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QTLs for branching, floret formation, and pre-flowering floret abortion of rice panicle in a temperate *japonica* × tropical *japonica* cross

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Abstract A large panicle with numerous florets is essential for improving rice (*Oryza sativa* L.) yield. Rice panicle size is determined by such underlying morphogenetic processes as: (1) primary branch formation on the panicle axis; (2) floret formation on the primary branches (mainly determined by the secondary branch formation); and (3) pre-flowering abortion of florets in the panicle. We examined QTLs for these processes to understand how they are integrated into panicle size. We developed 106 backcross-inbred lines (BC_1F_4) from a cross between 'Akihikari' (a temperate *japonica*) and 'IRAT109' (a tropical *japonica*) and constructed a genetic map. One QTL detected on chromosome 2, with a large effect (R=0.30) on the number of florets per panicle, affected both primary branch formation on the panicle axis and floret formation on the primary branches. In addition, three QTLs that affect only one of these two processes were identified on chromosomes 4, 9, and 11, each having a subsidiary effect on the number of florets per panicle (R^2=0.04–0.07). QTLs for pre-flowering floret abortion were detected at three different regions of the genome (chromosomes 1, 10, and 11). This is the first report on QTLs for pre-flowering floret abortion in grasses. The absence of a co-location between QTLs suggests that floret formation and abortion are not directly linked causally. These results demonstrate that studying the partitioning of panicle size into these underlying morphogenetic components would be helpful in understanding the complicated genetic control of panicle size.

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Introduction

A large panicle with numerous florets is essential for improving the sink capacity of rice (*Oryza sativa* L.) (Khush 2000). In the past 40 years, breeding efforts toward high-yielding rice varieties have increased the source capacity (e.g., erect leaves and the resultant high canopy photosynthesis rate) over the sink capacity. As a result, sink capacity is increasingly becoming a major constraint to grain yield. This is most pronounced in temperate *japonica* rice varieties, which have a relatively low potential for sink capacity (Takeda 1984). In theory, the sink capacity of rice can be increased by both a large panicle and profuse tillering. However, the former strategy has proven to be more effective for increasing yield (Peng et al. 1994; Akita 1999). Despite its agronomic importance, our knowledge of the genetic control of panicle size is still insufficient. Although many studies have reported the QTLs that control rice panicle size (see Mackill 1999 for a review), very little is known on how they are involved in the morphogenetic process of panicle development.

It takes about 1 month for a rice panicle to progress from initiation to flowering. This process of rice panicle morphogenesis can be divided into three major stages. In the first stage, "primary branches" are generated on successive nodes of the main panicle axis, which results in the establishment of the basic panicle skeleton. Considerable genetic variation in the number of primary branches (usually 8–20) exists among cultivars. In the second stage, individual primary branches vigorously branch to form many florets. Some florets originate as direct offspring from the primary branch, but most florets

are generated from higher order branches ("secondary branches") generated from the primary branches. The number of florets in a primary branch also genetically varies (usually 15–40), depending on the extent of branching of the primary branch. These two processes (primary branch formation on the panicle axis and the floret formation on individual primary branches) determine the potential panicle size as their multiplicative product, and produce considerable genetic variation in the number of florets (usually 80–500) in a panicle (Senanayake et al. 1994; Yamagishi et al. 2003).

The third stage is characterized by the development of individual florets (i.e., development of palea, lemma, anthers, and ovary in each floret). In this stage, panicle size is strongly downregulated by the abortion of young florets. This "pre-flowering floret abortion" (Senanayake et al. 1991) frequently occurs at the basal portion of the individual primary branch (Matsushima 1966). There is also genetic variation in the frequency of floret abortion (3–50%, Senanayake et al. 1994; Kobayashi and Imaki 1997). Pre-flowering floret abortion is an important component of grain yield of many cereals, the elimination of which is expected to be a promising breeding strategy for increasing grass sink capacity (Kernich et al. 1997).

