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Identification of quantitative trait loci for yield and yield components in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*

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Abstract A BC_2F_2 population developed from an interspecific cross between *Oryza sativa* (cv IR64) and *O. rufipogon* (IRGC 105491) was used in an advanced backcross QTL analysis to identify and introduce agronomically useful genes from this wild relative into the cultivated gene pool. The objectives of this study were: (1) to identify putative yield and yield component QTLs that can be useful to improve the elite cultivar IR64; (2) to compare the QTLs within this study with previously reported QTLs in rice as the basis for identifying QTLs that are stable across different environments and genetic backgrounds; and (3) to compare the identified QTLs with previously reported QTLs from maize to examine the degree of QTL conservation across the grass family. Two hundred eighty-five families were evaluated in two field environments in Indonesia, with two replications each, for 12 agronomic traits. A total of 165 markers consisting of 131 SSRs and 34 RFLPs were used to construct the genetic linkage map. By employing interval mapping and composite interval mapping, 42 QTLs were identified. Despite its inferior performance, 33% of the QTL alleles originating from *O. rufipogon* had a beneficial effect for yield and yield components in the IR64 background. Twenty-two QTLs (53.4%) were located in similar regions as previously reported rice QTLs, suggesting the existence of stable QTLs across genetic backgrounds and environments. Twenty QTLs (47.6%) were exclusively detected in this study, uncovering potentially novel alleles from the wild, some of which might improve the performance of the tropical *indica* variety IR64. Additionally, several QTLs for plant height, grain weight, and flowering time detected in this study corresponded to homeologous regions in maize containing previously detected maize QTLs for these traits.

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Introduction

Most agronomically useful traits existing in nature have continuous phenotypic distributions, implying that many genes with relatively minor effects, termed quantitative trait loci (QTLs), control those traits. The identification of QTLs provides the starting point to dissect the molecular basis of natural allelic diversity, which in turn will be very useful for future crop improvement. By doing so, many valuable genes with subtle effects can be identified and characterized. There is a wealth of QTL information available on rice providing excellent targets for future study.

Comparing QTL data across different rice studies, as well as across different grass species, can provide preliminary (or suggestive) information upon which hypotheses can be tested. One hypothesis is that some QTL alleles will be expressed in similar ways across multiple genetic backgrounds, while others will interact with their genetic backgrounds. By comparing the phenotypic performance of lines carrying the same introgres-

sions in a range of different genetic backgrounds, the relationship between QTL expression and genetic background can be examined. If exotic or wild material is used, such comparisons may also be useful to identify novel beneficial alleles that can be added to the cultivated gene pool to widen its genetic base. Comparison among near isogenic lines (NILs) constructed for this purpose will assist in gaining insight into the conservation of gene function. Comparative QTL mapping also offers a powerful way to identify putatively orthologous QTLs across grass species, as in the example of loci affecting seed weight, shattering, short-day flowering time (Paterson et al. 1995), as well as plant height and maturity in rice, sorghum, and maize (Lin et al. 1995). Conservation of QTLs across the grasses provides a wealth of information for future studies into gene evolution in the grass family.

One of the strategies to broaden the genetic diversity of cultivated crops is to identify QTLs associated with beneficial traits such as yield, grain or fruit quality, and disease resistance in interspecific backcross populations involving wild germplasm and elite cultivars (Tanksley and McCouch 1997). Positive alleles from an otherwise undesirable background may be identified and rapidly transferred into elite cultivars, using the advanced backcross QTL strategy (AB-QTL; Tanksley and Nelson 1996). This method has been used in tomato to improve the phenotypes of modern cultivars (Tanskley et al. 1996; Fulton et al. 1997, 2000; Bernacchi et al. 1998). This method has also been applied to rice with promising results where trait-improving QTL alleles from an inferior phenotype, namely the wild rice relative *Oryza rufipogon,* were identified in the backgrounds of the elite Chinese hybrid V20/Ce64 (Xiao et al. 1998), the upland Brazilian rice variety Caiapo (Moncada et al. 2001), and the U.S. tropical *japonica* cultivar Jefferson (Thomson et al. 2003).

We have applied the AB-QTL strategy to improve the elite tropical cultivar IR64 by identifying trait-improving alleles derived from the wild relative *O. rufipogon* (IRGC 105491). We chose IR64, a high-yielding irrigated rice variety developed by the International Rice Research Institute (IRRI), because it is widely planted in our target environment in Indonesia (http://www.irri.org), and throughout the tropics. Following QTL analysis, putative beneficial QTLs can then be targeted for the development of NILs, both for germplasm improvement as well as for fine-mapping and QTL characterization. The results from this study will provide additional data for comparison of QTLs introgressed from the same *O. rufipogon* accession into multiple elite cultivars grown in widely divergent environments (McCouch et al. 2001). These efforts will provide the information and materials needed to continue to make yield improvements in modern cultivars, as well as to better understand the molecular mechanisms underlying quantitative traits.

Materials and methods

Population development

The *O. sativa* ssp. *indica* variety IR64, was used as the female parent in crosses with *O. rufipogon* (IRGC 105491), a wild relative of modern rice originating from Malaysia. The F_1 plants were backcrossed to IR64 as the recurrent parent to develop 200 BC_1F_1 plants. Minimal selection was performed in the BC_1 generation to discard sterile plants or those with weedy characteristics, and 80 BC_1F_1 plants were backcrossed to IR64 to develop BC_2F_1 seeds. Five BC_2F_1 seeds per BC_1F_1 individual were planted to generate a population of 400 individuals. This population was allowed to self, and the resulting BC_2F_2 seeds were harvested from individual BC_2F_1 plants. In the next generation, all 400 BC_2F_2 families were used without selection for phenotyping.

Field trials and trait evaluation

Yield and yield components were evaluated based on the performance of the 400 BC_2F_2 families, with both parents as controls. The population was planted in December 1997 in two different field environments, the Semplak Experiment Station in Bogor and the Sukamandi Research Institute for Rice in Sukamandi, Indonesia. Semplak is located at an elevation of 240 m above sea level, at 116°44′E longitude and 6°40′S latitude, with an average rainfall of 513.4 mm/month and temperature of 27.3°C during the planting season. Sukamandi is located at an elevation of 15 m above sea level, at 107°39′E longitude and 8°20′S latitude, with an average rainfall of 151.8 mm/month and temperature of 27.1°C during the planting season. Both of the fields were irrigated. Each BC_2F_2 family was planted in one plot, the plant spacing was 25 cm between each plant, and plots consisted of 3 rows by 25 plants per row. Randomized complete block design with two replications was used. For subsequent analysis, the two replications were averaged.

Ten plants from each plot were randomly chosen for the evaluation of 12 traits: (1) days to heading (dth), (2) days to maturity (dtm), (3) plant height (ph), (4) panicle length (pl), (5) panicles per plant (ppl), (6) spikelets per panicle (spp), (7) grains per panicle (gpp), (8) percent seed set (pss), (9) spikelets per plant (spl), (10) grains per plant (gpl), (11) 1,000-grain weight (gw), and (12) yield per plant (yld). The traits were measured in similar ways as described by Xiao et al. (1998) and Moncada et al. (2001).

