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Mapping quantitative trait loci for yield, yield components and morphological traits in an advanced backcross population between *Oryza rufipogon* and the *Oryza sativa* cultivar Jefferson

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Abstract An advanced backcross population between an accession of *Oryza rufipogon* (IRGC 105491) and the U.S. cultivar Jefferson (*Oryza sativa* ssp. *japonica*) was developed to identify quantitative trait loci (QTLs) for yield, yield components and morphological traits. The genetic linkage map generated for this population consisted of 153 SSR and RFLP markers with an average interval size of 10.3 cM. Thirteen traits were examined, nine of which were measured in multiple environments. Seventy-six QTLs above an experiment-wise significance threshold of $P < 0.01$ (corresponding to an interval mapping LOD > 3.6 or a composite interval mapping LOD > 3.9) were identified. For the traits measured in multiple environments, 47% of the QTLs were detected in at least two environments. The *O. rufipogon* allele was favorable for 53% of the yield and yield component QTLs, including loci for yield, grains per panicle, panicle length, and grain weight. Morphological traits related to the domestication process and/or weedy characteristics, including plant height, shattering, tiller type and awns, were found clustered on chromosomes 1 and 4. Comparisons to previous studies involving wild × cultivated crosses revealed *O. rufipogon* alleles with stable effects in multiple genetic backgrounds and environments, several of which have not been detected in studies between *Oryza sativa* cultivars, indicating potentially novel alleles from *O. rufipogon*. Some *O. rufipogon*-derived QTLs, however, were in similar regions as previously reported QTLs from *Oryza sativa* cultivars, providing evidence for conservation of these QTLs across the *Oryza* genus. In addition, several QTLs for grain weight, plant height, and flowering time were localized to putative homeologous regions in maize where QTLs for these traits have been previously reported, supporting the hypothesis of functional conservation of QTLs across the grasses.

Keywords Quantitative trait locus (QTL) · Advanced backcross QTL analysis (AB-QTL) · Rice · Domestication · Comparative genetics

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Introduction

Rice is a major crop well suited to the identification of quantitative trait loci (QTLs) across varieties and environments. In the past decade a considerable number of QTLs from *Oryza sativa* cultivars have been identified (McCouch and Doerge 1995; Yano and Sasaki 1997; http://www.gramene.org). The identification of QTLs represents the first step toward dissecting the molecular basis of naturally occurring genetic variation for complex traits of agronomic importance. The study of natural variation complements work performed using induced mutants and enhances the functional analysis of plant genomes (Alonso-Blanco and Koornneef 2000; Yano 2001). The ability to clone the genes underlying QTLs (Frary et al. 2000; Fridman et al. 2000; Yano et al. 2000; Takahashi et al. 2001), combined with the importance of natural variation in evolution, domestication, and modern plant breeding, creates the impetus for identifying diverse sets of QTLs in a wide variety of plant species, accessions and environments.

Although wild crop relatives have long been used in plant breeding (Harlan 1976), the use of wild *Oryza* species in QTL studies has been slower to develop. The advanced backcross QTL (AB-QTL) strategy was proposed to identify and transfer agronomically useful QTLs from wild relatives of crops to increase the genetic base available to breeders (Tanksley and Nelson 1996; Tanksley and McCouch 1997). Several studies have been performed to identify and introgress trait-enhancing alleles from wild species of rice into high-yielding elite cultivars. The first such study employed a cross between an accession of *O. rufipogon* (IRGC 105491) and the Chinese *indica* hybrid V20/Ce64 (Xiao et al. 1998). Although the *O. rufipogon* accession was phenotypically inferior for all 12 traits studied, transgressive segregation was observed for all traits, and 51% of the QTLs detected had beneficial alleles from *O. rufipogon* (Xiao et al. 1998). A second study using an advanced backcross population between the same *O. rufipogon* accession and the upland *japonica* rice cultivar Caiapo identified beneficial QTL alleles from *O. rufipogon* for 56% of the trait-enhancing QTLs detected (Moncada et al. 2001). By using a common donor parent in combination with different cultivars as recurrent parents and examining diverse environments, QTLs that are stable across a variety of backgrounds and environments may be identified.

Employing the presumed wild relative of rice, *O. rufipogon*, also provides an opportunity to study morphological traits under selection during domestication, such as shattering, dormancy, red pericarp, grain size, and grain weight. These and other traits comprise the domestication syndrome shared across all of the grasses that distinguishes wild and cultivated plants (Harlan et al. 1973). The genetic basis of the domestication process in several plant species is now being characterized. In maize, five loci have been identified that can explain most of the morphological differences between teosinte and maize, supporting a hypothesis earlier proposed by Beadle that a small number of loci with large effects contributed to the evolution of the teosinte progenitor of modern maize (Beadle 1939; Doebley and Stec 1991, 1993). In common bean, many of the loci controlling domestication are clustered in just three regions of the genome (Koinange et al. 1996). In rice, several recent QTL studies have detected QTLs for domestication-related traits in two different *O. rufipogon* accessions and in a temperate *japonica* weedy rice (Xiong et al. 1999; Cai and Morishima 2000; Bres-Patry et al. 2001; Cai and Morishima 2002). In addition, a comparative QTL study suggested that there had been convergent selection for large seeds, reduced shattering, and daylength-insensitive flowering across rice, sorghum, and maize (Paterson et al. 1995). These studies lead to the hypothesis that selection at a small number of loci can explain much of the phenotypic outcome of the domestication process.

In the present study, an advanced backcross population between the presumed wild relative of rice *O. rufipogon* (IRGC 105491) and the U.S. cultivar Jefferson (*O. sativa* ssp. *japonica*) was used to identify QTLs for yield, yield components, and morphological traits. The objectives of this study were: (1) to reliably identify regions of the genome controlling agronomic traits of interest as a foundation for future characterization of the molecular mechanisms underlying natural genetic variation; (2) to identify trait-enhancing alleles from *O. rufipogon* for yield and yield components, and selectively introgress novel genetic variation into the background of an elite U.S. rice cultivar to provide potentially useful breeding materials; (3) to identify QTLs that were the targets of selection during the domestication process, as well as those considered to confer weedy characteristics in comparison to cultivated varieties; (4) to determine the extent of functional conservation of QTLs detected in this study across other rice cultivars, and in comparison with maize.

Materials and methods

Population development

The recurrent parent in this study is the *O. sativa* cultivar Jefferson, a long-grain *tropical japonica* cultivar grown in the southern U.S. (McClung et al. 1997). Jefferson was chosen for this study because it is a high-yielding variety, with a semi-dwarf plant type, a high level of disease resistance, early maturity, and good grain quality, and therefore provides a starting point for further improvement. The donor parent is an accession of the presumed wild relative of rice, *O. rufipogon* (IRGC 105491), which was previously chosen to be a common donor parent for multiple wild QTL studies (Xiao et al. 1998; McCouch et al. 2001; Moncada et al. 2001).

Population development was carried out at the Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia, beginning with a cross between Jefferson as the female parent, and *O. rufipogon* as the male parent. The F_1 progeny were backcrossed to Jefferson, resulting in 166 BC_1 seeds, from which 33 BC_1 plants were selected based on phenotype to eliminate non-desirable characteristics, including very late- or non-flowering types, excessively tall plants, and sterile plants. After a second backcross to Jefferson, 353 BC_2F_1 plants were grown under quarantine in a greenhouse in Beaumont, Texas, and phenotyped for multiple traits. Selection against shattering and grain dormancy was performed, and 258 BC_2F_2 families that showed no shattering or dormancy were chosen for field trials. The 353 BC_2F_1 plants grown in the greenhouse can be traced back to the original 33 BC_1 plants with 2–15 BC_2F_1 plants per BC_1 plant. When the 258 BC_2F_2 families were selected for the field, one of the BC_1 plants was not represented, with 1–15 BC_2F_2 families tracing back to each of 32 BC_1 plants.

Field trials

Phenotypic evaluations were made on BC_2F_2 families grown in three field environments in the summer of 1998: Beaumont, Tex., Alvin, Tex., and Newport, Ark. In Beaumont, Tex., two replicates in a randomized complete block design were grown in the field by drill planting, and later thinned to a uniform spacing of 42 plants/m^2. For subsequent analyses, the two replicates were averaged. In Alvin, Tex., two field trials were conducted, one that was drill planted, and another that was transplanted. Because different seeding methods were used, the drilled and transplanted data sets were subsequently analyzed separately. The third field location was drill planted in Newport, Ark., with no replication possible due to a lack of available BC_2F_2 seed.

Trait evaluation

Traits were evaluated on BC_2F_1 individuals in the quarantine greenhouse, as well as on BC_2F_2 families (10 plants per family) in the field. Phenotypic measurements were performed for 13 traits, as follows: (1) *days to heading* was evaluated as the number of days from seeding to until 10% of the panicles had emerged; (2) *spikelets per panicle* was calculated as the average total number of spikelets (florets) per panicle measured on the primary panicle of each plant; (3) *grains per panicle* was measured as the average number of filled spikelets per panicle on the primary panicle of each plant; (4) *percent seed set* was determined as the number of filled grains per panicle divided by the total number of spikelets per panicle; (5) *panicle length* was measured as the average number of centimeters from the panicle neck to the panicle tip, excluding awns; (6) *panicles per plant* was calculated as the average number of panicles per plant at harvest; (7) *grain weight* was measured as the average weight of 100 kernels; (8) *yield per plant* was determined as the average weight of bulked harvested grain per plant from at least ten plants; (9) *plant height* was measured in centimeters from the soil surface to the tip of the tallest panicle, excluding the awns; (10) *shattering* was estimated using five categories ranging from non-shattering (seeds are difficult to pull off the panicle) to highly shattering (seeds fall freely without touching the panicle) at the time of harvest; (11) *percent germination* was determined using 30 kernels that had been harvested 30 days after the panicle had flowered, dried at 45 °C for 4 days, soaked in water for 2 days, and then transferred to moist filter paper in closed petri dishes for 4 days; (12) *awns* were ranked in five categories, from no awns to awns over 1 cm in length; (13) *tiller type* consisted of two categories – erect tiller type and lazy tiller type (greater than 10 degrees from the vertical).