To date, very little is known on how these underlying morphogenetic processes (primary branch formation on the panicle axis, floret formation on the primary branches, and pre-flowering abortion of florets in the panicle) are integrated into panicle size at the QTL level. Only a few QTL studies have examined primary and higher branches (Nagata et al. 2002; Yamagishi et al. 2002), and no information is available on the QTLs for pre-flowering floret abortion. To clarify these issues, we examined QTLs for these morphogenetic components, using a temperate *japonica* × tropical *japonica* cross. Previous QTL studies on panicle size predominantly made use of *indica* × *japonica* crosses (Mackill 1999). Recently, Yamagishi et al. (2003), who conducted a multivariate morphometry of panicle characters in 65 *japonica* cultivars from around the world, demonstrated that many tropical *japonica*s have much larger panicles than temperate *japonica*s. In the present study, QTLs that differentiate panicle characters (including pre-flowering floret abortion) between temperate and tropical *japonica*s were investigated. We developed 106 backcross-inbred lines (BILs) from a cross between 'Akihikari' (a temperate *japonica* with small panicles) and 'IRAT109' (a tropical *japonica* with large panicles) and constructed a genetic map with 112 simple sequence repeat (SSR) markers.

Materials and methods

Mapping population

A set of BILs derived from the cross between 'Akihikari' and 'IRAT109' was used. 'Akihikari' is a lowland temperate *japonica* variety developed in Japan, while 'IRAT109' is an upland tropical *japonica* variety developed in Cote d'Ivoire. In 1998, at the University of Tokyo, 'Akihikari' (as the maternal parent) was crossed to 'IRAT109'. The resultant F_1 plant (as the maternal parent) was backcrossed with 'Akihikari' in 1999. From the resultant BC_1F_1 ('Akihikari'/'IRAT109'//'Akihikari') population, the BILs (160 lines) were developed using the single-seed descent method at the University of Tokyo. Panicles were bagged for each generation to avoid outcrossing. In 2002, 106 BILs were extracted in the BC_1F_4 generation for marker analysis, and the resultant BC_1F_5 seeds were used for phenotypic evaluation.

Marker analysis

The DNA of the parents and 106 BC_1F_4 plants was extracted from fresh leaf tissue as described by Aoki et al. (2001). About 250 SSR markers (Chen et al. 1997; McCouch et al. 2002; Temnykh et al. 2001) were initially surveyed for polymorphism, using DNA from the parents. Additional SSR markers (about 400) were surveyed for chromosomal regions that were monomorphic for the initial markers. Using a selected set of polymorphic markers (112 markers) that are distributed evenly over the genome (9.3 markers per chromosome, with an average distance between markers of 14.6 cM), the 106 BC_1F_4 plants were genotyped. Polymerase chain reaction (PCR) amplifications were undertaken as described on the RGP homepage (http://rgp.dna.affrc.go.jp) and in Chen et al. (1997). The amplified products were separated on 3% agarose gel in 0.5 × TBE buffer. The patterns were visualized using ethidium bromide.

Phenotypic evaluation

The field experiment was conducted at the experimental farm of the University of Tokyo, Nishitokyo, in 2003. The 106 BILs and their parents were evaluated in a paddy field in randomized complete block design with two replications. Twelve 30-day-old seedlings for each entry were transplanted on 23 June in a one-row plot at one plant per hill. To reduce competition among individual plants, a wide spacing (30 cm row spacing and 30 cm hill spacing) was adopted. A chemical compound fertilizer (60-40-66 kg of N-P-K ha^{-1}) was applied before transplanting. At maturity, three plants from the center of each plot were sampled.

Measurements were made on the panicles of the main tillers. For each panicle, the number of florets (whether they survived or were aborted) per panicle (FPP) and the number of primary branches per panicle (BPP) were counted. We then calculated the number of florets on individual primary branches (FPB) as FPP/BPP. We also calculated the frequency of pre-flowering floret abortion (%FA) as 100 × (the number of aborted floret in the panicle/FPP). The aborted florets could be counted easily because they all remained on the mature panicles, as illustrated by Matsushima (1966). A total of six main-tiller

panicles (= 3 main-tiller panicles × 2 replications) were measured for each line at maturity, and the means of two replications were used for the QTL analysis. Broad-sense heritability (h_B^2) was calculated from the estimates of genetic (σ_G^2) and residual (σ_E^2) variances, which were derived from the expected mean squares of the analysis of variance, as $h_B^2=\sigma_G^2/(\sigma_E^2+\sigma_E^2/\kappa)$, where κ was the number of replications.

