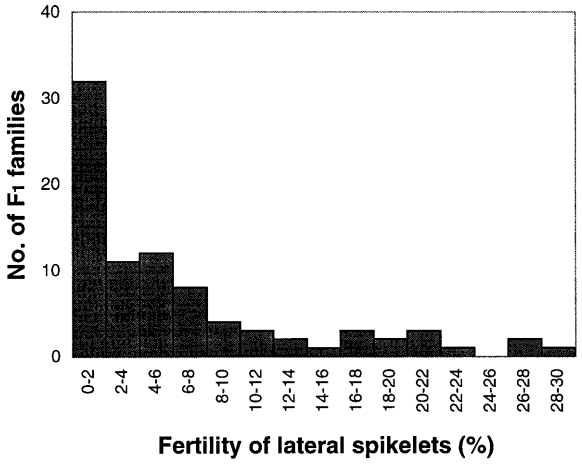

Fig. 1 Percentage of lateral fertility of F_1 families generated by the crosses of RILs × testers. The RILs (F_9) were developed from 'Azumamugi' (*Int-c.h*) × 'Kanto Nakate Gold' (*int-c.b*) by single-seed descent

Results

Mapping of the *int-c* locus

Figure 1 shows the frequency distribution of lateral fertility in the 85 F_1 families generated by the RIL × tester crosses. The distribution was continuous in the range between 0% and 30%. The F_1 family of the cross between 'Kanto Nakate Gold' (*int-c.b*) as female and RIL#73 (*int-c.b*) as male showed a lateral fertility of 2.7% (range, 1.3–3.8%), and the F_1 family of the reverse cross showed a lateral fertility of 2.2% (range, 1.3–3.2%). The F_1 family of the cross between 'Azumamugi' (*Int-c.h*) as female and 'Kanto Nakate Gold' (*int-c.b*) as male showed a lateral fertility of 9.7% (range, 9.3–12%), and the F_1 family of the reverse cross showed a lateral fertility of 18.9% (range, 15–22.2%).

First we mapped the *int-c* locus, assuming that a single gene controls lateral fertility. Based on the above F_1 data, we classified 32 F_1 families with a lateral fertility of 0–2.0% as homozygous *int-c.bint-c.b*, and 18 F_1 families with a lateral fertility of 10–30% as heterozygous *Int-c.hint-c.b* (Fig. 1). The genotypes of the remaining 35 F_1 families with a lateral fertility of 2.0–10% were ambiguous, so these lines were excluded from the linkage analysis to accomplish an accurate 'order' and map distance of the gene and marker loci. Figure 2 shows the linkage map of the *int-c* locus. The locus was situated at the distal end of chromosome 4HS and was most-closely linked to marker *MWG2033* at a map distance of 8.2 cM.

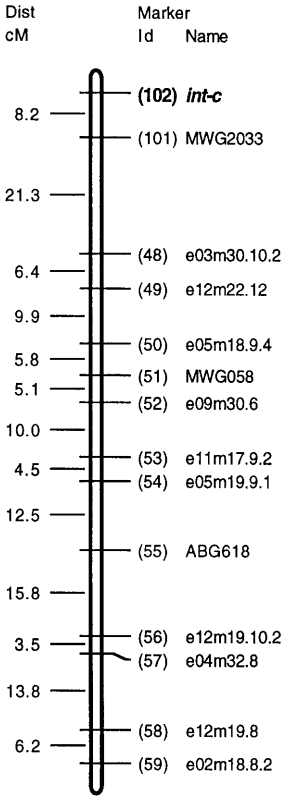

Fig. 2 Position of the *int-c* locus on a base map of chromosome 4H. The map displays marker distances in cM

