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# Quantitative trait locus analysis for rice panicle and grain characteristics

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**Abstract** The development of molecular genetic maps has accelerated the identification and mapping of genomic regions controlling quantitative characters, referred to as quantitative trait loci or QTLs. A molecular map derived from an $F_2$ population of a tropical japonica × indica cross (Labelle/Black Gora) consisted of 116 restriction fragment length polymorphism (RFLP) markers. Composite interval mapping was used to identify the QTLs controlling six panicle and grain characteristics. Two QTLs were identified for panicle size at LOD $> 3.0$, with one on chromosome 3 accounting for 16% of the phenotypic variation. Four loci controlling spikelet fertility accounted for 23% of the phenotypic variation. Seven, four, three and two QTLs were detected for grain length, breadth, shape and weight, respectively, with the most prominent QTLs being on chromosomes 3, 4, and 7. Grain shape, measured as the ratio of length to breadth, was mostly controlled by loci on chromosomes 3 and 7 that coincided with the most important QTLs identified for length and breadth, respectively. A model including three loci accounted for 45% of the phenotypic variation for this trait. The identification of economically important QTLs will be useful in breeding for improved grain characteristics.

**Key words** Quantitative trait locus (QTL) · *Oryza sativa* L. · Molecular markers · Grain dimensions · Panicle size

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## Introduction

Grain characteristics such as shape, size, translucency and color have a direct bearing on the marketability, and hence commercial success, of modern rice (*Oryza sativa* L.) cultivars. The breeding program at the California Rice Experiment Station has separate components for each of the USA market standards based on brown rice length: short, $\leqslant 5.5$ mm; medium, 5.51–6.60 mm; long, 6.61–7.50 mm; and extra long, $> 7.5$ mm (McKenzie et al. 1994). On the other hand, breeding efforts in the Southern USA are primarily geared towards the development of long-grain rice varieties (Gravois and McNew 1993). In most Asian countries, commercial cultivars belong to the medium- or long-grain class. Long- and slender-grained Basmati cultivars of India and Pakistan command premium prices in the international market while short- and bold-grained cultivars are preferred in Japan and Sri Lanka. Breeding for grain characteristics would, therefore, be principally influenced by consumer preference in the intended market. Hence, selection for a particular grain characteristic could go in either direction, depending on the breeding goal.

USA cultivars belong to the japonica subspecies based on RAPD (random amplified polymorphic DNA) analysis (Mackill 1995). Short- and medium-grain varieties of California cultivars are classified as temperate japonicas and long-grained southern USA cultivars as tropical japonicas. The genetic base of USA long-grain cultivars is considered very narrow (Dilday 1990). An infusion of new germplasm may be necessary to realize greater selection progress in breeding for improved varieties in this varietal group (Gravois 1992). Recently, there has been a renewed interest in hybrid rice production in the USA as a means for further increasing yields (Gravois and McNew 1993; Mackill 1995). Due to the limited genetic variation among japonicas at the molecular level (Glaszmann

1987; Zhang et al. 1992; Mackill 1995), successful exploitation of heterosis in temperate areas may have to involve the use of indica × japonica and temperate japonica × tropical japonica crosses. The impact of using such crosses on grain market standards is not clear. Mackill (1995) noted that a considerable breeding effort may be necessary before an acceptable grain type for $F_1$ hybrids can be produced.

The development of molecular genetic maps in rice (McCouch et al. 1988; Causse et al. 1994; Kurata et al. 1994) has facilitated the identification of QTLs controlling important quantitative characters (Wang et al. 1994). Rice grain characteristics such as size and shape are quantitatively inherited (McKenzie and Rutger 1983). The identification and chromosomal localization of QTLs for panicle and grain characteristics would elucidate their genetic control, thus facilitating conventional and heterosis breeding for these characters. In the present study, we used a molecular map based on RFLPs to determine the number, chromosomal location, magnitude of effects, and gene action of QTLs controlling important panicle and grain characteristics in a japonica × indica cross.