Marker genotype analysis and map construction

Out of 400 families evaluated in the two field environments, 285 BC_2F_2 families were randomly chosen for genotyping. Twenty-five individuals per family were planted in the greenhouse (Ithaca, NY), and leaf tissues were bulked for DNA extraction. Genotyping was primarily performed using SSRs markers, with RFLPs added to fill gaps and to facilitate comparative mapping with previous QTL studies. SSR analysis was as described in Chen et al. (1997), with a slight modification as described in Moncada et al. (2001). Silver staining was performed as described in Panaud et al. (1996). To perform RFLP analysis, DNA was digested with one of the four enzymes (*Eco*RI, *Eco*RV, *Hin*dIII, and *Dra*I), and subjected to Southern-blot analysis as described by McCouch et al. (1988). A total of 165 markers, consisting of 131 SSRs and 34 RFLPs, was used to construct the genotype map using the program MAPMAKER (Lander et al. 1987). SSR markers were ordered along the chromosomes as described in Chen et al. (1997) and Temnykh et al. (2000). Five novel SSR markers were also developed and mapped (Table 1), which were generated from rice genomic sequences from the International Rice Genome Sequencing Project, in order to close the gaps that still remained after using the existing SSR and RFLP markers. The order of the RFLP markers was consistent with that described in Causse et al. (1994). A significance threshold value of LOD >2 was applied to determine whether certain markers would be included in the framework map. However, markers with

Table 1 Marker information for five newly developed SSR markers[a]

No.	Locus	Primer sequence	Size (bp) in Nipponbare	Repeat type and length
1	RM626	CAACCTTGCATGCTGTCTTC TTGGATGGTCATTAGCCTCTG	260	(AAG)12
2	RM627	CGTTTGCGACACCATTACAG ATGCACTGGCGAGGAGATAC	242	(CT)10(T)4(C)2(T)22
3	RM628	GCAGTAGACCTCGTGCTGAA GGCCTCGGTTAATAAACACC	247	(G)5(GA)4(G)2(GA)5CA(CT)2(GT)8
4	RM629	TGAATGCTCGACCACGTAGA GCTGTTAATCAGTACCCTGCAT	146	(GA)16
5	RM630	GAGCCTTTTACGAGACGGATAG GCATGTGATAACCGCGTTG	229	(TA)48(TG)58

[a] Markers were developed based on Nipponbare genomic sequence

LOD values under the threshold, usually being tightly linked with flanking markers, were still positioned on the map to show their approximate position along the chromosomes, and were placed in parentheses. The statistical analysis was done using the 154 framework markers (not including the low-LOD markers in parentheses) with an average marker interval of 14.1 cM, and genome coverage of 96.8% according to Temnykh et al. (2001). To convert the value of recombination frequencies to map distance in centimorgans, the Kosambi mapping function was employed.

Statistical analysis

Genome proportion and length of segment introgression was calculated using the program QGene (Nelson 1997). Segregation ratios for the two genotypic classes (homozygous IR64 or heterozygous IR64/ *O. rufipogon*) were compared with expected Mendelian ratios (3:1), based on a χ^2 test ($P<0.01$) employing QGene. Correlation among the traits was also calculated using QGene, with a significance threshold value of 0.05.

Three different analyses were performed to identify putative QTLs in the BC_2F_2 population. Single point analysis (SPA), interval mapping (IM), and composite interval mapping (CIM) were used to examine the association between phenotype and marker genotype. In our study, by employing SPA and IM with the program QGene, all of the QTLs detected by SPA were identified by IM, though the reverse was not always the case. For this reason, only the results obtained from IM are presented here. The program QTL Cartographer was used in implementing the composite interval mapping (Basten et al. 1997) as described in Moncada et al. (2001). To declare a significant association between a marker locus and a QTL, significance thresholds were determined based on permutation tests at an experiment-wise significance level of 0.05. Based on 10,000 permutations for each trait, the experiment-wise threshold for IM corresponded to an average LOD score value of 2.89, and by conducting 1,000 permutations, the experiment-wise threshold for CIM corresponded to an average LOD score value of 2.95. QTLs detected by either IM or CIM were not always in agreement with each other. The QTLs reported in this study were identified by either or both of the methods. The estimated proportion of phenotypic variance explained (R^2), which shows the relative contribution of a particular locus to a specific trait, and the QTL effect (A), was determined for each QTL based on IM and CIM. Digenic interaction between marker loci for each trait was performed using the two-way interaction analysis from QGene.

Comparative QTL analysis

QTL results in the present study were compared to previously detected rice QTLs for all 12 traits by employing a framework map (S. Harrington, personal communication: http://www.gramene.org) that was constructed from three rice genetic linkage maps: the Cornell RFLP map (Causse et al. 1994), the Japanese Rice Genome Research Program RFLP map (Harushima et al. 1998), and the Cornell SSR map (Temnykh et al. 2000). The QTLs being compared were considered to be potentially homologous if they had a significant overlap.

Comparisons were also made with published maize QTLs, using the rice-maize comparative maps by Wilson et al. (1999) and the rice consensus map (S. Harrington, personal communication) to align the regions. Three traits (plant height, days to flowering, and grain weight) were chosen for further study, as these three were predicted to be parallel traits between rice and maize and would be predicted to share related genetic components. In cases where markers were not shared between Wilson et al. (1999) and the various maize QTL papers, the map of Davis et al. (1999) was used for indirect comparisons.

Results and discussion

Marker polymorphism

The RFLP probe survey detected polymorphism 40% of the time. This was higher than the rate of RFLP polymorphism reported by Xiao et al. (1998), which was 28%, but it was lower than that reported by Moncada et al. (2001), which was 60%. In this study, SSR markers detected polymorphism 62% of the time. This was similar to the SSR polymorphism frequency reported by Xiao et al. (1998), which was 59.6%, but it was significantly lower than the study by Moncada et al. (2001), which was 90%. All three of these studies used the same *O. rufipogon* accession (IRGC 105491) as a donor parent, but different recurrent parents. The study by Xiao et al. (1998) and this study evaluated crosses with *indica* recurrent parents, while Moncada et al. (2001) used a tropical *japonica* variety (Caiapo). In both this study and that by Xiao et al. (1998), the short arm of chromosome 10 had a particularly low level of polymorphism, while this pattern was not observed in the crosses involving *japonica* varieties. These results suggest that this region of the *O. rufipogon* (IRGC 105491) genome is more closely related to the *indica* than the *japonica* subgroup.