Marker analysis

Tissue was harvested in bulks of approximately 10–15 individuals from each of 353 BC_2F_2 families grown in the greenhouse at Cornell University (Ithaca, N.Y.), and DNA was extracted using a choloroform-based DNA extraction protocol as described in McCouch et al. (1988). Marker surveys were first conducted to identify polymorphic markers from the available rice simple sequence repeat (SSR) markers (Panaud et al. 1996; Chen et al. 1997; Temnykh et al. 2000). Polymerase chain reaction (PCR) conditions were as described in Panaud et al. (1996), with the following modifications: the total reaction volume was scaled down to 15 μl, and the following thermal cycle profile was used: 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s; lastly, 5 min at 72 °C. PCR products were run on 4% denaturing polyacrylamide gels, followed by silver staining as described in Panaud et al. (1996).

Genotypic ratios were evaluated for each marker locus using a chi-square test, with significant deviations from expected ratios reported at $P < 0.01$. The expected genotypic frequency was 0.25 for heterozygous BC_2F_2 families (Jefferson/*O. rufipogon*) at any single marker locus and 0.75 for homozygous Jefferson families. Because tissue from each family was harvested in bulk, homozygous *O. rufipogon* individuals were not detected, except as they contributed to the heterozygous BC_2F_2 class.

The initial linkage map was constructed based on segregation at 104 microsatellite marker loci using MAPMAKER software (Lander et al. 1987). Marker orders were confirmed using the published microsatellite map from Temnykh et al. (2000). Subsequently, marker surveys for restriction fragment length polymorphisms (RFLP) for rice and oat RFLP probes were conducted as previously described (McCouch et al. 1988; Van Deynze et al. 1998). Of the polymorphic markers, 49 RFLP markers were added to the map using the MAPMAKER "try" command to fill gaps and to aid in later comparisons to previous QTL studies. The genetic distances for the final map were obtained using the BC_2 mapping algorithm with MAP MANAGER QTX (Manly and Olson 1999; http://mapmgr.roswellpark.org/mmQTX.html).

QTL analysis

QTLs were identified using single-point analysis (SPA), interval mapping (IM) and composite interval mapping (CIM). The primary analysis using SPA and IM was performed using QGENE (Nelson 1997). The QTL detected by SPA and IM corresponded well (data not shown), therefore only the results from IM are presented. For the IM analysis, the following parameters were selected: the BC_2 population structure, 1-cM intervals, and the Kosambi function. To identify an accurate significance threshold for each trait, an empirical threshold was determined for IM using 10,000 permutations for each trait across all 12 chromosomes (Churchill and Doerge 1994). For IM, the experiment-wise significance level of $P < 0.01$ corresponded to an average LOD > 3.60 across traits, while the level of $P < 0.05$ corresponded to a LOD > 2.84.

To identify additional QTLs that may have been masked by the larger QTLs, CIM was employed (Zeng 1994). Automatic cofactor selection using a forward/backward regression (forward $P < 0.01$, backward $P < 0.01$) was performed with QTL CARTOGRAPHER v1.21 (Basten et al. 1997). Significance thresholds for CIM were determined using 1,000 permutations for each trait. For CIM, the experiment-wise significance level of $P < 0.01$ corresponded to an average LOD > 3.90, while the level of $P < 0.05$ corresponded to a LOD > 2.98. A putative QTL was reported if detected in at least one environment at an experiment-wise significance threshold of $P < 0.01$. QTLs were labeled as significant in multiple environments if detected in at least one environment at $P < 0.01$, and in supporting environments at $P < 0.05$.

Comparative QTL analysis

To compare the QTL locations from the present study with previously reported rice QTLs, the results from 32 previous rice QTL studies were first examined for data on any of the 14 traits to be compared (see above for descriptions of 13 traits, plus the additional trait of grains per plant). In total, 509 previously reported QTLs were found for these 14 traits, and QTLs on the same chromosome as a QTL in the present study were selected for detailed comparisons. Three rice genetic linkage maps were used to compare QTL locations: the Japanese Rice Genome Research Program RFLP map (Nipponbare × Kasalath; Harushima et al. 1998), the Cornell RFLP map (*O. sativa* × *O. longistaminata*; Causse et al. 1994), and the Cornell SSR map (IR64 × Azucena; Temnykh et al. 2000). The QTLs were placed on a framework map based on a cross map comparison between the three rice genetic linkage maps (S. Harrington, personal communication; http://www.gramene.org). QTLs were identified as potentially homologous if there was significant overlap in the QTL intervals being compared.

Comparisons of rice QTLs from the present study to maize QTLs were performed for flowering time, plant height, and grain weight. QTLs from the present study for these three traits that were detected in at least two environments were chosen for comparison. Putative homeologous maize segments were identified for each QTL region using the comparative map of Wilson et al. (1999). Previously reported maize QTLs from 15 published maize QTL studies were used for the comparison. Maize QTLs that aligned to the putative homeologous regions were identified through shared markers, or by indirect comparisons with the markers on the maize map of Davis et al. (1999) using both manual approaches and newly developed comparative map tools in http://www.gramene.org.

Results

Linkage map and marker segregation

The genetic linkage map for this study contained 153 microsatellite and RFLP markers, for a total length of

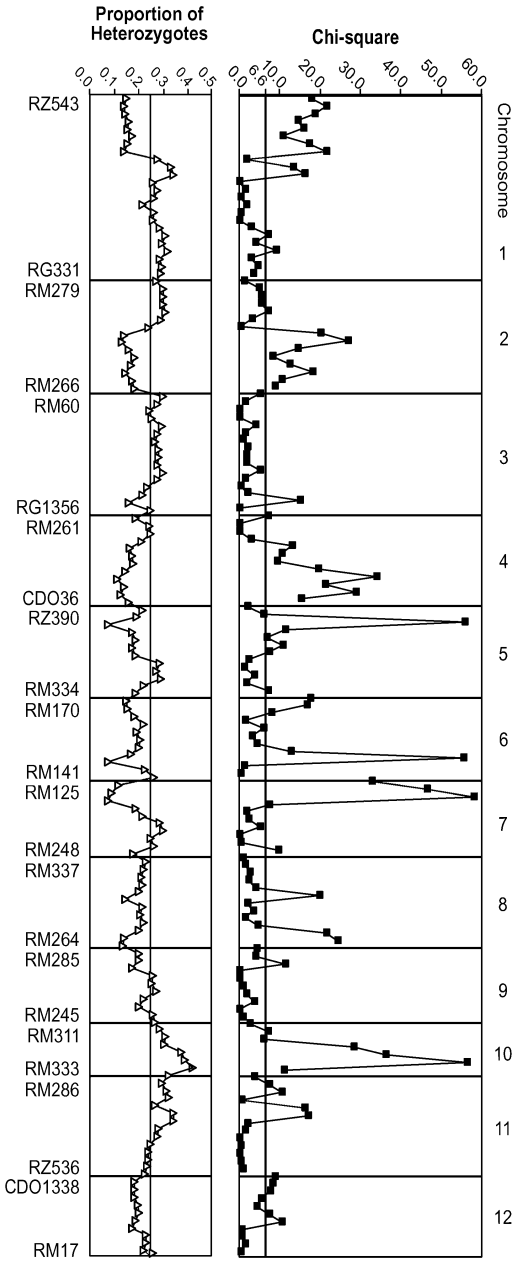

Fig. 1 Segregation distortion across all 12 rice chromosomes is shown as χ^2 values for deviation from the expected segregation ratio. The first and last markers for each chromosome are indicated on the *X-axis*, and χ^2 values are on the *Y-axis*. A value of $\chi^2 > 6.6$ corresponds to $P < 0.01$. The genotype frequency across all 12 chromosomes is also shown. The proportion of the Jefferson/*O. rufipogon* heterozygous class for each marker locus is depicted with *triangles*

1,457 cM (Kosambi) with an average interval size of 10.3 cM. Marker orders for the microsatellites were identical to the published map with the exception of an inversion of RM261 and RM307 on the top of chromosome 4. For this population, the average genome proportion is 23.2% *O. rufipogon* and 76.7% Jefferson, and the average length for *O. rufipogon* introgressions is 34 cM. Significant skewing of genotypic classes was observed for 42.5% of the markers used in this study: 33.3% of the total marker loci were skewed towards the homozygous Jefferson class, while 9.2% were skewed towards the heterozygous Jefferson/*O. rufipogon* class ($\chi^2 > 6.6$, $P < 0.01$). Eight chromosomal regions, on chromosomes 1, 2, 4, 5, 6, 7, 8, and 10, contained clusters of skewed markers with at least one marker in each region showing extreme distortion ($\chi^2 > 20$, $P < 0.0001$; Fig. 1). Of these, only one, on chromosome 10, showed extreme skewing towards the heterozygous class.

Trait correlations

Correlations between yield and yield components were calculated using the transplanted field trial from Alvin, Tex. as a representative environment, as this was the only field trial in which every yield component was evaluated. Correlations for morphological traits were based on greenhouse data. The strongest positive correlations with yield in the field environment were panicles per plant, grains per panicle, and spikelets per panicle (Table 1). The number of grains per panicle also had a strong positive correlation with percent seed set, panicle length, and days to heading. There was a small negative correlation between grains per panicle and grain weight. For the morphological traits, strong positive correlations were found between plant height and panicle length, and a negative correlation between panicle length and days to heading (Table 2). In addition, awns were weakly but positively correlated with shattering, plant height, panicle length, and grain weight, and negatively correlated with days to heading.