Next we performed composite interval mapping of QTLs to test the accuracy of the position of the *int-c* locus and to identify other gene loci with minor effects on lateral fertility. Data from all 85 RILs were analyzed. We detected one major QTL and two minor QTLs. The major QTL (peak LOD, 18.6) was located at exactly the same position as the *int-c* locus on chromosome 4HS (Fig. 2). It explained 49.0% of the phenotypic variance, and the 'Azumamugi' allele had a positive effect (+6.2°). One minor QTL resided on chromosome 2HL, within the interval between *MWG882* and *e15m31.10.3* (peak LOD, 3.8; for the position of markers see Mano et al. 2001). It explained 5.4% of the phenotypic variance, and the 'Azumamugi' allele had a negative effect (–2.1°). The other minor QTL was located on chromosome 5HL, in the interval between *e14m27.4.4* and *MWG2230* (peak LOD, 5.4; for the position of markers see Mano et al. 2001). It explained 6.8% of the phenotypic variance, and the 'Azumamugi' allele had a positive effect (+2.3°). RIL#73 had 'Azumamugi' alleles at the two minor QTLs.

Mapping of the *btr1* locus

Table 1 shows the segregation between the brittle and non-brittle rachis of 85 F_1 families. Forty nine families generated from the RILs × 'Kanto Nakate Gold' crosses were potentially useful for mapping the *btr1* locus. Forty six of the families segregated 24:22 into brittle:non-brittle, fitting the expected ratio of 1:1. The remaining three families showed variation from plant to plant and from spike to spike, so they were excluded from the mapping study. Figure 3 shows a molecular map of the *btr1* locus. The map shows that *btr1* is flanked by markers *e14m27.4.1* and *e15m19.7*, with map distances of 3.1 and 4.2 cM. The interval between the two marker loci was 7.3 cM. Excluding the *btr1* locus the interval was 7.9 cM (Mano et al. 2001). Therefore, no expansion of the map distance was detected after the addition of the *btr1* locus. This result indicates that the genotyping of the 46 RILs was accurately done, eliminating misclassification.

The test crosses of RILs × RIL#73 generated 36 families, which were potentially useful for mapping the *btr2* locus (Table 1). Thirty one of the F_1 families segregated 23:8 into non-brittle:brittle, showing a large deviation from the expected 1:1 ratio. The remaining five families showed variations within each family, so they were excluded from the mapping study. The *btr2* locus was assigned to the linkage group of chromosome 3H but could not be localized to the framework map of chromosome 3H. The most-likely position suggested by the MAPMAKER program was between markers *e15m19.7*

Table 1 Expected and observed segregation of brittle and non-brittle rachis F_1 families generated by the test crosses between RILs and testers

Genotype of gametes[a]			Phenotype of F_1 family	Frequency of RILs	
RIL[b]		Tester		Expected	Observed
RILs	×	'Kanto Nakate Gold'			
Btr1btr2 ***d***		*btr1Btr2* ***D***	Brittle	11.5	24
Btr1btr2 ***D***		*btr1Btr2* ***D***	Brittle	11.5	
btr1Btr2 ***d***		*btr1Btr2* ***D***	Non-brittle	11.5	22
btr1Btr2 ***D***		*btr1Btr2* ***D***	Non-brittle	11.5	
Ambiguous		*btr1Btr2* ***D***	Variable		3
RILs	×	RIL#73			
Btr1btr2 ***d***		*Btr1btr2* ***d***	Non-brittle	7.8	23
Btr1btr2 ***D***		*Btr1btr2* ***d***	Non-brittle	7.8	
btr1Btr2 ***d***		*Btr1btr2* ***d***	Non-brittle	7.8	
btr1Btr2 ***D***		*Btr1btr2* ***d***	Brittle	7.8	8
Ambiguous		*Btr1btr2* ***d***	Variable		5
Total					85

[a] ***D*** and ***d*** are alleles at an independently inherited locus, ***d***, and the homozygote ***dd*** inhibits rachis brittleness

[b] Theoretically, the occurrence of *Btr1Btr2* and *btr1btr2* gametes in the RILs could not be excluded, but they would have been very few and were excluded from this table for simplicity. In practice there were no *Btr1Btr2* RILs because all the RILs were non-brittle