## Materials and methods

An $F_2$ population derived from a cross between the USA cultivar Labelle (LB) and the Indian cultivar Black Gora (BG) was used in genetic map construction and in the measurement of panicle and grain characteristics. This population was also used for mapping QTLs underlying seedling vigor-related traits (Redoña and Mackill 1996 a). LB is a tropical japonica cultivar with slender grains while BG is an indica (*aus*) cultivar with bold (wide) grains and a black pericarp. Both cultivars have similar grain length.

$F_2$ plants were grown individually in pots in a greenhouse; 204 plants were used for marker segregation analysis and 195 plants were scored for panicle and grain characteristics. The number of spikelets per panicle (panicle size, PS) and spikelet fertility (SF), calculated as the number of filled grains divided by PS, were measured on five randomly selected panicles taken from each $F_2$ plant. Twenty random grain-samples per plant were used for measuring grain length (GL), grain width or breadth (GB), and grain shape (length/breadth ratio, GS), and 100 random grain-samples were used for obtaining grain weight (GW) data. Spikelet fertility (SF) was calculated as $100 \times (GP/PS)$. Length measurements were recorded to the nearest millimeter and grain weight was recorded in milligrams. Black pericarp color was scored as a dominant marker in the $F_2$.

DNA extraction and RFLP assays on parental and $F_2$ plants were as described in Redoña and Mackill (1996 a). The clones used for RFLP analysis were obtained from Dr. Steven Tanksley at Cornell University. Five restriction enzymes, *Eco*RI, *Eco*RV, *Hin*dIII, *Sca*I and *Xba*I, were used both in the initial parental RFLP survey and in assaying the $F_2$ population. Initial linkage mapping of RFLP markers, conducted using version 3.0 of MAPMAKER/EXP running on a unix computer (Lander et al. 1987) and version 2.0 of MAPMAKER for Macintosh (received from Scott Tingey, Dupont), were as described in Redoña and Mackill (1996 a). These markers were assigned to chromosomes by two-point linkage with RFLP markers (minimum LOD of 3.0 and recombination frequency $< 0.40$). The RFLP markers used to assign linkage groups to respective rice chromosomes were previously mapped by McCouch et al. (1988). For use in QTL analysis, markers which mapped at LOD = 2.0 but not LOD = 3.0 were placed in their most likely position.

Identification of factors controlling the quantitative traits measured was undertaken using composite interval mapping (CIM) (Jansen and Stam 1994; Zeng 1994) based on the multiple regression approach with flanking markers described by Haley and Knott (1992) and implemented in the DOS program PLABQTL (Utz Melchinger 1996). The cov (covariates) statement was set at "Select" to include the most important markers identified from simple interval mapping as covariates for CIM. The threshold for QTL detection was set at a LOD score of 3.0.

## Results and discussion

### Genetic map and trait distributions

The molecular map of 116 RFLP markers and one morphological marker (black pericarp) spanned all 12 rice chromosomes with a total length of 1576 cM and an average distance between markers of 15 cM. The black pericarp color gene was mapped to chromosome 4. This gene may, therefore, correspond to the *Pb* gene that was mapped earlier to this chromosome using conventional genetic analysis (Hsieh and Chang 1964) and RFLPs (Zhuang et al. 1994).

Trait distributions were continuous suggesting quantitative inheritance of the characters studied (Fig. 1). Traits generally followed a normal distribution with the exception of SF. The skewed distribution of SF, with many plants showing values close to zero, would be expected in indica × japonica crosses, which typically show high levels of sterility (Ikehashi and Araki 1986). In subsequent mapping studies, various transformations of the data gave similar results for QTL analyses. Transgressive segregation was observed for all traits and was especially pronounced for the higher values of PS, GL, GB and GW.

### Panicle characteristics

Two QTLs were identified for PS at LOD > 3.0 (Table 1, Fig. 2). The locus on chromosome 3 had the largest effect, accounting for 16% of the phenotypic variation with an additive effect of 26. The chromosome-6 allele was highly overdominant. In a multiple regression model, both loci accounted for 21% of the phenotypic variation. Both positive alleles for PS were contributed by the larger PS parent LB, which is a tropical japonica cultivar. Breeding programs attempting to increase the yield potential of indica rice cultivars have utilized tropical japonica cultivars as a source of higher PS (Peng et al. 1993). The chromosome-3 QTL could therefore be a valuable target for selection. PS was also mapped in the crosses studied by Li et al. (1997), Xiao et al. (1996) and Lin et al. (1996). None of these studies identified a similar locus on chromosome 3, but a locus in the same region as the one on chromosome 6 was detected by Lin et al. (1996). One suggestive QTL in the interval RG449–RZ565 on

