Analysis of QTLs for yield-related traits in Yuanjiang common wild rice (Oryza rufipogon Griff.)

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Abstract

Using an accession of common wild rice (Oryza rufipogon Griff.) collected from Yuanjiang County, Yunnan Province, China, as the donor and an elite cultivar 93-11, widely used in two-line indica hybrid rice production in China, as the recurrent parent, an advanced backcross populations were developed. Through genotyping of 187 SSR markers and investigation of six yield-related traits of two generations (BC4F2 and BC4F4), a total of 26 QTLs were detected by employing single point analysis and interval mapping in both generations. Of the 26 QTLs, the alleles of 10 (38.5%) QTLs originating from O. rufipogon had shown a beneficial effect for yield-related traits in the 93-11 genetic background. In addition, five QTLs controlling yield and its components were newly identified, indicating that there are potentially novel alleles in Yuanjiang common wild rice. Three regions underlying significant QTLs for several yield-related traits were detected on chromosome 1, 7 and 12. The QTL clusters were founded and corresponding agronomic traits of those QTLs showed highly significant correlation, suggesting the pleiotropism or tight linkage. Fine-mapping and cloning of these yield-related QTLs from wild rice would be helpful to elucidating molecular mechanism of rice domestication and rice breeding in the future.

Keywords: common wild rice; yield-related traits; advanced backcross population; QTL

Introduction

Rice (Oryza sativa L.) is one of the most important food crops in the world, and it is very important to increase the yield through broadening the genetic variation in the modern rice breeding. In the genus of Oryza, there are more than 20 wild species and two cultivated species (Vaughan, 1994), the wild species of rice has been well recognized as a primary gene pool that conserves a lot of specific genes which are presently not available for extinct in the cultivated rice, such as male sterility (Lin and Yuan, 1980) and several resistance genes, for example, resistance to grassy stunt virus from annual wild rice (O. nivara) (Kush et al., 1977), rice bacterial blight resistance gene Xa-21 from O. longistaminata (Kush et al., 1991; Song et al., 1995) and Xa-23 from O. rufipogon (Zhang et al., 2000).

Although wild relatives of crops were important source of genetic variation for cultivated crops ( Tanksley and McCouch, 1997; Zamir, 2001) and it have long been used...
in plant breeding (Harlan, 1976), in rice, some genes for qualitative trait were transferred from wild rice species (Brar and Khush, 1997), but the progress on using of wild *Oryza* species in QTL studies was slower. After advanced backcross QTL (AB-QTL) approach proposed by Tanksley et al. (1996), the QTL studies for mining favorable genes from wild rice species were paid for great attentions. Recently, several studies have been reported to identify and introduce the QTL of yield-related traits enhancing alleles from wild species of rice into high-yielding elite cultivars by AB-QTL approaches (Xiao et al., 1998; Moncada et al., 2001; Li et al., 2002; Thomson et al., 2003; Deng et al., 2004; He et al., 2006; Deng et al., 2007; Tan et al., 2008).

In addition, some QTLs related to rice quality traits were also detected using wild rice introgression lines (Septiningsih et al., 2003b; Hao et al., 2006; Garcia-Oliveira et al., 2009).

In this study, two generations of advanced backcross population (BC4F2 and BC4F4) derived from an accession of common wild rice collected from Yuanjiang County, Yunnan Province of China, as the donor and 93-11 (*O. sativa*), a two-line elite indica restorer, as the recurrent parent, were developed. QTLs for six yield-related traits were analyzed based on the genotype detected by 187 SSR markers and the phenotype data of BC4F2 and BC4F4. The objectives of this study were: 1) detect QTLs for yield-related traits in 93-11 background in the two BC4 generations; 2) compare the QTLs detected in populations between different wild species as donor.

**Materials and methods**

**Population development**

The donor plant, Yuanjiang common wild rice (YJCW, *O. rufipogon* Griff.), C21, was collected from Yuanjiang County, Yunnan Province of China (collected as rhizomes from its original habitat). The habitat of YJCW was well-isolated from cultivated rice up to now. The F1 plants, derived from a cross between YJCWR (as female parent) and 93-11(*O. sativa*), a two-line elite indica restorer, as the recurrent parent, were developed. QTLs for six yield-related traits were analyzed based on the genotype detected by 187 SSR markers and the phenotype data of BC4F2 and BC4F4. The objectives of this study were: 1) detect QTLs for yield-related traits in 93-11 background in the two BC4 generations; 2) compare the QTLs detected in populations between different wild species as donor.