Map construction and QTL analysis

Linkage analyses were performed with MAPL, using the "BC_1F_1-derived RI mode" (Ukai et al. 1995). QTLs were detected by composite interval mapping using Windows QTL Cartographer, version 2.0 (Wang et al. 2003). The significant threshold was estimated by performing 1,000 permutations (Churchill and Doerge 1994) of each character (P<0.05), as implemented by QTL Cartographer (threshold for FPP, BPP, FPB and %FA were 3.12, 2.97, 3.04 and 3.43, respectively). To identify interaction between QTLs detected, two-way analyses of variance (ANOVAs) were performed using the nearest marker of each QTL.

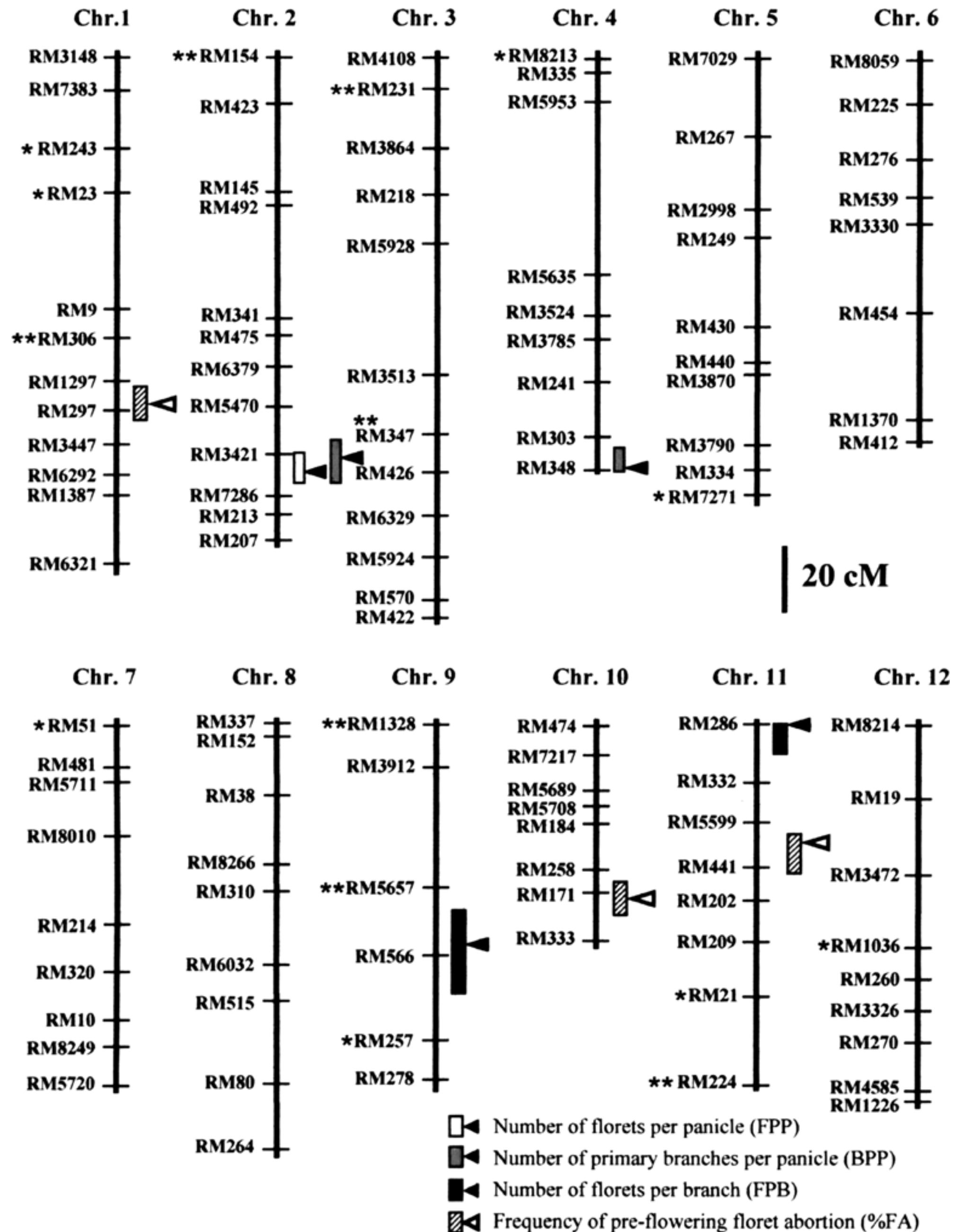

Fig. 1 Chromosomal location of QTLs for number of florets per panicle (*FPP*), number of primary branches per panicle (*BPP*), number of florets per branch (*FPB*) and frequency of pre-flowering floret abortion (*%FA*). QTLs with significant LOD scores determined by the permutations (P=0.05) are shown. *Bars to the right* of the chromosomes indicate 1-LOD likelihood intervals and *arrowheads* indicate the position of the peak LOD in the interval. * and ** indicate segregation distortion at the 0.05 and 0.01 significance levels, respectively.

Results

Linkage map and marker segregation of the 'Akihikari' × 'IRAT109' BILs

About 650 SSR markers were examined for polymorphism to construct a linkage map for the BILs derived from BC_1F_1 between 'Akihikari' and 'IRAT109'. As a result, about 150 markers appeared polymorphic on agarose gels between the two parents. From these, we selected and mapped 112 markers for 106 BILs, so that the markers would be distributed evenly over the genome. Finally, a genetic map of 12 linkage groups that spanned 1,437 cM, with an average marker distance of 14.6 cM, was obtained (Fig. 1). The distal half of the long arm of chromosome 9 remained uninformative due to the lack of polymorphic markers. The largest gap (52 cM) was found between markers RM5953 and RM5635 on chromosome 4. A similar gap was reported by Fujino et al. (2004), who constructed a temperate *japonica* × temperate *japonica* linkage