QTL identification

QTLs were identified for all 13 traits in this study. A total of 76 QTLs were detected above an empirically determined experiment-wise significance threshold equivalent to $P < 0.01$ (corresponding to an interval mapping LOD > 3.6 or a composite interval mapping LOD > 3.9; Fig. 2; Tables 3, 4). Nine of the 13 traits were measured across multiple environments. An experiment-wise significance threshold of $P < 0.05$ was used to declare a QTL significant for supporting environments if a QTL was already established at the same position in at least one environment at $P < 0.01$. For the traits measured in multiple environments, 47% of the QTLs (28 out of 60) were detected in at least two environments. The *O. rufipogon* allele was favorable for 53% of the yield and yield component QTLs (Fig. 2, Table 3).

Days to heading

Eleven QTLs were detected for days to heading: the *O. rufipogon* allele contributed to earliness at eight loci, while the *O. rufipogon* allele caused later heading at three

Table 1 Trait correlations for the Alvin, Tex. transplanted field environment[a]

Trait[b]	dth	pl	ppl	gpp	yld	gw	pss
pl	–						
ppl	–	–					
gpp	0.294	0.248	–				
yld	0.161	0.176	0.735	0.458			
gw	–	–	–	–0.257	–		
pss	–	–	–	0.434	0.174	–	
spp	0.313	0.284	–	0.961	0.446	–0.261	0.180

[a] $P < 0.01$
[b] Abbreviations: dth, days to heading; pl, panicle length; ppl, panicles per plant; gpp, grains per panicle; yld, yield per plant; gw, grain weight; pss, percent seed set; spp, spikelets per panicle

Table 2 Trait correlations for the greenhouse environment[a]

Trait[b]	awn	sh	tt	ph	pl	gw	dth
sh	0.204						
tt	–	–					
ph	0.227	–	–				
pl	0.280	–	0.160	0.573			
gw	0.209	0.293	–	0.289	0.214		
dth	–0.209	0.193	–	–0.177	–0.348	–	
grm	–	–	–	–	–	–	–

[a] $P < 0.01$
[b] Abbreviations: awn, awns; sh, shattering; tt, tiller type; ph, plant height; pl, panicle length; gw, grain weight; dth, days to heading; grm, percent germination

loci (Fig. 2, Table 3). The most stable QTL across environments was *dth7.1*, detected in all five environments measured for days to heading, with the largest effect in Newport, Ark., with 37.7% of the variance explained by this QTL. The most stable earliness QTL from *O. rufipogon* was *dth1.1*, detected in three environments, with 14.9% variance explained in the transplanted Alvin, Tex. trial (Table 3).

Yield components

Grains per panicle

Ten QTLs were detected for grains per panicle: the *O. rufipogon* allele increased the number of grains per panicle at four loci and decreased grains per panicle at six loci (Fig. 2, Table 3). The most stable QTL across environments was *gpp1.2* at marker RM5, detected in Alvin, Tex. and Beaumont, Tex. The most significant *O. rufipogon*-derived QTL associated with an increase of grains per panicle was *gpp3.1*, which explained 12.4% of the variance in the Alvin, Tex. drilled trial (Table 3).

Spikelets per panicle

Six QTLs were detected for spikelets per panicle: the *O. rufipogon* allele increased spikelets per panicle at *spp2.1, spp3.1*, and *spp9.1*, while it was associated with decreased spikelets per panicle at *spp1.1, spp1.2*, and *spp12.1* (Fig. 2, Table 3). All of the QTLs for spikelets per panicle corresponded with QTL regions for grains per panicle (Fig. 2).

Panicle length

Six QTLs for panicle length were detected, with the *O. rufipogon* allele contributing to increased panicle length at five of the six loci (Fig. 2). The QTL *pl1.1* was detected in three environments, including Alvin, Tex., Newport, Ark., and the greenhouse, with 28.7% of the variance explained for this trait in the greenhouse environment (Table 3).

Percent seed set

Seven QTLs for percent seed set were identified: the *O. rufipogon* allele at *pss5.1* increased seed set, while the *O. rufipogon* alleles the other six QTLs decreased seed set (Figure 2, Table 3). The most stable QTL was *pss4.1*, detected in Alvin, Tex., Beaumont, Tex., and Newport, Ark., with a maximum R^2 of 13.2%.

Grain weight

Eight QTLs for grain weight were identified: the *O. rufipogon* alleles at *gw1.1* and *gw5.1* were associated with increased grain weight, while the *O. rufipogon* alleles at the other six QTLs decreased grain weight (Fig. 2). The most stable QTL was *gw3.1*, detected at Alvin, Tex., Newport, Ark., and the greenhouse environments, with a maximum R^2 of 17.3%.

Panicles per plant

Two QTLs were detected for panicles per plant in the single environment for which this trait was measured. The *O. rufipogon* allele increased panicles per plant at both loci, *ppl3.1* and *ppl7.1* (Table 3).

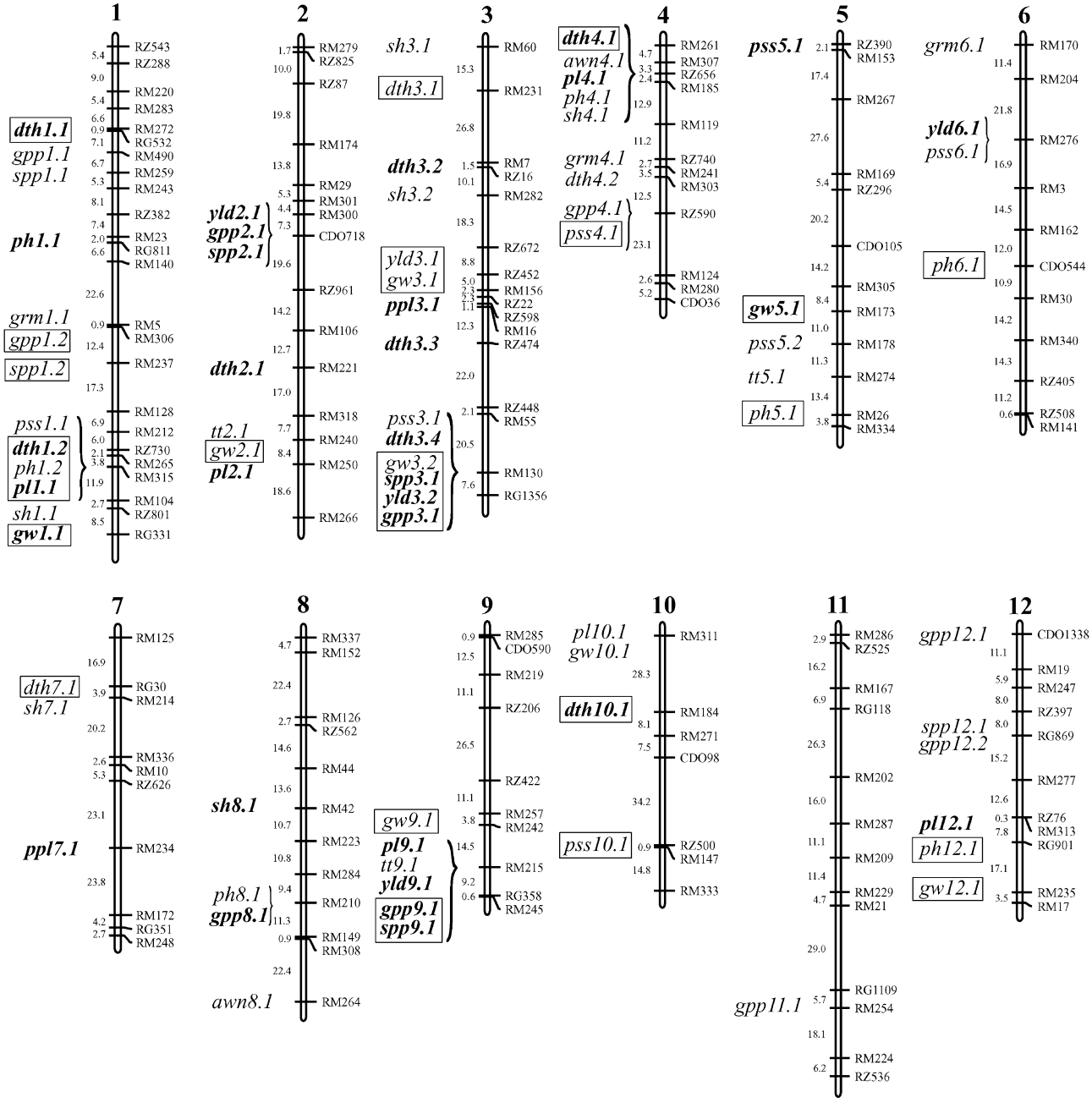

Fig. 2 Molecular linkage map with positions of QTLs for 13 traits. QTLs were detected by interval mapping and/or composite interval mapping at an experiment-wise threshold of $P < 0.01$ (corresponding to LOD > 3.6). QTLs detected in multiple environments, with at least one environment at LOD > 3.6 and supporting environments at LOD > 2.8, are *boxed*. QTLs with the desirable allele from *O. rufipogon* are in *bold*

Yield per plant

Five QTLs were detected for yield per plant, with the *O. rufipogon* allele increasing yield at *yld2.1, yld3.2, yld6.1, yld9.1*, and decreasing yield at *yld3.1* (Fig. 2). The strongest yield QTL, *yld3.2*, was detected in Alvin, Tex. and Beaumont, Tex., with an R^2 of 16.6% in the Beaumont, Tex. field trial (Table 3).

Morphological traits

Plant height

Seven QTLs were detected for plant height, with the *O. rufipogon* allele increasing plant height at all loci (Fig. 2). The long arm of chromosome 1 contained a major QTL for plant height, *ph1.2*, located between RZ730 and RG331, with a peak R^2 of 47.5% in the greenhouse environment (Table 4).