**DNA extraction and SSR analysis**

Fresh leaves of 20 plants from each family of the BC4F2 and BC4F4 generations were bulked and then ground in liquid nitrogen, respectively. DNA was extracted from the ground-tissues by the CTAB method (Rogers et al., 1988). Polymorphic marker survey was conducted using rice simple sequence repeat (SSR) markers (Panaud et al., 1996; Chen et al., 1997; Temnykh et al., 2000; McCouch et al., 2002). A total volume of 25 μL reaction mixture was applied for polymerase chain reaction (PCR), it composed of...
10 ng template DNA, 10 mmol Tris-HCl (pH 9.0),
50 mmol KCl, 1.5 mmol MgCl₂, 0.1% Triton X-100,
2 μmol of each primer, 2.5 mmol/L each of deoxynucleotide triphosphates (dNTP) and 1 unit of Taq DNA poly-
merase (Promega, USA). Amplification was carried out
using following program: the initial denaturing with 94 °C
for 5 min, followed by 35 cycles for 30 s at 94°C, 30 s at
55°C, 1 min at 72°C, with a final extension at 72 °C for
10 min. The PCR products were separated on 8% poly-
acrylamide denaturing gels and the bands were revealed
using the silver-staining protocol as described by Panaud
et al. (1996).

Construction of linkage groups and QTL analysis

The initial linkage map was constructed using the BC₄
mapping algorithm with MapManager QTXb17 (Manly et
al., 2001; http://mapmgr.roswellpark.org/mmQTL.html)
based on the segregation data of 187 SSR marker loci in
BC₄F₂ and BC₄F₄ population. The map’s orders of all 187
SSR markers were followed to the known map information
(Akagi et al., 1996; Chen et al., 1997; Temnykh et al.,
2000; McCouch et al., 2002).

The QTL was detected by single-point analysis (SPA)
and interval mapping (IM) using the software Map-
Manager QTXb17 (Manly et al., 2001). The statistical
thresholds for each trait were calculated based on permuta-
tion tests at an experiment-wise level of P < 0.005. The
experiment-wise threshold corresponded to an average
LOD of 2.06 (SPA) and 2.20 (IM), which was established
by a 10,000 permutation test in 1 cM steps. The proportion
of the observed phenotype variance attributable to a par-
ticular QTL was estimated by the coefficient of determina-
tion (R²) from the corresponding linear model analysis.

Results

Phenotypic evaluation of BC₄F₂ and BC₄F₄ generations

As shown in Table 1, there was a large range of pheno-
typic variation in six yield-related traits in the two popula-
tions (BC₄F₂ and BC₄F₄). Compared with recurrent parent
93-11, positive phenotypic transgressive variation was ob-
served for all traits in two different generations. The trans-
gressive variation suggested positive genotype × genotype
(G × G) variation where O. rufipogon alleles augment per-
formance in a largely 93-11 genetic background. Although
the mean of variation in BC₄F₂ was larger than that in BC₄F₄
in panicles per plant, the mean of variation in BC₄F₄ was
larger than that in BC₄F₂ in all other traits. Maximum varia-
tion was observed for grain yield per plant and grains per
panicle, while 1,000-grain weight had the least.

The correlations of grain yield per plant with all other
five yield components are significant positive (Table 2).
The number of grains per panicle also had strong positive
correlations with spikelets per panicle and percentage seed
set. But the number of panicl es per plant had significant
negative correlations with spikelets per panicle, grains per
panicle and 1,000-grain weight. In addition, there was a
significant negative correlation between panicles per plant
and percentage seed set only in BC₄F₄ population.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Beijing in 2005</th>
<th>Beijing in 2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>93-11</td>
<td>BC₄F₂</td>
</tr>
<tr>
<td>ppl</td>
<td>7.1 ± 2.0</td>
<td>7.8 ± 1.4</td>
</tr>
<tr>
<td>spp</td>
<td>159.8 ± 2.6</td>
<td>142.0 ± 26.2</td>
</tr>
<tr>
<td>gpp</td>
<td>130.4 ± 0.8</td>
<td>97.9 ± 25.0</td>
</tr>
<tr>
<td>pss (%)</td>
<td>81.6 ± 1.5</td>
<td>68.9 ± 12.5</td>
</tr>
<tr>
<td>kgw (g)</td>
<td>27.6 ± 0.3</td>
<td>25.8 ± 2.7</td>
</tr>
<tr>
<td>yld (g)</td>
<td>25.5 ± 0.9</td>
<td>19.5 ± 5.6</td>
</tr>
</tbody>
</table>

*ppl, panicles per plant; spp, spikelets per panicle; gpp, grains per panicle; pss, percentage seed set; kgw, 1,000-grain weight; yld, grain yield per plant.
Table 2
Trait correlations for yield and yield components in BC$_4$F$_2$ and BC$_4$F$_4$ populations $^a$