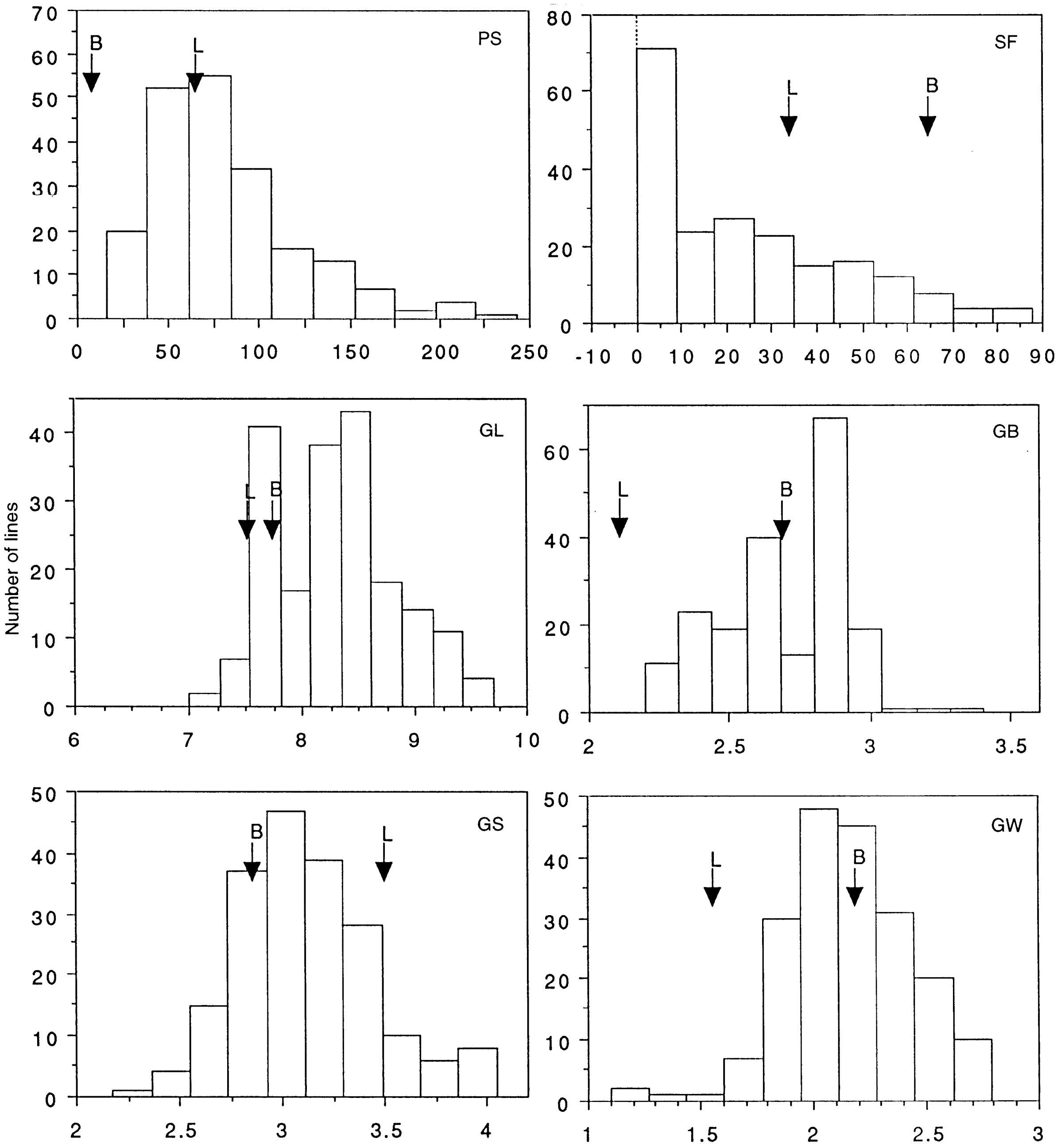

**Fig. 1** Histograms for six panicle and grain traits in a population of 204 $F_2$ plants from the cross Labelle (japonica) × Black Gora (indica-*aus*). *L* = Labelle value, *B* = Black Gora value. *PS* = panicle size in number of spikelets per panicle, *SF* = percent spikelet fertility (filled grains per panicle), *GL* = grain length (mm), *GB* = grain breadth (mm), *GS* = grain shape (GL/GB), *GW* = weight of 100 grains (g)