Table 3 Yield and yield component QTLs detected in a Jefferson/*Oryza rufipogon* BC_2 population[a]

QTL	Chr.	Peakmarker[b]	Flanking markers[c]	Increased effect[d]	IM or CIM	Alvin, Tex. (transplanted)[c]		Alvin, Tex. (drilled)		Beaumont, Tex.		Newport, Ark.		Greenhouse	
						LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %
Days to heading															
dth1.1	1	RG532	RZ288-RM140	Jefferson	IM	9.06	14.9	6.98	11.7					5.98	7.5
					CIM	6.91	9.2	6.59	8.5	4.01	4.0			5.96	5.7
dth1.2	1	RM315	RZ730-RZ801	Jefferson	IM	3.30	5.7	5.50	9.4						
					CIM			5.58	8.4						
dth2.1	2	RM221	RM106-RM221	Jefferson	CIM									4.06	4.4
dth3.1	3	RM231	RM60-RM231	*O. rufipogon*	IM					7.98	13.3			4.97	6.3
					CIM					10.24	12.7			7.37	7.1
dth3.2	3	RZ16	RM7-RM282	Jefferson	CIM									4.49	4.2
dth3.3	3	RZ474	RM16-RZ448	Jefferson	CIM			4.54	6.6						
dth3.4	3	RM130	RM130	Jefferson	IM	3.63	6.3								
dth4.1	4	RM307	RM307	Jefferson	IM	3.65	6.3	3.38	5.9						
dth4.2	4	RM303	RZ740-RM303	*O. rufipogon*	IM					4.82	8.2				
					CIM					3.19	3.2				
dth7.1	7	RM214	RM125-RM336	*O. rufipogon*	IM	6.21	10.5	10.52	17.1	16.72	25.8	12.10	22.8	13.52	16.2
					CIM	5.02	8.4	10.20	15.9	21.89	29.8	17.88	37.7	16.34	16.6
dth10.1	10	RM184	RM184-RM271	Jefferson	IM					3.24	5.6				
					CIM					6.57	7.6	3.84	5.7		
Grains per panicle															
gpp1.1	1	RM490	RM283-RM259	Jefferson	IM			6.17	10.4					–	–
					CIM			7.90	11.3					–	–
gpp1.2	1	RM5	RM5-RM237	Jefferson	IM	4.51	7.7	3.58	6.2	3.09	5.4			–	–
					CIM	6.35	9.7	4.34	6.9	3.34	6.5			–	–
gpp2.1	2	CDO718	CDO718	*O. rufipogon*	IM	4.57	7.8							–	–
gpp3.1	3	RG1356	RM130-RG1356	*O. rufipogon*	IM	4.53	7.8	2.96	5.2					–	–
					CIM	5.51	9.5	7.02	12.4			3.02	5.3	–	–
gpp4.1	4	RZ590	RZ740-RZ590	Jefferson	IM					6.69	11.3			–	–
					CIM					4.41	7.9			–	–
gpp8.1	8	RM210	RM210	*O. rufipogon*	CIM					4.44	7.2			–	–
gpp9.1	9	RM215	RM215	*O. rufipogon*	IM	4.03	6.9			3.61	6.2			–	–
gpp11.1	11	RM254	RM254	Jefferson	IM	3.93	6.9							–	–
gpp12.1	12	CDO1338	CDO1338	Jefferson	CIM					3.59	5.1			–	–
gpp12.2	12	RG869	RG869	Jefferson	CIM							3.60	7.4	–	–
Spikelets per panicle															
spp1.1	1	RM490	RM283-RM259	Jefferson	IM			4.76	8.2					–	–
					CIM			5.40	7.2					–	–
spp1.2	1	RM237	RM237-RM128	Jefferson	IM	3.73	6.4	3.17	5.5					–	–
					CIM	5.84	8.5	4.75	7.9					–	–
spp2.1	2	CDO718	CDO718	*O. rufipogon*	IM	5.91	10.0							–	–
					CIM	3.69	5.7							–	–
spp3.1	3	RM130	RM130-RG1356	*O. rufipogon*	IM	4.73	8.1	5.58	9.5			2.82	5.9	–	–
					CIM	5.82	9.5	10.46	15.1	3.30	4.8	3.30	6.5	–	–
spp9.1	9	RM215	RM215	*O. rufipogon*	IM	4.68	8.0			4.59	7.9			–	–
					CIM					4.84	8.2			–	–
spp12.1	12	RG869	RG869	Jefferson	CIM							3.82	8.6		

Table 3 (continued)

QTL	Chr.	Peakmarker[b]	Flanking markers[c]	Increased effect[d]	IM or CIM	Alvin, Tex. (transplanted)[c]		Alvin, Tex. (drilled)		Beaumont, Tex.		Newport, Ark.		Greenhouse	
						LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %
Panicle length															
pl1.1	1	RM315	RZ730-RZ801	*O. rufipogon*	IM	3.41	5.9			–	–	3.47	7.2	18.30	21.2
					CIM					–	–	6.68	13.7	22.53	28.7
pl2.1	2	RM250	RM221-RM250	*O. rufipogon*	IM	4.81	8.2			–	–				
					CIM	4.78	7.6			–	–				
pl4.1	4	RZ656	RM307-RM185	*O. rufipogon*	IM					–	–			5.62	7.1
pl9.1	9	RM215	RM215	*O. rufipogon*	IM			4.87	8.3	–	–				
					CIM			5.15	7.5	–	–				
pl10.1	10	RM311	RM311	Jefferson	CIM					–	–			3.98	4.3
pl12.1	12	RG901	RG901	*O. rufipogon*	IM			4.02	6.9	–	–				
					CIM			5.38	9.8	–	–				
Percent seed set															
pss1.1	1	RM315	RM265-RM315	Jefferson	IM							4.42	9.1	–	–
					CIM							4.84	10.0	–	–
pss3.1	3	RM130	RM130	Jefferson	IM			4.00	6.9					–	–
					CIM			4.31	6.0					–	–
pss4.1	4	RZ590	RZ740-RZ590	Jefferson	IM			3.57	6.2	7.96	13.2	3.43	7.1	–	–
					CIM					10.04	19.9			–	–
pss5.1	5	RM153	RM153	*O. rufipogon*	IM					3.91	6.7			–	–
pss5.2	5	RM178	RM173-RM178	Jefferson	IM							4.29	8.8	–	–
					CIM							4.68	11.5	–	–
pss6.1	6	RM276	RM276-RM3	Jefferson	CIM			5.69	18.6					–	–
pss10.1	10	RM147	CDO98-RM333	Jefferson	IM			9.72	15.9	3.17	5.5			–	–
					CIM			13.82	22.2					–	–
Grain weight															
gw1.1	1	RG331	RM104-RG331	*O. rufipogon*	IM					–	–			4.65	5.9
					CIM			4.55	6.3	–	–			5.82	8.0
gw2.1	2	RM250	RM240-RM266	Jefferson	IM					–	–	4.47	9.2		
					CIM					–	–	7.06	16.0	3.31	4.9
gw3.1	3	RZ452	RZ672-RZ474	Jefferson	IM			6.49	10.9	–	–	3.73	7.7	12.58	15.1
					CIM			7.54	10.2	–	–	5.86	10.5	15.83	17.3
gw3.2	3	RM130	RM130-RG1356	Jefferson	IM	3.75	6.5	6.69	11.3	–	–				
					CIM	3.72	6.0	6.42	8.8	–	–				
gw5.1	5	RM173	RM305-RM173	*O. rufipogon*	IM	4.29	7.4			–	–				
					CIM	4.01	6.2	2.94	3.7	–	–				
gw9.1	9	RM242	RM242	Jefferson	IM	3.30	5.7	3.62	6.3	–	–				
					CIM			4.56	5.6	–	–				
gw10.1	10	RM311	RM311	Jefferson	CIM					–	–			4.66	7.6
gw12.1	12	RM235	RG901-RM17	Jefferson	IM	4.91	8.4			–	–	3.84	7.9		
					CIM	3.20	5.5			–	–	3.36	6.4		
Panicles per plant															
ppl3.1	3	RZ598	RM156-RM16	*O. rufipogon*	IM	4.56	7.8	–	–	–	–	–	–	–	–
					CIM	5.85	8.7	–	–	–	–	–	–	–	–
ppl7.1	7	RM234	RM234	*O. rufipogon*	IM	3.71	6.4	–	–	–	–	–	–	–	–
					CIM	5.36	18.0	–	–	–	–	–	–	–	–

Table 3 (continued)

QTL	Chr.	Peakmarker[b]	Flanking markers[c]	Increased effect[d]	IM or CIM	Alvin, Tex. (transplanted)[e]		Alvin, Tex. (drilled)		Beaumont, Tex.		Newport, Ark.		Greenhouse	
						LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %
Yield per plant															
yld2.1	2	CDO718	CDO718	*O. rufipogon*	IM	7.35	12.3					–	–	–	–
					CIM	4.77	9.8					–	–	–	–
yld3.1	3	RZ452	RZ452-RM16	Jefferson	CIM			4.88	8.0	3.43	4.3	–	–	–	–
yld3.2	3	RG1356	RM130-RG1356	*O. rufipogon*	IM			3.80	6.6	10.10	16.5	–	–	–	–
					CIM			5.60	8.4	11.56	16.6	–	–	–	–
yld6.1	6	RM276	RM276	*O. rufipogon*	IM					3.74	6.5	–	–	–	–
yld9.1	9	RM215	RM215	*O. rufipogon*	IM	4.28	7.4					–	–	–	–

[a] QTLs at an experiment-wise $P < 0.01$ (IM LOD > 3.60, CIM LOD > 3.90), with supporting environments at $P < 0.05$ (IM LOD > 2.84, CIM LOD > 2.98)
[b] Peak marker is the marker closest to the peak LOD score in the most significant environment
[c] Flanking markers are the markers within the significance threshold at each border of the QTL range in the most significant environment
[d] Increased effect is the source of the allele causing an increase in the trait measurement (whether favorable or unfavorable)
[e] Traits were measured in four field trials, and one greenhouse trial; traits not measured in a specific environment are marked with "–"

Shattering

Six QTLs for shattering were identified, with the *O. rufipogon* introgression increasing shattering at *sh1.1, sh3.1, sh3.2, sh4.1, sh7.1*. For one locus, at *sh8.1*, the *O. rufipogon* allele decreased shattering (Fig. 2).