map, and this suggests that this chromosomal region might be generally monomorphic between *japonica* cultivars. Other gaps larger than 30 cM were RM23–RM9 on chromosome 1 (35 cM), RM492–RM341 on chromosome 2 (34 cM), RM5928–RM3513 on chromosome 3 (40 cM), and RM3912–RM5657 on chromosome 9 (36 cM). The estimated genome coverage of the map developed in this study was about 87.3% (excluding the interval RM5953–RM5635 on chromosome 4) of the rice high-density linkage map (Harushima et al. 1998). Of the 112 markers, 16 (14%) (mainly on chromosomes 1, 3 and 9) showed significant deviations ($P<0.05$) from the expected segregation ratios based on the χ^2 test. Among the 16 markers, 11 and five showed an excess of the 'IRAT109' and 'Akihikari' homozygotes, respectively. The average frequency of the heterozygous genotype per marker was 5.6%, which is close to the expected value (6.3%).

A genetic map using a cross between temperate and tropical *japonica*s was first constructed by Redoña and Mackill (1996) using 'Labelle' (tropical *japonica*) and 'Italica Livorno' (temperate *japonica*). Interestingly, chromosome 10 of their map was particularly polymorphic, with a greater percentage of markers (RAPDs), suggesting that this chromosome might be essentially involved in the differentiation of temperate and tropical *japonica*s. However, polymorphism of the markers that were initially surveyed (about 250 markers) showed that no particular chromosome was highly polymorphic in our cross.

Trait variation

We measured panicle characters for the 106 BILs and the two parents (Fig. 2). All characters generally followed a continuous and unimodal distribution, and transgressive segregation was observed for all characters.

QTL analysis

Using QTL Cartographer, we detected one QTL for FPP on chromosome 2 (Table 1; Fig. 1). We then mapped QTLs for primary branch formation on the panicle axis and floret formation on primary branches. For BPP, two QTLs were detected on chromosomes 2 and 4. The QTL on chromosome 2 coincided with the QTL for FPP (Table 1; Fig. 1). No digenic interaction was found