chromosome 4 with a LOD score of 2.72 (and therefore excluded from the table) was in the same region as a QTL identified by Xiao et al. (1996). The japonica allele of their locus contributed a higher PS, as was observed in the present study.

Four loci were associated with SF, which is generally low in inter-subspecific crosses. The two loci on chromosome 1 showed strong underdominance (Table 1, Fig. 2), with the heterozygote having much lower fertility than either homozygote, which is typical for indica × japonica crosses. The most common gene affecting this type of genetic sterility is the $S_5$ locus on chromosome 6 (Ikehashi and Araki 1986), but no locus on chromosome 6 was detected in the present study. Being a tropical japonica, however, it is probable that LB possesses the wide compatibility allele at this locus. Lin et al. (1996) detected loci on chromosome 1 in two different crosses that may be allelic to both of those identified here. However, they studied an indica × indica population. A SF locus identified by Xiao et al. (1996) on chromosome 5 might be allelic to the one

Table 1 Chromosome, position measured as distance from first marker per chromosome, RFLP markers bracketing the interval, LOD score, coefficient of determination ($R^2$), additive (A) and dominance (D) effects for putative QTLs for panicle and grain characters in a japonica × indica rice cross. Only markers with LOD > 3.0 were considered by composite interval mapping (CIM). Positive values of additive/dominance effects indicate a contribution of positive effect by the male parent Black Gora and negative values indicate a contribution from the female parent Labelle

| Chromosome | Position (cM) | Markers | LOD | $R^2$ | Additive effect | Dominance effect |
|---|---|---|---|---|---|---|
| *Panicle size (PS)* | | | | | | |
| 3 | 60 | RZ448-RZ403 | 7.72 | 16.0 | −26.1 | −6.6 |
| 6 | 118 | RZ612-RZ144 | 3.86 | 8.3 | −5.2 | 20.8 |
| *Spikelet fertility (SF)* | | | | | | |
| 1 | 88 | CDO920-RZ776 | 4.96 | 10.6 | −7.3 | −17.2 |
| 1 | 208 | RZ566-RG350 | 4.46 | 9.7 | −1.7 | −11.7 |
| 3 | 78 | RZ403-RZ452 | 4.61 | 9.9 | 9.2 | 0.6 |
| 5 | 34 | RG182-RZ296 | 3.41 | 7.4 | 7.1 | 3.4 |
| *Grain length (GL)* | | | | | | |
| 2 | 178 | CDO1091-RG520 | 3.42 | 8.0 | −0.18 | 0.00 |
| 3 | 4 | CDO457-RZ142 | 4.63 | 10.4 | 0.44 | −0.16 |
| 3 | 92 | RZ452-RZ284 | 9.95 | 20.9 | −0.29 | −0.13 |
| 4 | 14 | RZ656-RG449 | 5.71 | 12.7 | 0.14 | 0.21 |
| 4 | 130 | RG476-RG620 | 3.77 | 8.6 | 0.20 | −0.11 |
| 7 | 38 | RG711-RG650 | 8.00 | 17.2 | −0.23 | 0.11 |
| 10 | 34 | RZ625-RZ337 | 3.66 | 8.4 | −0.22 | −0.09 |
| *Grain breadth (GB)* | | | | | | |
| 2 | 148 | RG139-CDO686 | 4.01 | 9.1 | −0.08 | 0.00 |
| 3 | 62 | RZ448-RZ403 | 3.50 | 7.9 | 0.08 | 0.07 |
| 7 | 32 | RG711-RG650 | 10.54 | 22.0 | 0.13 | −0.02 |
| 8 | 6 | RZ143-RG333 | 3.24 | 7.5 | −0.08 | −0.01 |
| *Grain shape (GS)* | | | | | | |
| 3 | 82 | RZ403-RZ452 | 10.19 | 21.4 | −0.18 | −0.11 |
| 4 | 16 | RZ656-RG449 | 4.84 | 10.9 | 0.05 | 0.15 |
| 7 | 36 | RG711-RG650 | 12.89 | 26.2 | −0.21 | 0.04 |
| *Grain weight (GW)* | | | | | | |
| 4 | 118 | Pericarp-RG476 | 4.52 | 10.2 | 0.12 | −0.01 |
| 8 | 24 | RG333-RZ562 | 3.35 | 7.7 | −0.08 | 0.06 |