Percent germination

Three QTLs were detected, with *O. rufipogon* decreasing percent germination at all loci: *grm1.1, grm4.1*, and *grm6.1* (Fig. 2).

Awns

Two QTLs were identified for awns: the *O. rufipogon* allele increased awn size at *awn4.1* and *awn8.1* (Fig. 2). The QTL on chromosome 4, *awn4.1*, explained 27.3% of the variance, compared to an R^2 of 7.9% for *awn8.1* (Table 4).

Tiller type

Three QTLs were detected for tiller type: with the *O. rufipogon* allele contributing to a lazy plant type at all loci: *tt2.1, tt5.1*, and *tt9.1* (Fig. 2). Thus, except for *sh8.1*, all of the QTLs associated with weedy characters were increased by the presence of *O. rufipogon* alleles and had apparently been eliminated in the Jefferson parent.

Discussion

As more QTL data is accumulated in the literature and as subsequent research begins to build from this data, stringent criteria for supporting the validity of reported QTLs are essential. Such criteria include (1) empirically determined experiment-wise thresholds of significance, (2) supporting data from multiple replicates and/or multiple environments for the same population, and (3) confirmation of QTL effects through near-isogenic lines. For the present study, to reliably identify QTLs segregating in the Jefferson/*O. rufipogon* population, the risk of reporting false positive QTLs (Type-I error) was minimized using permutation tests to define an empirical detection threshold at an experiment-wise *P*-value <0.01. For the primary QTL analysis, IM was employed, followed by CIM as a complement to IM to aid in identifying QTLs that may have been masked by the effect of the larger QTLs (Zeng 1994). Using the combined IM and CIM QTLs (at $P < 0.01$) as a core set of QTLs, a less stringent experiment-wise significance threshold of $P < 0.05$ was used across the other environments to identify supporting QTLs detected in different environments at the same loci. Therefore, while 76 independent QTLs were detected at $P < 0.01$, 60 of

Table 4 Morphological and weediness QTLs detected in a Jefferson/*O. rufipogon* BC_2 population[a]

QTL	Chr.	Peakmarker[b]	Flanking markers[c]	Increased effect[d]	IM or CIM	Alvin, Tex. (transplanted)[c]		Alvin, Tex. (drilled)		Beaumont, Tex.		Newport, Ark.		Greenhouse	
						LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %	LOD	R^2 %
Plant height															
ph1.1	1	RG811	RG811	Jefferson	CIM	–	–					–	–	3.97	2.4
ph1.2	1	RM315	RZ730-RZ331	*O. rufipogon*	IM	–	–	11.32	18.6			–	–	30.97	33.2
					CIM	–	–	9.19	13.4			–	–	51.14	47.5
ph4.1	4	RZ656	RM307-RM185	*O. rufipogon*	IM	–	–					–	–	7.11	8.8
ph5.1	5	RM26	RM178-RM334	*O. rufipogon*	IM	–	–					–	–	8.19	10.1
					CIM	–	–	3.31	4.2			–	–	13.27	10.7
ph6.1	6	CDO544	RM162-RM30	*O. rufipogon*	IM	–	–					–	–	3.50	4.5
					CIM	–	–	5.09	10.0			–	–	15.46	12.2
ph8.1	8	RM210	RM210-RM308	*O. rufipogon*	CIM	–	–					–	–	5.52	5.3
ph12.1	12	RG901	RG901	*O. rufipogon*	IM	–	–	3.06	5.4			–	–	3.67	4.7
Shattering															
sh1.1	1	RZ801	RM315-RG331	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	5.16	6.5
					CIM	–	–	–	–	–	–	–	–	4.85	6.0
sh3.1	3	RM60	RM60	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	4.97	6.3
					CIM	–	–	–	–	–	–	–	–	5.83	7.2
sh3.2	3	RM282	RM282	*O. rufipogon*	CIM	–	–	–	–	–	–	–	–	4.03	4.3
sh4.1	4	RM185	RZ656-RM185	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	3.44	4.4
					CIM	–	–	–	–	–	–	–	–	3.92	4.7
sh7.1	7	RM214	RG30-RM214	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	3.67	4.7
					CIM	–	–	–	–	–	–	–	–	7.70	8.5
sh8.1	8	RM42	RM44-RM42	Jefferson	IM	–	–	–	–	–	–	–	–	4.24	5.4
					CIM	–	–	–	–	–	–	–	–	3.99	4.8
Percent germination															
grm1.1	1	RM5	RM5-RM306	Jefferson	IM	–	–	–	–	–	–	–	–	5.23	6.6
					CIM	–	–	–	–	–	–	–	–	4.44	6.4
grm4.1	4	RZ740	RM119-RM303	Jefferson	IM	–	–	–	–	–	–	–	–	8.69	10.7
					CIM	–	–	–	–	–	–	–	–	8.01	10.2
grm6.1	6	RM170	RM170-RM204	Jefferson	IM	–	–	–	–	–	–	–	–	8.90	11.0
					CIM	–	–	–	–	–	–	–	–	7.20	8.4
Awns															
awn4.1	4	RZ656	RM307-RM185	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	24.36	27.3
awn8.1	8	RM264	RM264	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	6.27	7.9
Tiller type															
tt2.1	2	RM240	RM318-RM250	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	7.51	9.3
					CIM	–	–	–	–	–	–	–	–	4.37	3.8
tt5.1	5	RM274	RM274	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	3.25	4.2
					CIM	–	–	–	–	–	–	–	–	4.70	5.0
tt9.1	9	RM215	RZ422-RM245	*O. rufipogon*	IM	–	–	–	–	–	–	–	–	32.19	34.3
					CIM	–	–	–	–	–	–	–	–	45.24	46.3

[a] QTLs at an experiment-wise $P < 0.01$ (IM LOD > 3.60, CIM LOD > 3.90), with supporting environments at $P < 0.05$ (IM LOD > 2.84, CIM LOD > 2.98)
[b] Peak marker is the marker closest to the peak LOD score in the most significant environment
[c] Flanking markers are the markers within the significance threshold at each border of the QTL range in the most significant environment
[d] Increased effect is the source of the allele causing an increase in the trait measurement (whether favorable or unfavorable)
[e] Traits were measured in four field trials, and one greenhouse trial; traits not measured in a specific environment are marked with "–"

these were evaluated in multiple environments, and of those, 28 (47%) were detected in more than one environment, adding up to a total of 185 QTLs detected across all environments at $P < 0.05$ (Tables 3, 4). Two thresholds for reporting QTLs were chosen because (1) an experiment-wise threshold of $P < 0.01$ provides a stringent level of security against Type-I error and (2) if there is already strong evidence ($P < 0.01$) for a QTL in one environment, this increases the chance that a slightly less significant QTL ($P < 0.05$) detected in the same population but evaluated in another environment at the same locus is valid (i.e., not a false positive).

Significant segregation distortion, which is the deviation from the expected Mendelian segregation ratio, was observed in this study for 42.5% of the marker loci (33.3% of the total markers were skewed towards the homozygous Jefferson class, while 9.2% were skewed towards the heterozygous Jefferson/*O. rufipogon* class). The amount of distortion was similar to the wild QTL study between Caiapo and *O. rufipogon*, which had 28% skewed towards the recurrent parent and 8.8% skewed towards the heterozygous class containing *O. rufipogon* alleles (Moncada et al. 2001). The segregation distortion was clustered in eight regions, with extreme skewing towards the heterozygous Jefferson/*O. rufipogon* class apparent only on chromosome 10.

Skewed segregation ratios can result from loci causing gamete competition or the abortion of male or female gametes (Sano 1990; Lyttle 1991), or from selection in the BC_1 population. A comparison of the skewed regions from this study with those seen in previous rice linkage maps revealed that four regions of distortion were shared across studies. These include chromosome 2 near RM300 and RG171 shared with one study (Huang et al. 1997), chromosome 6 near RM276 and RG213 shared with three studies and possibly linked to numerous sterility and gametophyte loci (Harushima et al. 1996; Xu et al. 1997; Doi et al. 1998), chromosome 7 near RM172 and RG351 possibly shared with one study (Xiao et al. 1996), and chromosome 10 near RM184 and CDO98 shared by two studies (Harushima et al. 1996; Huang et al. 1997). In contrast, two other distorted regions, on chromosomes 1 and 4, were not shared across studies but may be explained by selection at QTLs in those regions. The skewed segregation on chromosome 1, near RM104 and RZ801, and on chromosome 4, near RM185 and RZ656, may be explained by selection against *O. rufipogon* alleles at QTLs for plant height that occurred during development of the BC_1 population and shattering which was selected against following the second backcross. In addition, one region, on chromosome 5, was shared by two studies and is potentially linked to the gametophytic gene *ga-15* (t) (Xiao et al. 1996; Huang et al. 1997; Xu et al. 1997), but also could have resulted from selection against the plant height QTL in this region. Lastly, one region, on chromosome 8 near RM337, could not readily be explained by either linkage with sterility or gametophyte loci or with selection against QTLs.

One of the objectives in the present study was to identify trait-enhancing alleles from the wild rice relative *O. rufipogon* for yield and yield components. In this study, the *O. rufipogon* alleles were favorable for 53% of the yield and yield component QTLs, including loci for yield, grains per panicle, panicle length, heading date, and grain weight. This compares to previously reported proportions of favorable *O. rufipogon* alleles of 51% for the V20/Ce64/*O. rufipogon* hybrid testcross population (Xiao et al. 1998) and 56% for the Caiapo/*O. rufipogon* population (Moncada et al. 2001). Of the four yield QTLs identified with an increase in yield from the *O. rufipogon* allele, *yld2.1* and *yld6.1* were not linked to any known negative QTLs and would presumably be directly useful for developing breeding materials. The third, *yld3.2*, is linked to a grain weight QTL where the *O. rufipogon* allele decreases grain weight, (potentially compromising grain quality), while *yld9.1* is linked to a QTL that affects the tiller type and is nearby an *O. rufipogon* QTL decreasing grain weight. For these two loci, the yield QTL may still be useful if negative linkages can be broken, but may not be useful if these effects are due to pleiotropy at a single locus causing an increased number of smaller-sized grains. Additional trait-enhancing QTLs from *O. rufipogon* were detected for yield components: those detected in multiple environments include *dth1.1,dth1.2, dth4.1*, and *dth10.1* providing early heading date and *gw1.1* providing an increase in grain weight. All of these QTLs, however, are also linked to negative *O. rufipogon* QTLs and would require breaking the negative linkage before being used in a breeding program.