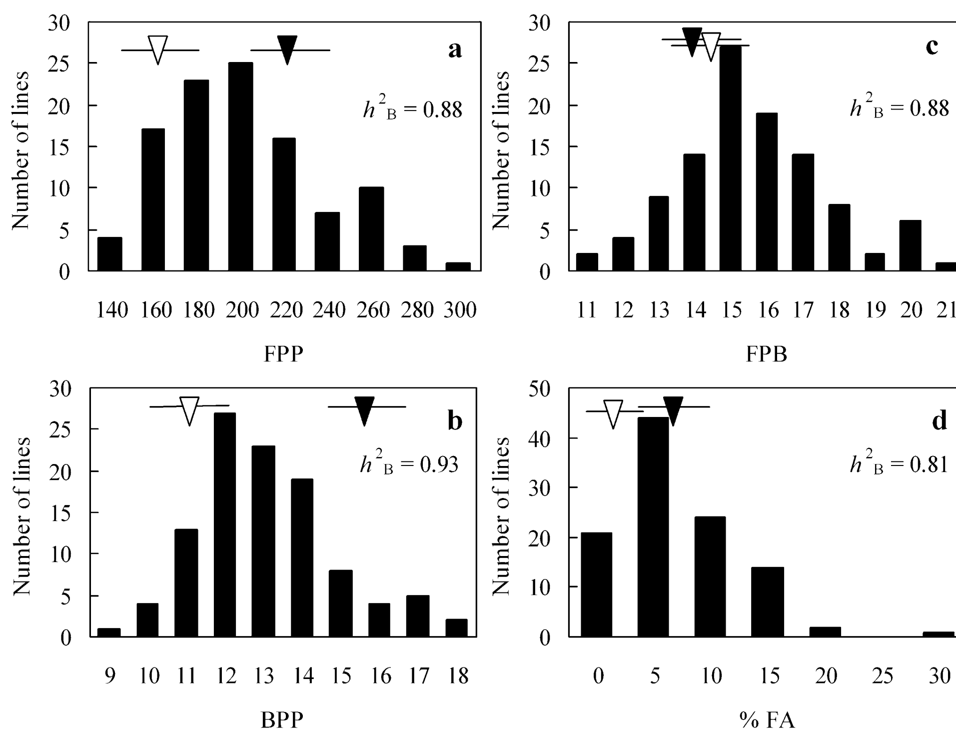

Fig. 2 Frequency distribution of 106 backcross-inbred lines (BC_1F_5) for **a** FPP, **b** BPP, **c** FPB, and **d** %FA. The values of FPP were 163±19 (n=18) and 223±22 (n=18) for 'Akihikari' (*open triangle* ±SD) and 'IRAT109' (*closed triangle*± SD), respectively. The BPP values of 'Akihikari' and 'IRAT109' were 11.3±1.1 and 15.9±0.9, respectively. The FPB values of 'Akihikari' and 'IRAT109' were 14.5±0.8 and 14.0±1.2, respectively. The %FA of 'Akihikari' and 'IRAT109' was 2.0±2.4 and 5.9 ±3.0, respectively. h_B^2 Broad-sense heritability

between these two QTLs, using two-way ANOVA. For FPB, two QTLs were detected on chromosomes 9 and 11 (Table 1; Fig. 1). No digenic interaction was found between these two QTLs. Although below the significance level, the third-largest QTL for FPB (LOD=2.67, additive effect = −0.71, R^2=0.09) was detected in the FPP QTL region on chromosome 2 (RM7286–RM213).

We also mapped QTLs for %FA. Three QTLs for %FA were detected on chromosomes 1, 10, and 11 (Table 1; Fig. 1). Digenic interactions were suggested between QTLs on chromosomes 1 and 11 (F-value = 4.28, P<0.01) and between those on chromosomes 10 and 11 (F-value = 3.27, P<0.05).