Table 2 Phenotype performance of BC_2F_2 population

Trait	Sukamandi			Bogor			*df*	*t*-test
	Data range	Mean	CV	Data range	Mean	CV		
Days to heading (*dth)*	74.0–94.0	82.6	3.36	63.0–91.0	71.7	8.62	568	27.391**
Days to maturity (*dtm*)	93.0–120.0	103.6	2.36	79.0–116.0	96.4	6.42	568	18.231**
Plant height (*ph*)	105.1–172.7	128.0	11.58	102.8–191.6	122.0	13.06	568	4.665**
Panicle length (*pl*)	21.2–26.7	24.1	4.17	18.2–29.4	24.2	6.17	568	0.861[ns]
Panicles per plant (*ppl*)	9.1–18.0	13.2	12.20	5.3–18.6	9.6	18.71	568	25.127**
Spikelets per panicle (*spp*)	59.6–131.6	89.4	14.75	56.3–177.6	117.9	15.63	568	17.963**
Grains per panicle (*gpp*)	17.9–104.8	68.9	19.63	21.4–95.2	62.0	21.01	568	7.654**
Percent seed set (*pss)*	26.1–88.0	76.4	9.16	30.0–76.6	52.7	15.67	568	37.050**
Spikelets per plant (*spl*)	720.7–1,990.2	1,172.2	18.13	449.0–1,836.4	1,129.3	22.27	568	2.201
Grains per plant (*gpl*)	237.0–1,711.1	904.0	23.25	181.4–1,091.9	591.8	25.43	568	20.391**
1,000-grain weight (*gw*)	2.2–3.1	2.6	6.02	2.2–3.1	2.7	5.81	568	3.023*
Yield per plant (*yld*)	6.3–42.9	23.7	22.59	4.8–29.5	15.7	24.81	568	20.487**

[*] Significant at $P<0.01$
[**] Significant at $P<0.001$
[ns] Not significant
[a] All correlations shown are significant at $P<0.05$

Table 3 Trait correlations for yield and yield components[a]

Trait	dth[b]	dtm	ph	pl	ppl	gpp	spp	pss	gpl	spl	gw
dtm	0.931**										
ph	–	–									
pl	0.129	0.13	0.234**								
ppl	–	0.12	–	–							
gpp	0.21**	0.195**	–	0.275**	0.144						
spp	0.208**	0.19**	–	0.265**	–	0.664**					
pss	–	–	–	0.127	–	0.694**	–				
gpl	0.197**	0.203**	–	0.198**	0.589**	0.674**	0.419**	0.536**			
spl	0.185*	0.19**	–	0.159*	0.741**	0.303**	0.579**	–	0.769**		
gw	–	–	0.243**	–	–	–0.212**	–0.128	–0.138	–0.23**	–0.152*	
yld	0.21**	0.213**	–	0.207**	0.583**	0.637**	0.411**	0.505**	0.961**	0.757**	–

[*] Significant at $P<0.01$
[**] Significant at $P<0.001$
[a] All correlations shown are significant at $P<0.05$
[b] Abbreviations: *dth* days to heading, *dtm* days to maturity, *ph* plant height, *pl* panicle length, *ppl* panicles per plant, *gpp* grains per panicle, *spp* spikelets per panicle, *pss* percent seed set, *gpl* grains per plant, *spl* spikelets per plant, *gw* grain weight, *yld* yield

Phenotypic data analysis

The phenotypic data used in the QTL analysis were obtained from two field environments in Bogor and Sukamandi, Indonesia (Table 2). Field data from Bogor, Indonesia were used to measure trait correlations (Table 3). Most of the correlations conformed to expectations, such as the previously known inverse relationship between grain number and grain weight.

Marker segregation

Without selection, the expected genotypic ratio in the BC_2 generation would be 3 to 1 for the homozygous IR64 to heterozygous IR64/*O. rufipogon* genotype classes (or 87.5% IR64 alleles to 12.5% *O. rufipogon* alleles). Out of 154 marker loci, 21.4% (33 markers) were skewed toward one or the other parent: 8.4% (13 markers) showed overrepresentation of IR64 alleles, while 13.0% (20 markers) were skewed toward *O. rufipogon* ($P<0.01$). Some of the distorted markers were randomly distributed along the chromosomes, but most occurred in clusters of at least three adjacent loci, located on chromosomes 2, 5, 6, 7, 9 and 12 (Fig. 1). The skewing toward IR64 was expected, due to the selection carried out in the BC_1 (presumably favoring the cultivated IR64 alleles for reducing shattering, dormancy, and plant height). However, the skewing toward *O. rufipogon* was not expected. The interspecific population may be responsible for linkage drag in some regions, possibly influenced by sterility genes.

Comparison of the distorted regions in the current study with the previous studies revealed several regions in common (Table 4). Some other regions of the chromosomes may have been distorted because of selection imposed upon the BC_1 plants. For instance, a region close to RM315 on the long arm of chromosome 1, distorted toward IR64, can be explained by selection for semidwarf plant height (*sd-1*) and non-shattering (*sh-2*) in this region, while the region on chromosome 4 close to RZ590, may be caused by selection for non-shattering at a major shattering locus (*sh-3*) (Kinoshita, 1995). Because

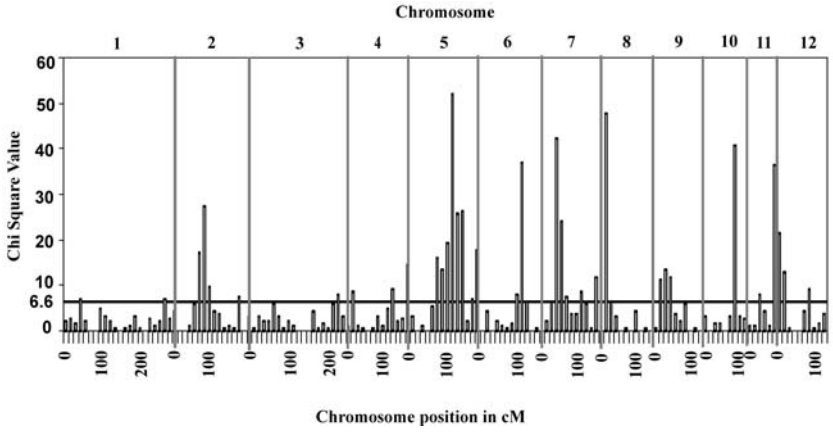

Fig. 1 Segregation distortion detected along the 12 rice chromosomes. The chromosomal position in centimorgans is on the *x-axis*, and chi-square values are on the *y-axis*. A value of χ^2 >6.6 corresponds to $P< 0.01$

Table 4 Comparative study of segregation distortion

Genomic regions	Chr	Previous studies having common distorted regions	Parents	Direction of skewness		Population
				Current study	Previous study	
RG157-RM331	2	Thomson et al. 2003	*Jefferson*[b]/*O. rufipogon*	IR64	Japonica	BC_2F_2
		Huang et al. 1997	IR64/Azucena	–	Japonica	DH
RM516-RM13	5	Huang et al. 1997	IR64/Azucena	*O. rufipogon*	Indica	DH
RM345-RZ405	6	Thomson et al. 2003	Jefferson/*O. rufipogon*	IR64	Japonica	BC_2F_2
RM253-RM314[a]	6	Harushima et al. 1996	Nipponbare/Kasalath	*O. rufipogon*	Indica	F2
		Xu et al. 1997	Zhai-Ye-Qing 8/Jing-Xi 17	–	Japonica	DH
		Doi et al. 1998	Taichung 65/*O. glaberrima*	–	O. glaberrima	BC1F1
		Kinoshita et al. 1995	N/A[c]	–	–	
RM234-RM336	7	Xiao et al. 1996	LH422/9024	*O. rufipogon*	Japonica	RIL
RM264-CDO99	8	Huang et al. 1997	IR64/Azucena	IR64	Indica	DH
RM215-RM257	9	Xiao et al. 1996	LH422/9024	*O. rufipogon*	Indica	RIL

[a] Potential gametophyte and sterility genes are ga-4, ga-5, s-1, or s-8
[b] Skewed towards the underlined parent
[c] Not available

of selection imposed at the BC_1 generation, not all segregating QTLs would be detected in the BC_2F_2 generation, as some *O. rufipogon* introgressions may have been selected against. For example, at marker CDO99 on the long arm of chromosome 8, only 19 (6.6%) of the 285 BC_2F_2 families that were genotyped had *O. rufipogon* alleles. Segregation distortion in this region has been previously reported in an IR64/Azucena population by Huang et al. (1997).