With three rice wild QTL studies using the same *O. rufipogon* accession as the donor parent now completed, comparisons can be made as to the effects of wild QTLs in different genetic backgrounds and environments. For yield and yield components, one potential region in common between the wild studies is on the long arm of chromosome 1, where *yld1.1* and *gpl1.1* were detected by Xiao et al. (1998) and Moncada et al. (2001), both of which show increases in yield and grains per plant from *O. rufipogon*. Interestingly, the same region in the current study, at *gpp1.2* and *spp1.2*, shows a decrease in the number of grains per panicle associated with the *O. rufipogon* allele, rather than an increase, possibly indicating a superior Jefferson-derived allele in this cultivated background (Fig. 2, Table 3). In another instance, the *O. rufipogon* allele associated with days to heading, *dth1.1*, at RG532 on the short arm of chromosome 1 from Xiao et al. (1998) increases days to heading, while the *O. rufipogon* allele for *dth1.1* at RG532 provides earliness in three environments for the Jefferson/*O. rufipogon* population (Table 3). These cases point to the possibility of an allelic series, where the same *O. rufipogon* allele is superior to one cultivated allele, but inferior to another one. Alternatively, the different genetic backgrounds may interact with the *O. rufipogon* allele in different ways.

In many other instances, however, the *O. rufipogon* alleles showed the same effects in the different genetic backgrounds and environments between the three pub-

lished rice wild QTL studies. For instance, the *O. rufipogon* allele increased grain number at *gpp8.1* in this study and at *gpl8.2* in Xiao et al. (1998) at RM210 on chromosome 8. For panicle length, four QTLs were in common between the Jefferson and V20/Ce64 populations, all of which showed an increase in panicle length from *O. rufipogon*: *pl1.1* at RZ730 on chromosome 1, *pl4.1* above RZ656 on chromosome 4, *pl9.1* between RZ422 and RG358 on chromosome 9, and *pl12.1* above RG901 on chromosome 12 (Xiao et al. 1998; Fig. 2).

For heading date, the *O. rufipogon* allele increased days to heading at *dth3.1* above RM7 on chromosome 3 in the Caiapo/*O. rufipogon* population as reported by Moncada et al. (2001) as well as in Jefferson/*O. rufipogon* (Fig. 2). Likewise, the *O. rufipogon* allele increased days to heading at *dth7.1* at RG30 on chromosome 7 in both the Caiapo and Jefferson studies (Moncada et al. 2001; Fig. 2). Near RZ500 on chromosome 10, Moncada et al. (2001) reported a sterility QTL, *ste10.2*, which compares to the percent seed set QTL, *pss10.1*, in the Jefferson study, both of which show decreased seed set associated with the *O. rufipogon* allele. In the centromeric region of chromosome 3, near RZ672 and RZ452, both the Jefferson and V20/Ce64 populations have a QTL where the *O. rufipogon* allele decreases grain weight (Xiao et al. 1998; Fig. 2).

For plant height, the *O. rufipogon* allele increased plant height in the region on chromosome 1 near RZ730 and RZ801 for all three studies, and all were of large effect: 44.8% in V20/Ce64/*O. rufipogon*, 21% in Caiapo/*O. rufipogon*, and 33.2% in the present study (Xiao et al. 1998; Moncada et al. 2001; Table 4). In addition, the *O. rufipogon* allele also increased plant height for *ph8.1* at RM210 on chromosome 8 and for *ph12.1* near RG901 on chromosome 12 in both the Jefferson and V20/Ce64 populations (Xiao et al. 1998; Fig. 2). Likewise, a QTL near the end of chromosome 5 was detected in both the Caiapo and Jefferson populations, although the lack of shared markers prevents a precise comparison of QTL location (Moncada et al. 2001). These results confirm the existence of *O. rufipogon*-derived QTLs that are significant in different genetic backgrounds and widely different environments, from a hybrid testcross in an irrigated field environment in China to an inbred cross in an upland environment in Colombia and an inbred cross in an irrigated environment in the Southern United States.

Another objective of the present study was to identify QTLs potentially involved in the domestication process, such as those associated with shattering, grain dormancy, and grain weight, as well as those considered to confer undesirable weedy characteristics in comparison to cultivated varieties, including excessive plant height, awns, and tiller angle. All of the QTLs detected for these traits had the expected wild or weedy effect associated with introgressions from *O. rufipogon* except for three: two QTLs for increased grain weight from *O. rufipogon* (*gw1.1* and *gw5.1*) and a QTL for reduced shattering from *O. rufipogon* (*sh8.1*; Table 4).

Several clusters of linked domestication and weediness QTLs were identified, echoing the previous finding of linked sets of genes conferring the domestication syndrome in common bean (Koinange et al. 1996). First, the region around RZ730 and RZ801 on the long arm of chromosome 1 contained QTLs for plant height and shattering. A second cluster is located on chromosome 4, near RZ656, with QTLs for plant height, shattering, and awns. Of these, two were QTLs of large effects – the plant height QTL *ph1.1* (R^2 = 33.2%) and the QTL for awns, *awn4.1* (R^2 = 27.3%). Although these traits do not seem to be related, it is still possible that a single gene has pleiotropic effects on all three traits. One precedent for this is the *ttg1* mutant in Arabidopsis that affects three seemingly unrelated traits: trichome cell-fate determination, root hair spacing, and anthocyanin secondary metabolism (Walker et al. 1999; Payne et al. 2000). Fine mapping of these clusters would be needed to differentiate between gene linkage and pleiotropy. Four other *O. rufipogon* QTLs for shattering, three QTLs for dormancy, and a QTL of large effect for tiller angle were also detected, but these were not clustered with other domestication or weediness QTLs.

Comparison of these domestication clusters with other QTL studies reveals previously reported QTLs in similar regions. For chromosome 1, two reported QTLs for shattering overlap the *sh1.1* region near RZ801, one from a weedy *japonica* (Bres-Patry et al. 2001) and a shattering-resistant locus induced from an *indica* (Fukuta 1995). Two other QTL studies, both employing *O. rufipogon* as one of the parents, also located shattering QTLs to the long arm of chromosome 1, but these are located slightly above the *sh1.1* region and may not be overlapping (Xiong et al. 1999; Cai and Morishima 2000). In addition, a major gene for shattering, *sh-2*, has previously been mapped to this region (Ogi et al. 1993; Fukuta 1995). In this same region, 11 other QTL studies have located a plant height QTL near RZ730 and RZ801 (Fukuta 1995; Huang et al. 1996; Tan et al. 1996; Wu et al. 1996; Kohn et al. 1997; Zhuang et al. 1997; Xiao et al. 1998; Yan et al. 1998; Xiong et al. 1999; Moncada et al. 2001; E.M. Septiningsih, personal communication). This is the same region that the semi-dwarf gene *sd1* has previously been located (Cho et al. 1994; Monna et al. 2002; Sasaki et al. 2002). For the chromosome 4 region containing *ph4.1, sh4.1*, and *awn4.1*, a major gene for awns, *an-1*, has been reported (Nagao and Takahashi 1963), as well as a QTL for plant height (Huang et al. 1996). Clusters of QTLs for domestication traits were also reported by Cai and Morishima (2002), though there are limited regions shared with the current study, in part because many of the traits examined by Cai and Morishima were not measured in the present study.

Selection for larger grain size is also associated with domestication in most cereals (Harlan et al. 1973). Eight grain weight QTLs were identified in this study, with the dominant *O. rufipogon* allele contributing to smaller grains at six of them (Fig. 2). The wild alleles associated with small grains may have been selected against during the domestication process to produce the heavier grains of the cultivated varieties. The locus with the largest effect,

gw3.1, near the centromere on chromosome 3 (near RZ672), was also detected in the V20/Ce64 population (Xiao et al. 1998). It remains to be seen whether the cultivated allele is similar in both V20, an *indica* variety, and Jefferson, which is a *japonica* variety.

The last objective of this study was to determine the extent of functional conservation of QTLs across rice cultivars and across grass genera. Where QTLs are detected across cultivars, species, and genera, the data provide an additional level of confirmation for the existence of conserved genes controlling the traits of interest. Within *Oryza*, the *O. rufipogon*-derived yield QTL *yld2.1* shares the same region as a yield QTL from a cultivated rice population reported by Lin et al. (1996), while the QTL *yld3.2* is located in the same region as QTLs for grain number and grain weight per panicle from Li et al. (1997). The grains per panicle QTL *gpp4.1* shares the same region as a grains per panicle QTL from Xiao et al. (1995, 1996), as well as a QTL for grain number from Li et al. (1997).

For panicle length, *pl2.1* shares a region with QTLs from Zhuang et al. (1997) and Wu et al. (1996), while *pl9.1* is in the same region as two other *O. rufipogon*-derived panicle length QTLs from Xiao et al. (1998) and Kohn et al. (1997), as well as a QTL from Xiao et al. (1995, 1996). The QTL *gw1.1*, with *O. rufipogon* increasing grain weight, shares a region with grain weight QTLs from Li et al. (1997) and Huang et al. (1997). In addition, three grain weight QTLs with *O. rufipogon* decreasing grain weight also shared regions with previously reported grain weight QTLs: *gw3.1* with Yu et al. (1997), Li et al. (1997), Xiao et al. (1998), and Li et al. (2000); *gw3.2* with Lu et al. (1997), Li et al. (1997), and Moncada et al. (2001); *gw9.1* with Yu et al. (1997) and Bres-Patry et al. (2001).