Discussion

QTLs for floret number of a rice panicle in the ‘Akihikari’ × ‘IRAT109’ BILs

We developed BILs from the temperate *japonica* ‘Akihikari’ and the tropical *japonica* ‘IRAT109’. Permanent mapping population derived from this type of cross would be useful, because most existing rice populations are derived from an *indica* × *japonica* or an *indica* × *indica* crosses (Xu 2002). QTL information from our BILs would be directly comparable with the two existing mapping populations, the ‘Akihikari’ × ‘Milyang 23’ (*indica*) recombinant inbred lines (Fukuta et al. 1997) and the ‘Koshihikari’ (temperate *japonica*) × ‘Akihikari’ doubled haploid lines (Takeuchi et al. 2001), from which many important agronomic characters were mapped. Using these new BILs, we detected a major QTL for FPP located on chromosome 2 (Table 1; Fig. 1). QTLs for FPP have been repeatedly identified on the centromeric regions of chromosomes 4 and 8 (Mackill 1999). However, no QTLs for FPP were detected in these chromosomal regions in our study. The QTL on chromosome 2, where the ‘IRAT109’ allele increased the number of florets, explained as much as 30% of the total phenotypic variation. No comparable QTL was detected in the ‘Akihikari’ × ‘Milyang 23’ recombinant inbred lines (Yagi et al. 2001; Nagata et al. 2002) and in the ‘Koshihikari’ × ‘Akihikari’ doubled haploid lines (Yamagishi et al. 2002). The large additive effect (about 20 florets) of this QTL makes it a possible target for marker-assisted selection and positional cloning.

Although this QTL has not been reported from any other *indica* × *japonica* cross (Mackill 1999), it seemed to be at the same location as a small QTL that was detected in an *indica* × *indica* intrasubspecific cross (Zhuang et al. 2002). This unexpected result might be explained by the differential gene action between intersubspecific and intrasubspecific crosses. As demonstrated by Zhuang et al. (2002), the main effects of an epistatic QTL depend on the extent to which other interacting loci become fixed. Thus, some epistatic QTLs without main effects in a more diverse background (e.g., intersubspecies crosses) might behave as main effect QTLs in a less diverse genetic background (e.g., intrasubspecies cross) (Zhuang et al. 2002). This could be the reason why this QTL was detected in the *japonica* × *japonica* and *indica* × *indica* intrasubspecific crosses, but not in the *japonica* × *indica* intersubspecific crosses. From these results, we suggest that QTL information from *japonica* × *japonica* crosses would be necessary for discovering useful main-effect QTLs for the breeding of *japonica* rice (i.e., many important QTLs might be masked by the action of epistasis in *japonica* × *indica* crosses).

Genetic control of branch and floret formation

The FPP is determined by two underlying morphogenetic processes: primary branch formation on the panicle axis (as scaled by BPP) and floret formation on the primary branch (as scaled by FPB) (see “Introduction”). The co-location of QTLs for these two processes suggests that some QTLs affect both processes, while others affect only one process, as follows (Table 1: Fig. 1):

1. *QTLs that promote primary branch formation on the panicle axis, but do not (or only slightly) affect floret formation on the primary branches.* This class includes the QTL for BPP on chromosome 4 (RM303–RM348). The ‘IRAT109’ allele acts as a favorable allele at this QTL. This QTL might be the

Table 1 Location, peak LOD, additive effects, and percent of the phenotypic variation explained (R^2) for QTLs detected for panicle characters in back-cross-inbred lines from the cross ‘Akihikari’ × ‘IRAT109’

Chromosome	Marker interval	Position [a]	Peak LOD	Add [b]	R^2
Number of florets per panicle					
2	RM3421–RM7286	4.7	8.88	−22.1	0.30
Number of primary branches per panicle					
2	RM3421–RM7286	0.0	5.66	−0.88	0.16
4	RM303–RM348	9.8	5.80	−0.95	0.18
Number of florets per primary branch					
9	RM5657–RM566	15.7	3.26	0.95	0.14
11	RM286–RM332	0.0	4.27	−0.92	0.14
Frequency of pre-flowering floret abortion					
1	RM1297–RM297	6.5	6.23	−2.60	0.19
10	RM171–RM333	0.0	8.49	−3.24	0.22
11	RM5599–RM441	8.1	5.76	−2.33	0.16

[a] Distance from the left flanking marker in cM
[b] Positive value indicates additive effect of the ‘Akihikari’ allele

same locus that for the number of florets per panicle reported in Xiao et al. (1996).