Length of *O. rufipogon* segment introgression and genome proportion

The length of segment introgression from *O. rufipogon* ranged from 2.5 cM to 184.5 cM, with an average introgression size of 36.3 cM (Fig. 2). The proportion of the genome corresponding to *O. rufipogon* introgressions per individual ranged from 0% to 97.8%, with an overall average of 26.2% (Fig. 3). The average was only slightly different from the expected heterozygous portion of an unselected BC_2F_2 population, which would be 25% (12.5% *O. rufipogon* alleles). The ten individuals with extreme proportions of *O. rufipogon* genetic material, near 0% or 100%, may represent parental selfs.

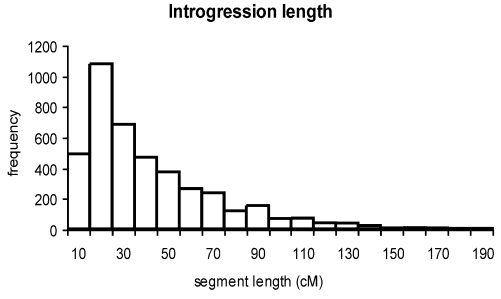

Fig. 2 Numbers of *Oryza rufipogon* introgression segments in given cM length classes across the whole genome and all individuals. Segment length in centimorgans is on the *x-axis*, and the number of introgressions of the given cM length is on the *y-axis*

The average segment length of 36.3 cM for *O. rufipogon* introgressions in the BC_2 population, combined with the number of different introgressions for any specific region, determines the resolution of the QTL analysis. Therefore, for the first stage of QTL analysis,

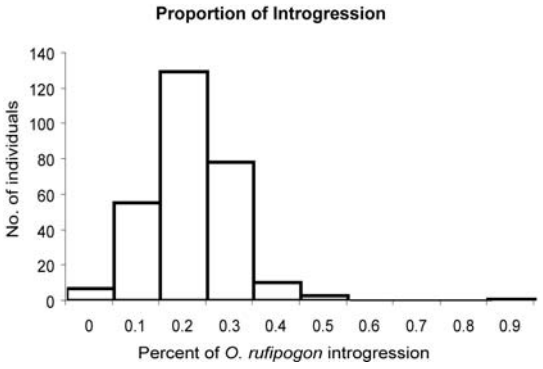

Fig. 3 Proportion of the genome containing *O. rufipogon* introgressions per individual. Genome proportion of *O. rufipogon* genetic material (stated as a percent) is on the *x-axis*, and the number of individuals having a given proportion is on the *y-axis*

the resolution is limited. These large blocks of *O. rufipogon* introgressions also present problems of linkage drag, as negative traits may still be linked to regions containing beneficial QTLs. However, by choosing the smallest available introgressions in target regions as the basis for near-isogenic line (NIL) development, and by selecting for new recombination events in subsequent generations, the introgressions can be shortened and the resolution can be increased for specific QTL targets of interest.

The average genome proportion of 26.2% of *O. rufipogon* genetic material in any single individual accurately reflected the minimal selection imposed in this population. As a whole, this population exhibited most of the characteristics of the wild species in at least some of the individual families. Theoretically, one of the advantages of the AB-QTL strategy is to reduce the donor parent in the progeny. When using wild material with negative characteristics, the smaller genome proportion will limit the negative phenotypes that may otherwise mask positive QTLs from the wild relative. Targeted backcrossing and selection using molecular markers then allows for the rapid development of NILs, after selecting for individuals in the BC_2 population with the smallest amount of *O. rufipogon* introgressions in the background.

QTL analysis

In this study, a total of 47 QTLs were detected using IM and CIM, five of which were detected in both field environments (*ph1.1*, *pl1.1*, *pl3.1*, *spp3.1*, and *gw1.1*), resulting in 42 QTLs with independent positions (Fig. 4, Table 5). IM analysis detected fewer QTLs (29) than CIM (41). Twenty-three QTLs (48.9%) were common for both methods, while six QTLs (12.8%) were exclusively detected by IM, and 18 QTLs (38.3%) were only identified by CIM. Detection of more QTLs using CIM could result from the use of cofactors in CIM that accounted for the variation from the major QTLs, thereby increasing the power of detection of minor QTLs. Different values between QTLs detected by IM and CIM has been previously reported (Moncada et al. 2001). Despite discrepancy between both methods, together they provide hypotheses to be tested in future genetic experiments to confirm the usefulness of the QTLs.

Interaction among QTLs

A test for interactions between marker loci for all traits identified a relatively small number of potential epistatic interactions between loci (Table 6). The small number of identified interactions may be due to the BC_2F_2 population structure, which would limit the number of *O. rufipogon* introgressions per individual and therefore decrease the statistical power available for detecting two-way interactions.

Useful *O. rufipogon*-derived QTLs for yield improvement

Despite its inferior performance, 33% of the QTLs alleles originating from *O. rufipogon* had a beneficial effect for yield and yield components in the IR64 background, increasing panicle length (*pl1.1*, *pl9.1*, *pl10.1*), panicles per plant (*ppl2.1*), percentage of seed set (*pss1.1*), grains per plant (*gpl1.1*), grain weight (*gw1.1*, *gw3.1*, *gw3.2*) and yield (*yld1.1*) while decreasing days to heading (*dth2.1*, *dth11.1*, *dth12.1*) and days to maturity (*dtm4.2*). This was a lower percentage than reported in previous studies using the same donor parent (Xiao et al. 1998, Moncada et al. 2001, and Thomson et al. 2003). In the three previous studies, *O. rufipogon* alleles accounted for 51%, 56%, and 53% of the beneficial alleles, respectively. The smaller percentage in this study may be explained by the higher degree of genetic similarity between IR64 and *O. rufipogon* or the IR64 cultivar may have more favorable alleles than *O. rufipogon* at most of the identified loci, compared to the three other cultivars used in the previous studies. Alternatively, *O. rufipogon* QTLs may interact with the genetic background of IR64 differently than they do with other backgrounds. For the IR64/*O. rufipogon* population, there was no selection at the BC_2 generation, unlike the previous studies using *O. rufipogon* as a donor parent where a second round of selection for return to parental type was imposed (Xiao et al. 1998; Moncada et al. 2001; Thomson et al. 2003). This lower amount of selection may lead to fewer opportunities for positive interaction between *O. rufipogon* and recurrent parent alleles, which is the basis for transgressive segregation.