For days to heading, the *O. rufipogon*-derived QTL for earliness, *dth1.1*, shares a region with *O. rufipogon*-derived QTLs from Kohn et al. (1997), Xiao et al. (1998), and Cai and Morishima (2002), with an *O. glaberrima*-derived QTL from Doi et al. (1998) and with a cultivated QTL from Maheswaran et al. (2000). Two QTLs with *O. rufipogon* providing lateness were also strongly supported by previously reported QTLs: *dth3.1* with *O. rufipogon* QTLs from Xiao et al. (1998) and Moncada et al. (2001), a weedy *japonica* QTL from Bres-Patry et al. (2001), and cultivated QTLs from Xiao et al. (1995, 1996), Li et al. (1995) and Price et al. (1997); while *dth7.1* matches QTLs from Yano et al. (1997), Maheswaran et al. (2000), and Moncada et al. (2001). Lastly, the *O. rufipogon*-derived plant height QTL *ph6.1* matches a QTL from Xiao et al. (1995, 1996), and the QTL *ph8.1* matches QTLs from Xiao et al. (1998) and from Yan et al. (1999).

On the other hand, *O. rufipogon*-derived QTLs that have not been detected in previous QTL studies between *O. sativa* cultivars may indicate potentially novel alleles from *O. rufipogon*. For example, *gpp8.1*, with *O. rufipogon* increasing the number of grains per panicle, shares the same region as the *O. rufipogon*-derived QTL from Xiao et al. (1998), but not with other previously reported QTLs. In addition, *pss3.1* with *O. rufipogon* increasing the percent seed set and the *O. rufipogon*-derived earliness QTL *dth3.3* also did not share regions with any cultivar-derived QTL.

In addition to conservation across *Oryza* cultivars and species, several QTLs for grain weight, plant height, and flowering time were localized in putative homeologous regions in maize, lending credence to the hypothesis of functional conservation of QTLs across the grasses. For example, the *O. rufipogon* grain weight QTL *gw1.1*, flanked on the rice map by RZ444 and CDO394 on the long arm of chromosome 1, shares an inverted homeologous region with maize chromosome 3, flanked by UMC175 and UMC60, and including UMC18a. QTLs for kernel weight in maize in this region on chromosome 3 have been reported by Doebley et al. (1994), Veldbom and Lee (1994), Paterson et al. (1995), and Austin and Lee (1996).

For plant height, the *O. rufipogon* QTL *ph1.2*, mapped in rice near RZ444, RZ538, and CDO251, shares homeologous regions with maize chromosomes 3 (near BNL10.24a and UMC60) and 8 (near NPI268a and CSU38b). Two maize QTLs map to this region on chromosome 3 (Schon et al. 1994; Khairallah et al. 1998), and two other maize QTLs for plant height map to the homeologous region on maize chromosome 8 (Austin and Lee 1996; Khairallah et al. 1998). Lastly, the region containing flowering time QTL *dth3.1*, flanked in rice by CDO20 and CDO1387 and including RZ329, shares a homeologous region with maize chromosome 9, flanked by CSU59a and CSU54b and including NPI209a, BNL14.28a, and BNL5.09a. This region on maize chromosome 9 contains five previously reported QTLs for flowering time (Koester et al. 1993; Veldoom et al. 1994; Ribaut et al. 1996; Khairallah et al. 1998; Austin et al. 2001). Further confirmation of the conservation of QTLs between rice and maize would require further mapping of maize probes and candidate genes in rice and vice versa, and could only be proved once the genes underlying the QTLs were cloned.

The QTLs detected in this study provide a rich source of information about the natural genetic variation underlying the evolution, domestication, and breeding of rice. The fine mapping and cloning of selected *O. rufipogon*-derived QTLs may ultimately provide the means to explore the molecular mechanisms underlying quantitative variation in rice and the grasses.

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References

Alonso-Blanco C, Koornneef M (2000) Naturally occurring variation in *Arabidopsis*: an underexploited resource for plant genetics. Trends Plant Sci 5:22–29

Austin DF, Lee M (1996) Comparative mapping in $F_{2:3}$ and $F_{6:7}$ generations of quantitative trait loci for grain yield and yield components in maize. Theor Appl Genet 92:817–826

Austin DF, Lee M, Veldboom LR (2001) Genetic mapping in maize with hybrid progeny across testers and generations: plant height and flowering. Theor Appl Genet 102:163–176

Basten CJ, Weir BS, Zeng Z-B (1997) QTL CARTOGRAPHER: a reference manual and tutorial for QTL mapping. Department of Statistics, North Carolina State University, Raleigh, N.C.

Beadle GW (1939) Teosinte and the origin of maize. J Hered 30:245–247

Bres-Patry C, Lorieux M, Clement G, Bangratz M, Ghesquiere A (2001) Heredity and genetic mapping of domestication-related traits in a temperate japonica weedy rice. Theor Appl Genet 102:118–126

Cai HW, Morishima H (2000) Genomic regions affecting seed shattering and seed dormancy in rice. Theor Appl Genet 100:840–846

Cai HW, Morishima H (2002) QTL clusters reflect character associations in wild and cultivated rice. Theor Appl Genet 104:1217–1228

Causse MA, Fulton TM, Cho YG, Ahn SN, Chunwongse J, Wu K, Xiao J, Yu Z, Ronald PC, Harrington SE, Second G, McCouch SR, Tanksley SD (1994) Saturated molecular map of the rice genome based on an interspecific backcross population. Genetics 138:1251–1274

Chen X, Temnykh S, Xu Y, Cho YG, McCouch SR (1997) Development of a microsatellite framework map providing genome-wide coverage in rice (*Oryza sativa* L.). Theor Appl Genet 95:553–567

Cho YG, Eun MY, McCouch SR, Cae YA (1994) The semidwarf gene, *sd-1*, of rice (*Oryza sativa* L.): II. molecular mapping and marker-assisted selection. Theor Appl Genet 89:54–59

Churchill GA, Doerge RW (1994) Empirical threshold value for quantitative trait mapping. Genetics 138:963–971

Davis GL, McMullen MD, Baysdorfer C, Musket T, Grant D, Staebell M, Xu G, Polacco M, Koster L, Melia HS, Houchins K, Chao S, Coe EH Jr (1999) A maize map standard with sequenced core markers, grass genome reference points and 932 expressed sequence tagged sites (ESTs) in a 1,736-locus map. Genetics 152:1137–1172

Doebley J, Stec A (1991) Genetic analysis of the morphological differences between maize and teosinte. Genetics 129:285–296

Doebley J, Stec A (1993) Inheritance of the morphological differences between maize and teosinte: comparison of results for two F_2 populations. Genetics 134:559–570

Doebley J, Bacigalupo A, Stec A (1994) Inheritance of kernel weight in two maize-teosinte hybrid populations: implications for crop evolution. J Hered 85:191–195

Doi K, Yoshimura A, Iwata N (1998) RFLP mapping and QTL analysis of heading date and pollen sterility using backcross populations between *Oryza sativa* L. and *Oryza glaberrima* Steud. Breed Sci 48:395–399

Frary A, Nesbitt TC, Frary A, Grandillo S, van der Knaap E, Cong B, Lui J, Meller J, Elber R, Alpert KB, Tanksley SD (2000) *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. Science 289:85–88

Fridman E, Pleban T, Zamir D (2000) A recombination hotspot delimits a wild-species quantitative trait locus for tomato sugar content to 484 bp within an invertase gene. Proc Natl Acad Sci USA 97:4718–4723

Fukuta Y (1995) RFLP Mapping of a shattering-resistance gene in the mutant line, SR-1 induced from an *indica* rice variety, Nanjing 11. Breed Sci 45:15–19

Harlan JR (1976) Genetic resources in wild relatives of crops. Crop Sci 16:329–333

Harlan JR, DeWet JMJ, Price EG (1973) Comparative evolution of cereals. Evolution 27:311–325

Harushima Y, Kurata N, Yano M, Nagamura Y, Sasaki T, Minobe Y, Nakagahra M (1996) Detection of segregation distortion in an *indica-japonica* rice cross using a high-resolution molecular map. Theor Appl Genet 92:145–150

Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush GS, Sasaki T (1998) A high-density rice genetic linkage map with 2,275 markers using a single F_2 population. Genetics 148:479–494

Huang N, Courtois B, Khush GS, Lin H, Wang G, Wu P, Zheng K (1996) Association of quantitative trait loci for plant height with major dwarfing genes in rice. Heredity 77:130–137

Huang N, Parco A, Mew T, Magapantay G, McCouch S, Guiderdoni E, Xu J, Subudhi P, Angelos ER, Khush GS (1997) RFLP mapping of isozymes, RAPD and QTLs for grain shape, brown planthopper resistance in a doubled haploid rice population. Mol Breed 3:105–113

Khairallah MM, Bohn M, Jiang C, Deutsch JA, Jewell DC, Mihm JA, Melchinger AE, Gonzalez DLD, Hoisington DA (1998) Molecular mapping of QTLs for southwestern corn borer resistance, plant height and flowering in tropical maize. Plant Breed 117:309–318

Koester RP, Sisco PH, Stuber CW (1993) Identification of quantitative trait loci controlling days to flowering and plant height in two near isogenic lines of maize. Crop Sci 33:1209–1216

Kohn JR, Leyva N, Dossey R, Sobral B, Morishima H (1997) Quantitative trait locus analysis of trait variation among annual and perennial ecotypes of *Oryza rufipogon*. Int Rice Res Notes 22:4–5

Koinange EMK, Singh SP, Gepts P (1996) Genetic control of the domestication syndrome in common bean. Crop Sci 36:1037–1045

Lander R, Green P, Abrahamson L, Barlow A, Daley M, Lincoln S, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Li JX, Yu SB, Xu CG, Tan YF, Gao YJ, Li XH, Zhang Q (2000) Analyzing quantitative trait loci for yield using a vegetatively replicated F_2 population from a cross between the parents of an elite rice hybrid. Theor Appl Genet 101:248–254