2. *QTLs that do not (or only slightly) affect primary branch formation on the panicle axis, but promote floret formation on the primary branches.* This class includes the two QTLs for FPB on chromosomes 9 (RM5657–RM566) and 11 (RM286–RM332). The 'Akihikari' allele acts as a favorable allele at the former QTL, whereas the 'IRAT109' allele acts as a favorable allele at the latter QTL. The actual target of these QTL actions is probably secondary branch formation. The two QTLs on chromosomes 9 and 11 coincided with the LOD peaks for the number of secondary branches per primary branch (data not shown).
3. *QTLs that promote both the formation of primary branches on the panicle axis and floret formation on the primary branches.* The QTL for FPP on chromosome 2 represents this class. At this QTL, the 'IRAT109' allele promotes the formation of both primary branches (BPP) (Table 1) and florets (FPB) (see "Results"). This QTL has a much larger effect on FPP than the *class 1* and *class 2* QTLs, which had only a subsidiary effect on FPP individually (R^2=0.04–0.07). This is not surprising, because FPP is the multiplicative function of primary branch formation on the panicle axis and floret formation on the primary branch (i.e., small effects of these two components would result in a large multiplicative effect on floret number). This QTL on chromosome 2 could possibly be tightly linked to two genes: one for primary branch formation (*class 1*) and one for floret formation on the primary branches (*class 2*). This possibility should be tested further by fine mapping of this QTL.

Growth duration and the corresponding whole plant size may also affect the formation of branches and florets. Long-duration (late-flowering) cultivars tend to have larger panicles than short-duration (early flowering) cultivars (Xiao et al. 1998). The co-location of QTLs in the previous study (Yamagishi et al. 2002) indicated that certain panicle size QTLs actually control flowering time. In our study, however, this pleiotropism is less likely to occur, because the 'Akihikari' × 'IRAT109' BILs exhibited a relatively narrow range of flowering time (about 3 weeks) compared with the 'Koshihikari' × 'Akihikari' doubled haploid lines used in the previous study (nearly 2 months, as reported by Takeuchi et al. 2001). In fact, no significant correlation existed between flowering time and FPP (r=−0.09, P=0.36) for the BILs. Flowering time in the BILs is controlled by such heading date loci (Yano et al. 2001) as *Hd9* on chromosome 3, *Hd8* on chromosome 3, *Hd3* on chromosome 6, and *Hd4* on chromosome 7 (data not shown), and none of the FPP, BPP, and FPB QTLs coincided with these *Hd* loci. Long-duration rice varieties are generally not preferred, and QTLs that increase yield without delaying maturity are desirable (Xiao et al. 1998). Thus, QTLs detected in the present study might serve as useful yield-improving QTLs.

Genetic control of %FA

Final panicle size is determined not only by the formation of branches and florets, but also by the abortion of florets during panicle development. This event, pre-flowering floret abortion, is an important component of panicle size in many cereal grasses and a potential breeding target for improving sink size. In barley, for example, there is a greater genetic potential to reduce %FA than to increase floret formation (Kernich et al. 1997). Using the new BILs, we detected three QTLs for %FA on chromosomes 1, 10 and 11, each of which explained 16–22% of the total phenotypic variation (Table 1, Fig. 1). In these QTLs, the 'IRAT109' alleles increased abortion. This is the first report on QTLs for %FA in grasses.

Abortion is generally believed to be under the control of the sink–source balance and the corresponding competition between florets (Otegui and Melon 1997). However, the QTLs for %FA did not coincide with any of the QTLs for floret or branch formation (FPP, BPP, and FPB), which indicated that floret formation and abortion were not directly linked causally. A possible mechanism might be that the QTLs for %FA are involved in "apical dominance" in developing panicles (Matsushima 1966). During panicle development, the florets are generated acropetally on young primary branches, beginning from one that is positioned on the basal region of the primary branch. As the panicle grows, however, distal florets, which are formed later, grow vigorously and thereby suppress the basal florets (thus, florets open in the reverse order of their initiation). This suppression of basal florets is consistent with the fact that abortion frequently occurs in these florets.

In conclusion, our results demonstrate that partitioning of panicle size into the underlying morphogenetic components would be helpful in understanding the complicated genetic control of panicle size. One could identify many supplemental QTLs for panicle size by partitioning it into such components. Although only major floret number QTLs have been targeted for marker-assisted selection, our study suggests that pyramiding QTLs for these supplemental QTLs (including the elimination of floret abortion QTLs) would be an alternative strategy for increasing rice panicle size. Because this study was conducted in a single year at one location, additional studies over years and locations should be conducted to verify the constancy of these QTLs across environments.

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