Despite the late heading date and maturity of *O. rufipogon* compared to IR64, four putative QTLs introgressed from *O. rufipogon* were associated with earliness, located at *dth2.1, dth11.1, dth12.1* and *dtm4.2*. QTL alleles from *O. rufipogon* at *pl1.1*, *pl9.1*, and *pl10.2* conferred an increase in panicle length. In addition, *gw1.1* on chromosome 1 and *gw3.3* and *gw3.2* on chromosome 3 were associated with an increase in grain weight from the *O. rufipogon* introgression. A region at *yld1.1* resulted in

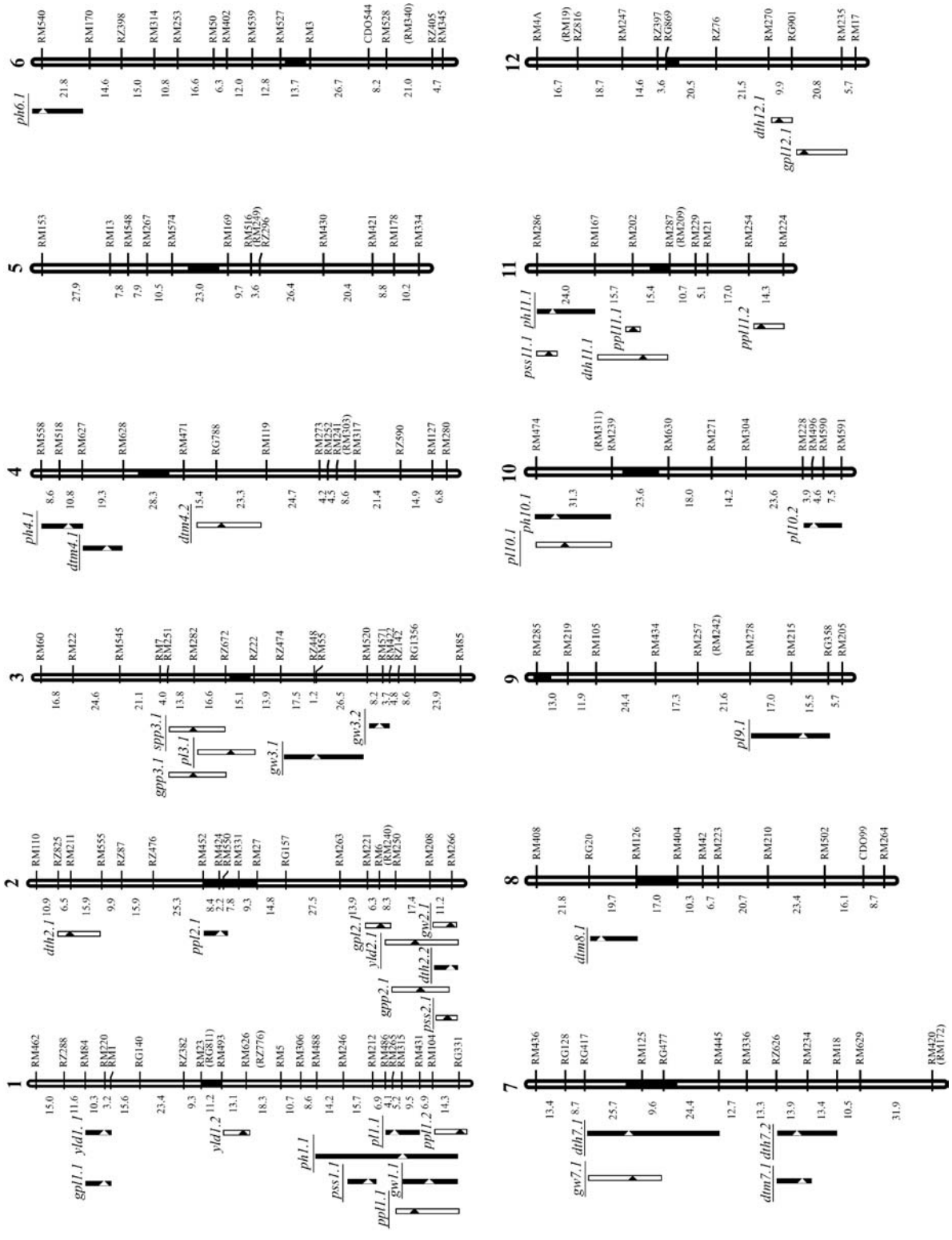

Fig. 4 Molecular linkage map of a BC_2F_2 population derived from a cross between IR64 and *O. rufipogon* along with the positions of QTLs for 12 yield and yield component traits of rice. Centromeres are indicated by *black bars* within each chromosome figure. *Filled black boxes* indicate increased effects from *O. rufipogon* and *white boxes* indicate decreased effects from *O. rufipogon*. The peak of the QTL interval plot is indicated by a *triangle*. The QTL boundaries are defined by the closest flanking markers that reach the empirically determined significance threshold for each trait (P<0.05). *Underlined names* indicate QTLs identified in both environments in this study or QTLs previously identified in other rice QTL studies

Table 5 Yield and yield component QTLs detected in an IR64/ *O. rufipogon* BC_2F_2 population

QTL	Chr	Peak marker	Increased effect	Sukamandi						Bogor					
				IM			CIM			IM			CIM		
				LOD	R^2 (%)	A	LOD	R^2 (%)	A	LOD	R^2 (%)	A	LOD	R^2 (%)	A
Days to heading															
dth2.1	2	RM211	IR64	2.96[a]	4.60	0.75	3.07	4.30	1.31						
dth2.2	2	RM266	*O. rufipogon*	2.90	4.70	–1.47	3.42	4.80	–1.46						
dth7.1	7	RM125	*O. rufipogon*	*2.35*[b]	*3.70*	*–0.92*	4.95[c]	12.20	–2.54						
dth7.2	7	RM234	*O. rufipogon*							*2.77*	*4.40*	*–1.45*	3.04	5.00	–2.86
dth11.1	11	RM202	IR64	3.71	5.80	0.83	4.84	7.10	1.76						
dth12.1	12	RM270	IR64							*2.24*	*3.40*	*1.40*	3.11	5.00	3.15
Days to maturity															
dtm4.1	4	RM627	*O. rufipogon*	*1.85*	*3.00*	*–0.70*	3.26	6.40	–1.16						
dtm4.2	4	RG788	IR64	*1.28*	*1.60*	*0.38*	3.48	6.70	1.25						
dtm7.1	7	RM234	*O. rufipogon*	*2.69*	*4.30*	*–0.75*				3.11	4.90	–1.64	3.46	5.20	–2.90
dtm8.1	8	RG20	*O. rufipogon*	*2.19*	*3.50*	*–0.84*	3.40	7.40	3.65						
Plant height															
ph1.1	1	RM315	*O. rufipogon*	**50.12**[d]	**55.5**	**–14.66**	**64.18**	**73.90**	**–32.09**	**30.22**	**38.60**	**–13.23**	**34.97**	**49.60**	**–29.01**
ph4.1	4	RM518/ RM627	*O. rufipogon*							4.44	6.90	–4.96	6.13	8.10	–8.76
ph6.1	6	RM540	*O. rufipogon*							2.97	4.70	–4.82			
ph10.1	10	RM474	*O. rufipogon*	3.82	6.00	–7.09									
ph11.1	11	RM286	*O. rufipogon*	4.29	6.70	–7.24				**2.13**	**3.40**	**–5.60**			
Panicle length															
pl1.1	1	RM315/ RM265	*O. rufipogon*	*2.71*	*4.30*	*–0.24*	**6.86**	**9.90**	**–0.85**	**4.49**	**7.00**	**–0.50**	**5.63**	**8.70**	**–1.09**
pl3.1	3	RZ672	IR64	*2.29*	*3.60*	*0.23*	5.09	7.60	0.63	*2.31*	*3.70*	*0.36*	**3.46**	**5.30**	**0.78**
pl9.1	9	RM215	*O. rufipogon*							4.07	6.40	–0.44	4.26	7.60	–0.87
pl10.1	10	RM474	IR64	*1.04*	*1.70*	*0.28*	4.21	25.00	1.10						
pl10.2	10	RM496	*O. rufipogon*							3.43	5.40	–0.41			
Panicles/plant															
ppl1.1	1	RM431/ RM315	IR64	6.62	10.10	0.68	6.50	10.10	1.27						
ppl1.2	1	RG331	IR64							*2.66*	*4.40*	*0.71*	3.64	5.60	0.83
ppl2.1	2	RM424	*O. rufipogon*							*2.57*	*4.10*	*–0.46*	3.28	5.00	–0.87
ppl11.1	11	RM202	IR64							2.97	4.70	0.48			
ppl11.2	11	RM254	IR64							2.92	4.60	0.47			
Grains/panicle															
gpp2.1	2	RM208	IR64	3.82	5.20	4.26	3.17	6.10	7.32						
gpp3.1	3	RM282	IR64	3.30	5.20	2.88	4.17	7.10	8.92						
Spikelets/panicle															
spp3.1	3	RM282	IR64	**3.76**	**5.90**	**7.93**	**3.93**	**6.60**	**9.47**	**3.50**	**5.50**	**10.71**	**3.81**	**5.70**	**11.51**
Percent seed set															
pss1.1	1	RM212	*O. rufipogon*							*2.33*	*3.70*	*–1.94*	3.12	5.90	–4.23
pss2.1	2	RM266	IR64	5.28	8.20	2.55	5.94	9.80	4.65						
pss11.1	11	RM286	IR64	*1.56*	*0.80*	*2.01*	2.97	8.30	4.89						
Grains/plant															
gpl1.1	1	RM220	*O. rufipogon*	*1.53*	*2.40*	*–40.43*	3.10	5.00	–117.77						
gpl2.1	2	RM6	IR64	3.04	4.80	56.07	3.12	4.80	104.87						
gpl12.1	12	RG901	IR64							*2.75*	*4.40*	*40.89*	2.96	5.70	85.42
Grain weight															
gw1.1	1	RM431/ RM104	*O. rufipogon*	**3.85**	**6.00**	**–0.05**	**6.72**	**10.30**	**–0.13**	**7.44**	**11.30**	**–0.06**	**7.45**	**11.40**	**–0.12**
gw2.1	2	RM266	IR64	3.05	4.80	0.08	4.25	6.30	0.10						
gw3.1	3	RZ448	*O. rufipogon*							3.14	5.00	–0.04	3.06	5.50	–0.08
gw3.2	3	RM571	*O. rufipogon*							3.11	4.90	–0.04	3.15	4.00	–0.07
gw7.1	7	RM125	IR64							5.20	8.10	0.05	5.55	7.10	0.11