Li Z, Pinson SRM, Stansel JW, Park WD (1995) Identification of quantitative trait loci (QTL) for heading date and plant height in cultivated rice (*Oryza sativa* L.). Theor Appl Genet 91:374–381

Li Z, Pinson SRM, Park WD, Paterson AH, Stansel JW (1997) Epistasis for three grain yield components in rice (*Oryza sativa* L.). Genetics 145:452–465

Lin HX, Qian HR, Zhuang JY, Lu J, Min SK, Xiong ZM (1996) RFLP mapping of QTLs for yield and other related characters in rice. Int Rice Res Notes 21:17–19

Lu C, Shen L, Tan Z, Xu Y, He P, Chen Y, Zhu L (1997) Comparative mapping of QTLs for agronomic traits of rice across environments by using a doubled-haploid population. Theor Appl Genet 94:145–150

Lyttle TW (1991) Segregation distorters. Annu Rev Genet 25:511–557

Maheswaran M, Huang N, Sreerangasamy SR, McCouch SR (2000) Mapping quantitative trait loci associated with days to flowering and photoperiod sensitivity in rice (*Oryza sativa* L.). Mol Breed 6:145–155

Manly KF, Olson JM (1999) Overview of QTL mapping software and introduction to MAP MANAGER QT. Mammalian Genome 10:327–334

McClung AM, Marchetti MA, Webb BD, Bollich CN (1997) Registration of 'Jefferson' Rice. Crop Sci 37:629–630

McCouch SR, Doerge RW (1995) QTL mapping in rice. Trends Genet 11:482–487

McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffman RW, Tanksley SD (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829

McCouch SR, Thomson MJ, Septiningsih EM, Moncada P, Li J, Xiao J, Martinez C, Tohme J, Moelpojawiro S, Yuan LP,

McClung A, Tai T, Guimaraes E, Moon HP, Ahn SN (2001) Wild QTLs for rice improvement. In: Rockwood W (ed) Proceedings of the Chandler symposium: rice research and production in the 21st century, June 15–17, 2000. IRRI, Philippines, pp 151–169

Moncada P, Martinez CP, Borrero J, Chatel M, Gauch H, Guimaraes E, Tohme J, McCouch SR (2001) Quantitative trait loci for yield and yield components in an *Oryza sativa* × *Oryza rufipogon* BC_2F_2 population evaluated in an upland environment. Theor Appl Genet 102:41–52

Monna L, Kitazawa N, Yoshino R, Suzuki J, Masuda H, Maehara Y, Tanji M, Sato M, Nasu S, Minobe Y (2002) Positional cloning of rice semidwarfing gene, *sd-1*: rice "green revolution gene" encodes a mutant enzyme involved in gibberellin synthesis. DNA Res 9:11–17

Nagao S, Takahashi M (1963) Trial construction of twelve linkage groups in Japanese rice. Genetical studies on rice plant. 27. J Fac Agric Hokkaido Univ 53:72–130

Nelson JC (1997) QGENE: software for marker-based genomic analysis and breeding. Mol Breed 3:239–245

Ogi Y, Kato H, Maruyama K, Saito A, Kikuchi F (1993) Identification of RFLP markers closely linked to the semidwarfing gene at the sd-1 locus in rice. Jpn J Breed 43:141–146

Panaud O, Chen X, McCouch SR (1996) Development of microsatellite markers and characterization of simple sequence length polymorphism (SSLP) in rice (*Oryza sativa* L.). Mol Gen Genet 252:597–607

Paterson AH, Lin YR, Li Z, Schertz KF, Doebley JF, Pinson SRM, Liu SC, Stansel JW, Irvine JE (1995) Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. Science 269:1714–1718

Payne CT, Zhang F, Lloyd AM (2000) GL3 encodes a bHLH protein that regulates trichome development in *Arabidopsis* through interaction with GL1 and TTG1. Genetics 156:1349–1362

Price AH, Young EM, Tomos AD (1997) Quantitative trait loci associated with stomatal conductance, leaf rolling and heading date mapped in upland rice (*Oryza sativa*). New Phytol 137:83–91

Ribaut JM, Hoisington DA, Deutsch JA, Jiang C, Gonzalez-de-Leon D (1996) Identification of quantitative trait loci under drought conditions in tropical maize. 1. Flowering parameters and the anthesis-silking interval. Theor Appl Genet 92:905–914

Sano Y (1990) The genic nature of gamete eliminator in rice. Genetics 125:183–191

Sasaki A, Ashikari M, Ueguchi-Tanaka M, Itoh H, Nishimura A, Swapan D, Ishiyama K, Saito T, Kobayashi M, Khush GS, Kitano H, Matsuoka M (2002) A mutant gibberellin synthesis-gene in rice. Nature 416:701–702

Schon CC, Melchinger AE, Boppenmaier J, Brunklaus-Jung E, Herrmann RG, Seitzer JF (1994) RFLP mapping in maize: quantitative trait loci affecting testcross performance of elite European flint lines. Crop Sci 34:378–389

Takahashi Y, Shomura A, Sasaki T, Yano M (2001) *Hd6*, a rice quantitative trait locus involved in photoperiod sensitivity, encodes the alpha subunit of protein kinase CK2. Proc Natl Acad Sci USA 98:7922–7927

Tan Z, Shen L, Kuang H, Lu C, Chen Y, Zhou K, Zhu L (1996) Identification of QTLs for lengths of the top internodes and other traits in rice and analysis of their genetic effects. Acta Genet Sin 23:439–446

Tanksley SD, McCouch SR (1997) Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277:1063–1066

Tanksley SD, Nelson JC (1996) Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. Theor Appl Genet 92:191–203

Temnykh S, Park W, Ayres N, Cartinhour S, Hauck N, Lipovich L, Cho YG, Ishii T, McCouch SR (2000) Mapping and genome organization of microsatellite sequences in rice (*Oryza sativa* L.). Theor Appl Genet 100:697–712

Van Deynze AE, Sorrells ME, Park WD, Ayres NM, Fu HY, Cartinhour SW, Paul E, McCouch SR (1998) Anchor probes for comparative mapping of grass genera. Theor Appl Genet 97:356–369

Veldboom LR, Lee M (1994) Molecular-marker-facilitated studies of morphological traits in maize. II: Determination of QTLs for grain yield and yield components. Theor Appl Genet 89:451–458

Veldboom LR, Lee M, Woodman WL (1994) Molecular marker-facilitated studies in an elite maize population: I. Linkage analysis and determination of QTLs for morphological traits. Theor Appl Genet 88:7–16

Walker AR, Davison PA, Bolognesi WAC, James CM, Srinivasan N, Blundell TL, Esch JJ, Marks DM, Gray JC (1999) The TRANSPARENT TESTA GLABRA1 locus, which regulates trichome differentiation and anthocyanin biosynthesis in *Arabidopsis*, encodes a WD40 repeat protein. Plant Cell 11:1337–1349

Wilson WA, Harrington SE, Woodman WL, Lee M, Sorrells ME, McCouch SR (1999) Inferences on the genome structure of progenitor maize through comparative analysis of rice, maize and the domesticated panicoids. Genetics 153:453–473

Wu P, Zhang G, Huang N (1996) Identification of QTLs controlling quantitative characters in rice using RFLP markers. Euphytica 89:349–354

Xiao J, Li J, Yuan L, Tanksley SD (1995) Dominance is the major genetic basis of heterosis in rice as revealed by QTL analysis using molecular markers. Genetics 140:745–754

Xiao J, Li J, Yuan L, Tanksley SD (1996) Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific cross. Theor Appl Genet 92:230–244

Xiao J, Li J, Grandillo S, Ahn SN, Yuan L, Tanksley SD, McCouch SR (1998) Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon*. Genetics 150:899–909

Xiong LZ, Liu KD, Dai XK, Xu CG, Zhang Q (1999) Identification of genetic factors controlling domestication-related traits of rice using an F_2 population of a cross between *Oryza sativa* and *O. rufipogon*. Theor Appl Genet 98:243–251

Xu Y, Zhu L, Xiao J, Huang N, McCouch SR (1997) Chromosomal regions associated with segregation distortion of molecular markers in F_2, backcross, doubled haploid, and recombinant inbred populations in rice (*Oryza sativa* L.). Mol Gen Genet 253:535–545

Yan J, Zhu J, He C, Benmoussa M, Wu P (1998) Molecular dissection of developmental behavior of plant height in rice (*Oryza sativa* L.). Genetics 150:1257–1265

Yan J, Zhu J, He C, Benmoussa M, Wu P (1999) Molecular marker-assisted dissection of genotype × environment interaction for plant type traits in rice (*Oryza sativa* L.). Crop Sci 39:538–544

Yano M (2001) Genetic and molecular dissection of naturally occurring variation. Curr Opin Plant Biol 4:130–135

Yano M, Sasaki T (1997) Genetic and molecular dissection of quantitative traits in rice. Plant Mol Biol 35:145–153

Yano M, Harushima Y, Nagamura Y, Kurata N, Minobe Y, Sasaki T (1997) Identification of quantitative trait loci controlling heading date in rice using a high-density linkage map. Theor Appl Genet 95:1025–1032

Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y, Sasaki T (2000) *Hd1*, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the *Arabidopsis* flowering time gene *CONSTANS*. Plant Cell 12:2473–2483

Yu SB, Li JX, Xu CG, Tan YF, Gao YJ, Li XH, Zhang Q, Maroof MAS (1997) Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. Proc Natl Acad Sci USA 94:9226–9231

Zeng ZB (1994) Precision mapping of quantitative trait loci. Genetics 136:1457–1468

Zhuang JY, Lin HX, Lu J, Qian HR, Hittalmani S, Huang N, Zheng KL (1997) Analysis of QTL × environment interaction for yield components and plant height in rice. Theor Appl Genet 95:799–808