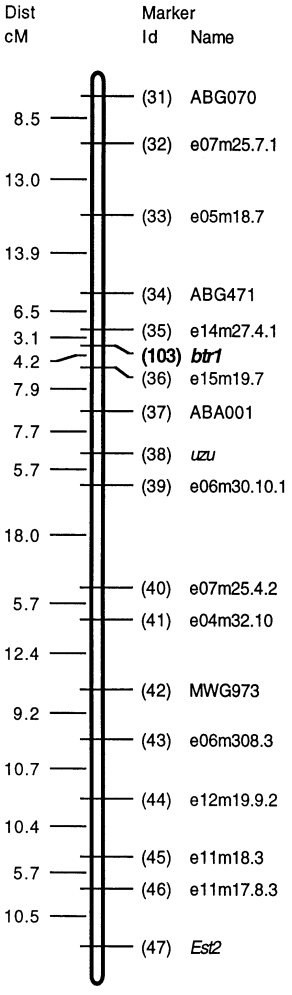

Fig. 3 Position of the *btr1* locus on a base map of chromosome 3H. The map displays marker distances in cM

and *ABA001*, a neighbor of the *btr1* locus. However, this position was accompanied by many lines in which "recombination" took place at each side of the *btr2* locus (data not shown), suggesting an inconsistency between phenotype and genotype at the *btr2* locus.

The following explanation is based on the theory that the *btr1* and *btr2* loci are very closely linked, as no recombination between the two loci was observed (Takahashi and Hayashi 1964). For simplicity, therefore, recombinants between the loci are not considered here. Let us consider one independently inherited gene locus, ***d***, and two alleles, ***D*** and ***d***, at the locus, and that the homozygote ***dd*** inhibits rachis brittleness. We assume that RIL#73 and 'Azumamugi' have ***dd*** and 'Kanto Nakate Gold' ***DD***. In this scenario, the expected ratio of brittle to non-brittle families is 1:1 in the test cross RILs × 'Kanto Nakate Gold' and 1:3 in the test cross RILs × RIL#73, which the observed ratios fit well (Table 1).

In line with this explanation, we inferred the position of the ***d*** locus by examining the 31 F_1 families generated from RILs × RIL#73 and the corresponding 31 RILs (Table 1). Of the 31 RILs, we assumed that 17 had 'Kanto Nakate Gold' alleles at both the *e14m27.4.1* and *e15m19.7* loci, or *btr1btr1Btr2Btr2*. In that case, although all 17 F_1 families have *Btr1btr1Btr2btr2*, they segregated into nine non-brittle (***dd***) and eight brittle (***Dd***). Then we searched for marker loci that correlated with the ***d*** locus throughout the linkage map (Mano et al. 2001). As a result, the ***d*** locus was correlated with eight AFLP markers between *e15m28.7.2* and *e15m19.6* on chromosome 7H, giving only one recombinant among the 17 RILs (for the positions of markers see Mano et al. 2001). For the other markers, four or more RILs among the 17 had an incongruent genotype with the ***d*** locus. Therefore, the ***d*** locus is most probably located in a region of about 30 cM on chromosome 7H. RIL#73 had homozygous 'Azumamugi' alleles for the AFLP markers, indicating that the tester was ***dd***.

Discussion

We treated lateral spikelet fertility as a qualitative trait as well as a quantitative trait. Lateral fertility was evaluated by using roughly 1,000 spikelets for each RIL. The position of *int-c* as a qualitative trait locus was identical to that of the major QTL detected. The *int-c* locus was mapped at 46-cM distal from a centromeric marker, *MWG058*, on chromosome 4H (Fig. 2). This position is in good agreement with that of the *int-c* locus presented in the linkage maps for morphological markers (Franckowiak 1997). The *int-c* locus was 8.2-cM distal from the *MWG2033* marker, itself 32-cM proximal to telomeric markers (Graner et al. 1994), which suggests that the *int-c* locus was located around 24 cM from the telomere. This position is in good agreement with the results of other studies (25 cM: Franckowiak 1997; Kleinhofs 1997; Marquez-Cedillo et al. 2000), indicating that the *int-c* locus is consistently located 24–25 cM from the telomere over the different cross combinations.