Table 5 (continued)

QTL	Chr	Peak marker	Increased effect	Sukamandi						Bogor					
				IM			CIM			IM			CIM		
				LOD	R^2 (%)	A	LOD	R^2 (%)	A	LOD	R^2 (%)	A	LOD	R^2 (%)	A
Yield/plant															
yld1.1	1	RM220	*O. rufipogon*	*1.87*	*3.00*	*–2.30*	4.16	6.10	–3.18						
yld1.2	1	RM626	IR64	*1.72*	*2.70*	*1.01*	2.96	5.30	2.63						
yld2.1	2	RM208/ RM250	IR64	4.06	6.40	1.72	3.91	7.50	3.23						

[a] QTL detected at an experiment-wise $P<0.05$ (IM LOD>2.89, CIM LOD>2.95) unless otherwise indicated
[b] Italicized LOD scores were just below the experiment-wise significance level for IM but at or above that for CIM
[c] Underlined LOD scores were significant at an experiment-wise $P<0.01$ (IM LOD>3.62, CIM LOD>3.76)
[d] Bold LOD scores were significant in two environments, Bogor and Sukamandi

Table 6 Digenic interactions detected at $P<0.001$ by two-way interaction analysis based on marker genotypes

Trait	Locus 1[a]	Chrom	Locus 2	Chrom	Sukamandi F	Bogor F
Days to maturity (*dtm*)	RM234	7	RM42	8	–	24.68
Plant height (*ph*)	RM431	1	RM315	1	16.05	
			RM591	10	–	17.5
			RM286	11	–	24.64
Panicles per plant (*ppl*)	RM104	1	RM265	1	14.45	–
Percent seed set (*pss*)	RM266	2	RM493	1	13.21	–
			RZ87	2	13.79	–
			RM60	3	23.23	–
			RM445	7	13.88	–
			RM474	10	49.76	–
			RM17	12	13.94	–

[a] If several closely linked markers were significant, the marker with the highest level of significance is shown

an increase in yield and QTLs in other regions, *ppl2.1*, *pss1.1*, and *gpl1.1*, controlled an increase in several yield components: panicle per plant, percentage seed set, and grains per plant, respectively, from *O. rufipogon* introgressions. However, *pl1.1* and *gw1.1* were closely linked with a negative QTL introgressed from *O. rufipogon*, *ph1.1*, which is associated with a large increase in plant height. This effect may be explained by the *sd1* locus. Further QTL characterization, including fine-mapping, is needed to determine if pleiotropy or closely linked QTLs are the cause of these effects. In addition, some of these potentially beneficial QTLs are linked to other QTLs conferring negative grain quality characteristics (Septiningsih et al. 2003b). For example, *pl1.1* is in the same region as a QTL from *O. rufipogon* that increases the proportion of broken grains. Careful selection against these regions will be needed to avoid negative characteristics in the improvement process. If linkage drag can be broken, the positive QTLs from *O. rufipogon* represent potentially useful materials for breeding efforts. In addition, QTLs having small effects can be combined for breeding purposes, and combinations of NILs can be developed to confirm observed QTL × QTL interactions and as the foundation for identifying those that provide beneficial effects. As several potential epistatic interactions were detected in this QTL study (Table 6), NILs with clean background would need to be developed to eliminate negative epistatic effects during variety improvement.

Comparison with other wild QTL studies using the same donor parent

Four parallel rice QTL studies have been performed using the same accession of *O. rufipogon* (IRGC 105491) as a donor parent (McCouch et al. 2001). These studies use different elite varieties as the recurrent parents, including V20A/Ce64, an elite Chinese hybrid variety (Xiao et al. 1998), Caiapo, an upland rice variety from Brazil (Moncada et al. 2001), Jefferson, an elite tropical *japonica* rice variety from the United States (Thomson et al. 2003), and the present study, which used the elite *indica* rice variety IR64. These parallel studies enable comparisons to be made to identify *O. rufipogon*-derived alleles that are expressed across environments and genetic backgrounds (Table 7).