identified in the present study. The SF locus identified by Wu et al. (1996) on chromosome 1 appeared to be non-allelic to those identified here.

## Grain characteristics

Seven QTLs for GL were identified, of which two each were found on chromosomes 3 and 4 (Table 1, Fig. 2). Loci on chromosomes 3 (RZ452-RZ284) and 7 (RG650-RG146) had particularly high LOD values and coefficients of determination. Long-grain alleles were contributed by both parents. Huang et al. (1997) detected loci similar to the RZ452-RZ284 locus on chromosome 3 and the locus on chromosome 10, with a longer GL also being conferred by the japonica alleles. It is interesting to note that a gene designated "Fusayoshi long grain" (*Lk-f*) has been mapped on the classical linkage map in the central part of chromosome 3 (Takeda and Saito 1980; Takamure and Kinoshita 1991), which might be related to the QTL identified here (Fig. 2). Another gene, designated minute grain (*Mi*), maps about 40 cM away (Takeda and Saito 1977; Takamure and Kinoshita 1991). Similarly, the mutant 'IRAT 13' long grain (*lk-i-l*) maps to the same end of chromosome 4 on the classical linkage map as the QTL (RZ656-RG449) associated with GL in this study (Table 1) (Kinoshita and Takamure 1990; Kinoshita 1993; Causse et al. 1994). A multiple regression model with all seven QTLs explained 42% of the phenotypic variation while a model with only the two high-LOD loci explained 24%.

For BG, four QTLs were identified, with the locus in RG711-RG650 on chromosome 7 having a high LOD value and accounting for 22% of the phenotypic variation (Table 1). All four loci together explained 30% of the phenotypic variation. Loci identified by Huang et al. (1997) on chromosomes 2 and 3 appear to be non-allelic to the ones identified here. The three loci identified for GS, being the ratio of GL to GB, were naturally associated with loci for its component traits. The locus on chromosome 3 was associated with a long-grain QTL from LB; the locus on chromosome 4 was associated with an overdominant long-grain QTL from BG; and the locus on chromosome 7 was associated with QTLs for both long- and slender-grains