The molecular map located no AFLP markers in the telomeric region of chromosome 4HS (Fig. 2 and Mano et al. 2001). This result is consistent with at least two interpretations. One explanation is that the parental cultivars have a similar genetic constitution in that region (for pedigrees of the parents see Komatsuda et al. 1997). As we analyzed only 33 combinations of primers for the construction of AFLP maps (Mano et al. 2001), more primer combinations or the use of other molecular markers will be necessary for the construction of a high-density map of the *int-c* locus. An alternative explanation is that the physical length of this region is shorter than that expected by the genetic distance, because the megabase to centimorgan ratio of this region is less than one-fifth of the average value for the barley genome (Künzel et al. 2000).

The QTL analysis also detected two minor QTLs for lateral fertility. The presence of minor QTLs in addition to some environmental effects agrees with the continuous frequency distribution of lateral fertility (Fig. 1). The reciprocal F_1 hybrids between RIL#73 and 'Kanto Nakate Gold', despite being homozygous *int-c.bint-c.b*, did show

a 2–3% fertility of lateral spikelets. This result indicates that the two minor QTLs promoted the partial fertility. Induced mutants having altered development and fertility of lateral spikelets have been studied in detail, and the chromosomal locations of the gene loci has been determined as *int-b* on 5HL, *int-c* on 4HS, *vrs2* on 5HL, *vrs3* on 1HL and *vrs4* on 3HL (Gustafsson and Lundqvist 1980; Fukuyama et al. 1982; Lundqvist and Lundqvist 1987). Allelism between the minor QTL detected on chromosome 5HL and the *int-b* or *vrs2* locus needs further study. The other QTL detected on chromosome 2HL might be a newly identified gene locus, not previously detected by studies on mutants.

The *btr1* locus was mapped between two flanking AFLP loci, which opens a window to the high-resolution mapping of the locus. The *btr1* locus was located on chromosome 3HS, at approximately 44.5 cM from the telomeric region (Fig. 3). This distance roughly agrees with the 55 cM reported by Franckowiak (1997). The distance between the *btr1* locus and clustering centromeric markers of 12 cM is much shorter than the 39 cM reported by Franckowiak (1997), probably indicating the suppression of recombination in the proximal region of chromosome 3H in our mapping population. Because the molecular map we used included very few *MWG* markers, physical mapping of the *btr1* locus requires inclusion of *MWG* markers appearing in the physical map of Künzel et al. (2000).

We could not determine the position of the *btr2* locus precisely, but results were consistent with close linkage to the *btr1* locus. The subset data of F_1 families generated by the RILs × RIL#73 crosses showed a large excess of non-brittle families in favor of the *btr2* allele of 'Azumamugi' (Table 1). However, this should not be the case, because segregation distortion of molecular markers on chromosome 3H was in favor of 'Kanto Nakate Gold' alleles (Mano et al. 1999, 2001). We therefore hypothesised the presence of another gene.

Schiemann (1921) extensively analyzed segregation for brittleness by using a lot of cross combinations of wild × cultivar, and cultivar × cultivar, and suggested the presence of a non-allelic inhibitor gene of rachis brittleness. Our results also suggest the presence of a non-allelic inhibitor gene of rachis brittleness and indicate that this gene locus lies on chromosome 7H, although we did not analyze many RILs. Takahashi and Hayashi (1959) stated that effects of the inhibitor genes for rachis brittleness were weak and that classification of segregating plants was ambiguous in some cross combinations. Therefore, QTL mapping would be powerful for mapping major and minor genes for rachis brittleness, as shown here for lateral fertility.

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