In many instances, the *O. rufipogon* alleles give similar effects in different cultivar backgrounds and environments. In the case of plant height, the *ph1.1* locus was significantly detected in both environments, Sukamandi and Bogor. A QTL in a similar region under the same name was reported in the V20A/Ce64//*O. rufipogon* population (Xiao et al. 1998), and was reported as *ph1.2*

Table 7 Comparison of QTL results across the *Oryza* genus

QTL	Previous studies shared common regions
dth2.2	*dth2.1* (Moncada et al. 2001); *Dtf2a* (Maheswaran et al. 2000)
dth7.1	*dth7.1* (Moncada et al. 2001; Thomson et al. 2003), *Hd-4* (Yano et al. 1997; Yamamoto et al. 1998); *Dtf7b* (Maheswaran et al. 2000)
dth7.2	*dth7.1* (Xiao et al. 1998); *Dtf7b* (Maheswaran et al. 2000)
dtm4.1	*dth4.1* (Thomson et al. 2003); *dth4* (Xiao et al. 1995);
dtm4.2	*dtm4* (Xiao et al. 1995); *Dtf4* (Maheswaran et al. 2000)
dtm7.1	*dtm7.1* (Xiao et al. 1998); *tdm7* (Xiao et al. 1995)
dtm8.1	*hd8* (Xiong et al. 1999); *dtm8* (Xiao et al. 1995, 1996); *Hd5* (Yano et al. 1997; Yamamoto et al. 1998, 2000; Lin et al. 2000); *Qhd8a* (Li et al. 1995)
ph1.1	*ph1.1* (Xiao et al. 1998); *ph1.2* (Moncada et al. 2001; Thomson et al. 2003); *ph1* (Xiong et al. 1999; Kohn et al. 1997; Yan et al. 1998, 1999; Zhuang et al. 1997; Huang et al. 1996; Wu et al. 1996), *sd1*[a] (Cho et al. 1994)
ph4.1	*ph4.1* (Xiao et al. 1998; Thomson et al. 2003); *d-11*[a] (Kinoshita, 1995)
ph6.1	*d-4*[a] (Kinoshita, 1995)
ph11.1	*d-27(d-t)*[a] (Kinoshita, 1995)
pl1.1	*pl1.1* (Xiao et al. 1998; Thomson et al. 2003); *pl1* (Xiong et al. 1999)
pl9.1	*pl9.1* (Xiao et al. 1998; Thomson et al. 2003); Kohn et al. 1997; *pl9* (Xiao et al. 1995, 1996)
pl10.1	*pl10.1* (Thomson et al. 2003)
ppl1.1	*pn1* (Yan et al. 1999); *np1* (Zhuang et al. 1997)
pss1.1	*sf1* (Zhuang et al. 1997; Lin et al. 1996)
pss2.1	*pss2.1* (Xiao et al. 1998)
gw1.1	*gw1.1* (Thomson et al. 2003); *tgwt1a* (Zhuang et al. 1997); *gw-1* (Lu et al. 1997); Paterson et al. 1995
gw2.1	*gw2.1* (Xiao et al. 1998; Thomson et al. 2003)
gw3.1	*gw3a* (Yu et al. 1997)
gw3.2	*gw3.2* (Thomson et al. 2003); *gw3.1* (Moncada et al. 2001); *gw-3* (Lu et al. 1997)
gw7.1	*gw7* (Yu et al. 1997; Li et al. 2000)
yld2.1	*yld2.1* (Xiao et al. 1998)

[a] Major gene

in the Caiapo/*O. rufipogon* and Jefferson/*O. rufipogon* populations (Moncada et al. 2001; Thomson et al. 2003). The position of this QTL coincides with the major gene, *sd1* (Cho et al. 1994). Likewise a QTL similar to *ph4.1* was reported by Xiao et al. (1998) and overlapped with a QTL identified by Thomson et al. (2003). In all of these examples, alleles from *O. rufipogon* increased plant height.

For yield, alleles from *O. rufipogon* increased the percent seed set at *pss1.1*, and the beneficial effect of the wild introgression in this region of chromosome 1 coincided with an increase in grains per plant, *gpl1.1*, and yield, *yld1.1*, in the Caiapo background as reported by Moncada et al. (2001). In these studies, related QTLs, alleles from the wild parent were positively associated with trait improvement. On the other hand, the QTL *yld1.2* was in a position similar to another related yield component, grains per panicle at *gpp1.2*, as reported in the Jefferson/*O. rufipogon* population (Thomson et al. 2003). In both of these studies alleles originating from *O. rufipogon* reduced both yield and grains per panicle. In addition, other QTLs were shared between the present study and one or two of the other *O. rufipogon* studies, including *dth2.2* with the Caiapo/*O. rufipogon* study, *gw1.1* and *pl10.1* with the Jefferson/*O. rufipogon* study, *dtm7.1* and *dth7.2* with the V20A/Ce64 study, *dth7.1* with both the Caiapo and Jefferson studies, and *pl1.1*, *pl9.1* and *gw2.1* with both the V20A/Ce64 and Jefferson studies (Xiao et al. 1998; Moncada et al. 2001; Thomson et al., 2003).

In some instances, *O. rufipogon* alleles seem to behave differently in different genetic backgrounds and environments. For instance, the QTL associated with days to maturity, *dtm4.1* in this study, was in a similar position as the highly correlated QTL for days to heading, *dth4.1* in the Jefferson study (Thomson et al., 2003), but the *O. rufipogon* alleles at *dtm4.1* and *dth4.1* had opposite effects. This may be the result of G X G or G X E interaction, where the same allele has a different effect on the phenotype, depending on the genetic background and environment in which it is evaluated. It will be of interest to eventually identify the specific genes and gene products that interact with each other in this context and the molecular mechanisms that govern that interaction.

A similar situation was observed for QTLs that were clustered at the end of the long arm of chromosome 2, *pss2.1*, *gpl2.1*, and *yld2.1*, where the *O. rufipogon* alleles decreased the trait values in this study, but similar QTLs in the same region, i.e. *pss2.1*, *gpl2.1* and *yld2.1* reported by Xiao et al. (1998) or *gpl2.1* reported by Moncada et al. (2001) showed increased trait values associated with the wild introgressions. This suggests that the *O. rufipogon* alleles associated with the introgressions in this region interact differently in the IR64 background than in the Chinese hybrid or Brazilian upland cultivars.

Lastly, a QTL in a similar position as *gw3.2* in this study was reported under the same name in the Jefferson study, and also identified as *gw3.1* in the Caiapo study (Thomson et al. 2003; Moncada et al. 2001). The allele from the wild parent in the current study increases grain weight, similar to the effect observed by Moncada et al. (2001). However, the wild introgression was associated with a decrease in grain weight in the Jefferson background. It was interesting to note that an introgression from *O. rufipogon* in the same location could be associated with increased grain weight in the tropical *indica* variety, IR64, grown under irrigated conditions and in the tropical *japonica*, Caipo, grown under dry upland conditions, while the opposite effect on grain weight was observed in the tropical *japonica* Jefferson variety, grown under irrigated conditions in a sub-tropical environment. One explanation is that the Jefferson alleles are superior to the *O. rufipogon* alleles in this region, while the IR64 and Caipo alleles are inferior. It is also possible that multiple, closely linked genes are involved, and that there are interactions among several alleles in the introgressed region.

Comparison of QTL results across the *Oryza* genus

While there were only five QTLs (11.9%) at or above the significance threshold for both environments in this study (*ph1.1*, *pl1.1*, *pl3.1*, *spp3.1*, and *gw1.1*), 22 QTLs (53.4%) were located in regions where QTLs for the same traits have previously been reported. Positional coincidence across studies provides support for the validity of a QTL but requires further confirmation. In our study, 20 QTLs (47.6%) were reported for the first time, uncovering the existence of potentially novel alleles.

The results of this study may also be compared with previous work with different accessions of *O. rufipogon*, such as in the study by Kohn et al. (1997), which used annual and perennial types of *O. rufipogon*, and the study by Xiong et al. (1999), where an *O. rufipogon* accession named 'P16' was used. Such comparisons are helpful in determining whether alleles originating from *O. rufipogon* (IRGC 105491) are common among different types of *O. rufipogon*, and interpreting which alleles may be shared between *O. rufipogon* and *O. sativa* cultivars (Table 7). Such ascending levels of comparisons will deepen our understanding of how genes have divergently evolved among different varieties of rice and their ancestors.