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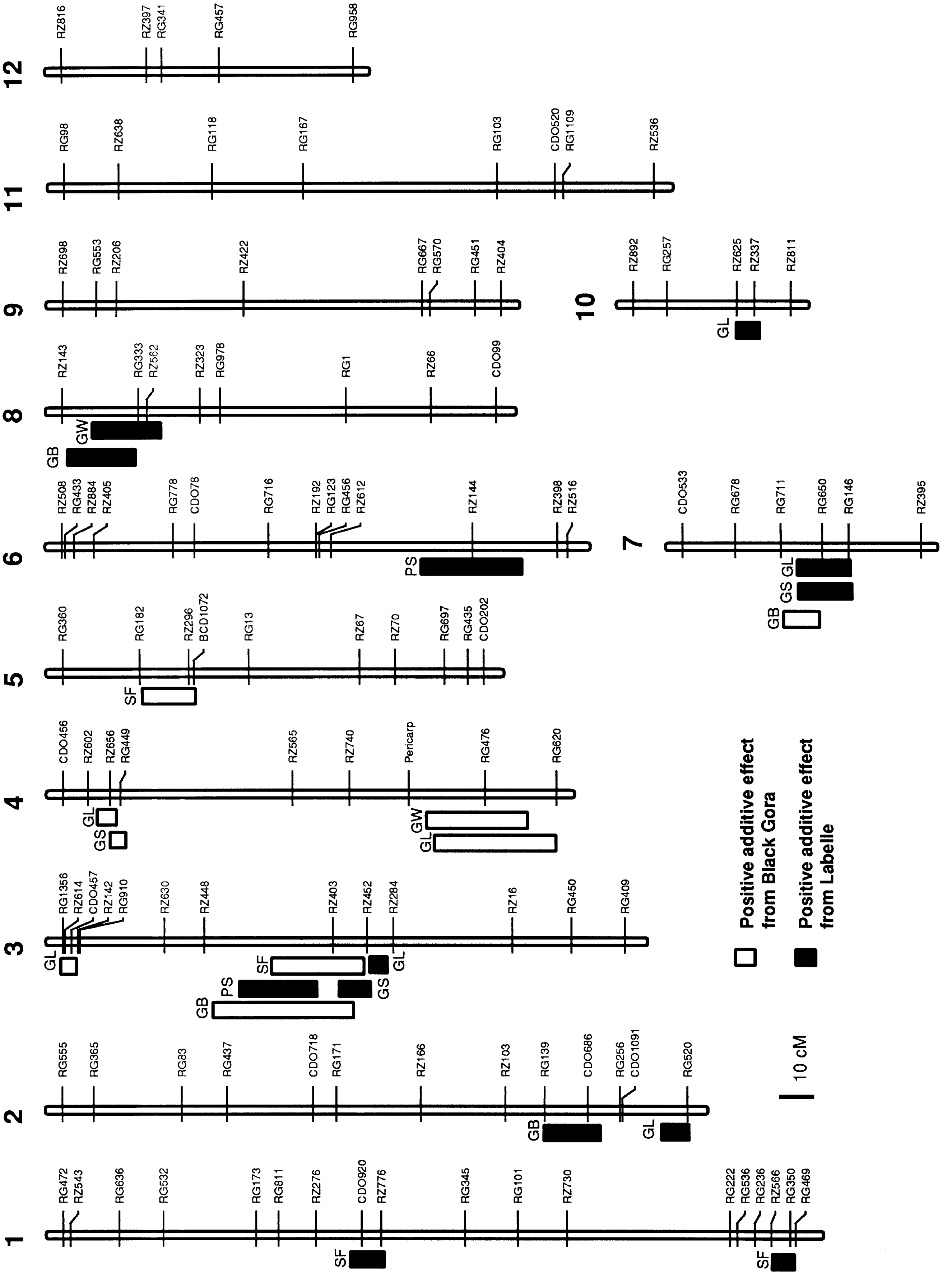
**Fig. 2** Marker maps for the $F_2$ population of the cross Labelle (japonica) × Black Gora (indica-*aus*) showing QTLs identified for six panicle and grain traits. *Lengths* of boxes indicate a one-LOD support interval for the identified QTL


1
RG472
RZ543
RG636
RG532
RG173
RG811
RZ276
CDO920
RZ776
RG345
RG101
RZ730
RG222
RG536
RG236
RZ566
RG350
RG469
SF
SF
2
RG555
RG365
RG83
RG437
CDO718
RG171
RZ166
RZ103
RG139
CDO686
RG256
CDO1091
RG520
GB
GL
10 cM
3
RG1356
RZ614
CDO457
RZ142
RG910
RZ630
RZ448
RZ403
RZ452
RZ284
RZ16
RG450
RG409
GL
GB
PS
SF
GS
GL
4
CDO456
RZ602
RZ656
RG449
RZ565
RZ740
Pericarp
RG476
RG620
GL
GS
GW
GL
5
RG360
RG182
RZ296
BCD1072
RG13
RZ67
RZ70
RG697
RG435
CDO202
SF
6
RZ508
RG433
RZ884
RZ405
RG778
CDO78
RG716
RZ192
RG123
RG456
RZ612
RZ144
RZ398
RZ516
PS
7
CDO533
RG678
RG711
RG650
RG146
RZ395
GB
GS
GL
8
RZ143
RG333
RZ562
RZ323
RG978
RG1
RZ66
CDO99
GB
GW
9
RZ698
RG553
RZ206
RZ422
RG667
RG570
RG451
RZ404
10
RZ892
RG257
RZ625
RZ337
RZ811
GL
11
RG98
RZ638
RG118
RG167
RG103
CDO520
RG1109
RZ536
12
RZ816
RZ397
RG341
RG457
RG958
□ Positive additive effect from Black Gora
■ Positive additive effect from Labelle

from LB. The two loci with the highest LOD values for GL and GB, RZ452-RZ284 on chromosome 3 and RG711-RG650 on chromosome 7, respectively, were the major loci for GS (Table 1). A two-locus model including both these loci accounted for 36% of the phenotypic variability for GS.

Taken together, the data indicate that these two loci on chromosomes 3 and 7 have a major effect on GL, GB, and GS in this cross. GL and GB did not appear to be directly related in the $F_2$ population ($r = 0.05$, $df = 193$) and all combinations of the two were recovered, as has also been observed in other studies (Chauhan and Chauhan 1994; Sarker et al. 1994). This would support the conclusions of Takita (1985) and Kato (1989) that these traits are controlled by separate genes, although linked or allelic QTLs on chromosomes 3 and 7 controlled both traits (Fig. 2).

Two loci were associated with GW, but together they accounted for only 12% of the phenotypic variation. The QTL identified by Xiao et al. (1996) and Lin et al. (1996) on chromosome 4 might be allelic to a locus near RG476 in this study. However, other QTLs identified by these authors and by Wu et al. (1996) and Li et al. (1997) were not associated with any of the markers detected in the present study. GW loci might be expected to be positively related with GL or GB loci, and this was observed here. The Japonica alleles of the QTL on chromosome 4 were associated with a higher GW and GL, and the indica alleles of the QTL on chromosome 8 were associated with a higher GW and GB (Table 1).

The gene action at the grain-dimension QTL was generally additive or partially dominant, but the GL/GS locus on chromosome 4 (RZ656-RG449) was overdominant (Table 1). Additive gene action has been reported to be more predominant for kernel length and kernel width (Singh and Singh 1985; Kato 1989), but both additive and non-additive gene actions were important for grain shape (Singh and Singh 1985). Short grains have been reported to be dominant or partially dominant over long grains (McKenzie and Rutger 1983; Kato 1989), while wide kernels were dominant or partially dominant over slender kernels (McKenzie and Rutger 1983; Chauhan and Chauhan 1994).

## Conclusions

The results of this study indicate that indica germplasm may be a good source of positive alleles for improving the kernel characteristics of japonica rice varieties. This is especially important for breeders in the USA where the germplasm pool is limited and an infusion of new germplasm has been recognized as a way to increase genetic gain in breeding for grain characters (Gravois 1992). The relatively high heritability estimates reported for GL and GB (McKenzie and Rutger 1983; Kato 1990; Chauhan and Chauhan 1994) suggest that selection for grain size would be effective in early generations. However, it has also been noted that environmental factors may greatly influence variation in grain size (Kamijima and Watanabe 1984). Greater genetic gain is, therefore, more likely if selection is based on the genotype, as identified by QTL analysis, rather than the phenotype. This study identified several QTLs from both parents that control the size and shape of rice kernals. Marker-aided introgression of these QTLs into desired genetic backgrounds would be a more effective approach in breeding for these traits in rice. Our use of a population also segregating for seedling vigor alleles, and the finding that positive alleles for both seedling vigor and some grain characters map to the same or adjacent chromosomal locations, also make it possible to introgress both seedling vigor and desired kernel traits simultaneously into desired genotypes. As discussed by Redoña and Mackill (1996 b), possible applications of mapped QTLs include their use in screening parentals for introgression or pyramiding purposes in new populations, the identification of recombinant lines segregating for the most QTLs and their use either as parentals or directly as varieties, as well as the backcrossing of recombinant lines to desired genetic backgrounds followed by marker-aided selection.

The identification of QTLs that appear to be similar to those detected in other crosses or mapped on the classical linkage map lends additional confidence to the importance of individual loci, as indicated by the loci on chromosome 3 for GL and GS. These loci may be attractive targets for inter-subspecific transfer. In addition, the QTLs for PS on chromosome 3 and GL/GS on chromosome 7 may be new loci that are attractive targets for marker-associated selection and map-based cloning.

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