Of the six putative QTLs detected for days to heading in this study, the wild alleles prolonged the heading date at three of them and all three had been identified previously (Table 7). It is interesting to note that all three QTLs where the *O. rufipogon* alleles delayed heading in interspecific crosses were also observed in inter-sub-specific (*indica* × *japonica*) crosses. This raises the possibility that many of the alleles discovered in *O. rufipogon* may be the same as those identified in specific cultivars of *O. sativa*. Alternatively, there may be many different alleles that can be distinguished phenotypically from one another in different wild and cultivated accessions of rice.

All four of the QTLs for days to maturity detected in the present study had previously identified counterparts in similar regions of the genome (Table 7). The QTL *dtm4.2* was the only instance where the allele from the wild decreased the number of days for the plants to reach maturity. The position of *dtm8.1* (R^2=7.4%) corresponded to *dtm8* (Xiao et al. 1995, 1996), where it was associated with an R^2 of 73.7%, suggesting that *dtm8* may be a major gene. It is possible that *dtm8.1* is a different, but closely linked gene to *dtm8*, or that it is the same gene, but confers an effect of very different magnitude in different genetic backgrounds.

For all of the QTLs associated with plant height, the wild alleles made the plants taller. Of the five QTLs, only *ph1.1* was significant in both Indonesian environments. It was also detected in many other QTL studies (Table 7). This QTL may be explained by the presence of the major gene *sd1* (Cho et al. 1994). A plant height QTL in chromosome 4, *ph4.1*, was identified in the region corresponding to the dwarfing gene, *d-11* (Kinoshita 1995). Another QTL found on chromosome 6, *ph6.1*, was in a similar region as the dwarfing gene, *d-4* (Kinoshita 1995). Lastly, QTL *ph11.1* was in a similar region to the previously reported dwarfing gene, *d-27(d-t)* (Kinoshita 1995).

Of the five QTLs identified for panicle length, two of the loci, *pl1.1* (in which *O. rufipogon* alleles increased panicle length) and *pl3.1* (in which *O. rufipogon* alleles decreased panicle length), were significant in both Sukamandi and Bogor. There were no previous reports of a QTL in the region containing *pl3.1*, suggesting that the recessive IR64 allele at this locus may be unusual in conferring increased panicle length, compared to other recurrent parents. The large body of evidence supporting the presence of genes associated with panicle length in the similar region as *pl9.1* suggested that in this case there is a predictable effect on phenotype across several different genetic background and environments (Table 7).

Of the five QTLs for panicles per plant, the wild alleles increased the number of panicles per plant at only one locus, *ppl2.1*. This is the first report of a QTL in this region. The QTL *gpp3.1* was located in the same region as the only QTL for spikelets per panicle, *spp3.1*, which was identified in both environments, Bogor and Sukamandi. Both traits were associated with increased numbers of spikelets or grains due to the presence of an IR64 allele at the same peak marker, RM282. A similar situation was observed for panicle length, *pl3.1*, found in a similar region on chromosome 3. There was no evidence of this QTL being previously reported. Again, this raises the possibility of a potentially novel set of alleles in this cultivar, since this QTL is stable in different environments.

A QTL for percentage seed set, *pss1.1*, was identified in a position similar to that of seed fertility, *sf1* (Lin et al. 1996; Zhuang et al. 1997) and also to the correlated traits, grains per plant, *gpl1.1*, and yield, *yld1.1*, reported by

Moncada et al. (2001), where alleles from the wild increased the effects of the traits, consistent with the effect observed in our study. A QTL in a similar region as *pss2.1* was reported by Xiao et al. (1998). In addition, on chomosome 11 there was positional overlap of a QTL for spikelets per plant, *spp11* (Xiao et al. 1995, 1996), grains per plant, *gpp11* and grain yield, *gy11* (Xiao et al. 1995) in the region containing *pss11.1* in our study. It is of interest to determine whether these are all pleiotrophic effects of a common gene or alternatively linked genes in the same region.

Of the three QTLs significantly associated with grains per plant, only at *gpl1.1* did the allele from *O. rufipogon* increase the number of grains per plant, and this QTL has not been previously reported. All of the QTLs for grain weight have potentially orthologous loci identified as QTLs in other studies (Table 7). In the current study, a QTL for yield, *yld1.1* was in the same region as *gpl1.1*, and had the same peak marker, RM220. For both traits, alleles from the wild relative were beneficial, increasing both yield and grains per plant. The QTL *yld1.2* was in a position similar to *gpp1.2* (Thomson et al. 2003), but in this case, alleles originating from *O. rufipogon* reduced the effects of both traits.

Comparison with maize QTLs

In addition to comparison within the *Oryza* genus, comparison was also done for flowering time, plant height, and grain weight QTLs detected in this study with the corresponding traits in previous QTL studies in maize. Here, we report rice QTLs that positionally coincide with two or more maize QTLs. Several QTL regions were shared between the two grass species, supporting the hypothesis of functional conservation of QTLs across grasses. For instance, the flowering time QTL *dth7.1* on rice chromosome 7 shared a previously identified homologous region with maize chromosome 2 (flanked by bnl18.44 and umc36, and near umc64a). There were three maize QTLs for days to flowering reported in this region (Koester et al. 1993; Ribaut et al. 1996; Austin et al. 2001).

For plant height, the QTL *ph1.1* on rice chromosome 1 shared common regions with maize chromosomes 3 (near bnl10.24a and umc60) and 8 (near npi268a and csu38b). The QTLs for plant height located on maize chromosome 3 were reported by Schon et al. (1994) and Khairallah et al. (1998), while those on chromosome 8 were reported by Austin and Lee (1996) and Khairallah et al. (1998). The QTL *ph4.1* on rice chromosome 4 shares homeologous regions with maize chromosome 2 (flanked by umc34 and umc36, or flanked by php10012 and umc98a, and near umc131) and 10 (near umc146 and umc64). The maize QTLs for plant height located on chromosome 2 were reported by Beavis et al. (1994), Austin and Lee (1996), Lubberstedt et al. (1998), and Austin et al. (2001). The QTL on maize chromosome 10 was reported by Lubberstedt et al. (1998). Another QTL, *ph6.1* on rice chromosome 6 corresponded with maize chromosome 9 (on the top of umc153 and near *wx1*). Two maize QTLs were reported in this region (Beavis et al. 1994; Austin et al. 2001).

A grain weight QTL, *gw1.1* on the long arm of rice chromosome 1 shares an inverted homeologous region with maize chromosome 3 (flanked by umc175 and umc18a). Four maize QTLs for kernel weight map to this region (Doebley et al. 1994; Veldboom and Lee 1994; Paterson et al. 1995; Austin and Lee 1996). Lastly, the QTL *gw3.2* on rice chromosome 3 is in a homeologous region with maize chromosome 1 (flanked by umc106 and bnl6.32, near umc161 and bnl8.29). The maize QTLs in this region were reported by two studies (Schon et al. 1994; Jiang et al. 1999). While these positional correspondences are suggestive, further confirmation will be needed to prove the conservation of QTLs between rice and maize by studies of conserved micro-synteny, gene isolation and comparative functional analysis.

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