<table>
<thead>
<tr>
<th>Trait $^b$</th>
<th>ppl</th>
<th>spp</th>
<th>gpp</th>
<th>pss</th>
<th>kgw</th>
</tr>
</thead>
<tbody>
<tr>
<td>spp</td>
<td>$-0.200^{*\ast}$</td>
<td>$-0.229^{*\ast}$</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>$0.702^{*\ast}$</td>
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<tr>
<td>gpp</td>
<td>$-0.176^{*\ast}$</td>
<td></td>
<td>$0.850^{*\ast}$</td>
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<tr>
<td>pss</td>
<td>$-0.276^{*\ast}$</td>
<td>$0.123^{*}$</td>
<td>$0.613^{*\ast}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>kgw</td>
<td>$-0.424^{*\ast}$</td>
<td>$-0.360^{*\ast}$</td>
<td></td>
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<tr>
<td></td>
<td>$0.278^{*\ast}$</td>
<td>$0.486^{*\ast}$</td>
<td>$0.825^{*\ast}$</td>
<td>$0.685^{*\ast}$</td>
<td>$0.177^{*\ast}$</td>
</tr>
<tr>
<td></td>
<td>$0.262^{*\ast}$</td>
<td>$0.609^{*\ast}$</td>
<td>$0.717^{*\ast}$</td>
<td>$0.457^{*\ast}$</td>
<td>$0.251^{*\ast}$</td>
</tr>
</tbody>
</table>

$^a$ Significant at $P < 0.001$; $^{*\ast}$ Significant at $P < 0.0001$. $^b$ All correlations shown are significant at $P < 0.005$. ppl, panicles per plant; spp, spikelets per panicle; gpp, grains per panicle; pss, percentage seed set; kgw, 1,000-grain weight; yld, grain yield per plant. $^c$ The value of each row is the correlation coefficient in BC$_4$F$_2$ population. $^d$ The value of each row is the correlation coefficient in BC$_4$F$_4$ population.

QTL analysis

Significant QTLs were identified for six yield-related traits as summarized in Table 3. A total of 26 QTLs were detected commonly in two different generations at $P < 0.005$ (SPA LOD > 2.06, IM LOD > 2.20). Of the 26 QTLs, the alleles of 10 (38.5%) QTLs originating from O. rufipogon had a beneficial effect for yield-related traits in the 93-11 genetic background (Table 3).

Panicles per plant

Five QTLs for panicles per plant were located on 5 chromosomes in both generations. The phenotypic variance explained by these 5 individual QTL varied from 3% to 7%. The O. rufipogon-derived alleles all increased panicles per plant in the 93-11 background. Of the five QTLs, four loci were significant at $P > 0.001$ level in two generations. The largest QTL (pp1.1) influenced panicle number per plant was located on the near of marker RM6574 of the short arm of chromosome 7, with an $R^2 > 5\%$ in both generations.

Spikelets per panicle

For spikelets per panicle, three QTLs were identified in both BC$_4$F$_2$ and BC$_4$F$_4$ generations, and one QTL, spp3.1, located on the short arm of chromosome 3, the O. rufipogon alleles contributed an increasing effect on spikelets per panicle.

Grains per panicle

Four QTLs for grains per panicle were detected at both generations. The O. rufipogon-derived alleles at gpp1.1, gpp3.1 were associated with increased grains per panicle, while the alleles from O. rufipogon at the other two loci decreased grains per panicle. Of the positive QTLs, gpp3.1, near the marker RM231 on chromosome 3 displayed 2% and 3% phenotypic variance, and the O. rufipogon-derived allele at gpp3.1 could increase 10.15/10.87 and 11.57/9.56 grains per panicle at the BC$_4$F$_2$ and BC$_4$F$_4$ generations, respectively. Moreover, the positive QTL for spikelets per panicle, spp3.1, was co-localized on the same region. Another positive QTL, gpp1.1, near the maker RM104 on the short arm of chromosome 1 also explained 4% phenotypic variance in both generations, and the O. rufipogon-derived allele increased 11.90/12.78 and 10.07/12.29 grains per panicle, respectively. This locus was close to sd1 locus and the allele from O. rufipogon increased plant height in both generations (data not shown).

1,000-grain weight

Nine QTLs for 1,000-grain weight were detected in both generations. Of the nine QTLs, a positive QTL, kgw1.2 was located on chromosome 1, and the QTL, kgw2.1, with largest LOD value detected in both generations, explaining 9% and 6% of total variance, respectively, but the allele from O. rufipogon decreased 1,000-grain weight in the 93-11 genetic background.

Percentage seed set

Only one QTL, pss12.1, was detected in both generations, with 4% and 6% variance explained, respectively, and the allele from O. rufipogon decreased percentage seed sets in the 93-11 genetic background.
### Table 3
Quantitative trait loci (QTLs) for yield-related traits detected commonly in both BC4F2 and BC4F4 generations

<table>
<thead>
<tr>
<th>Trait</th>
<th>Locus</th>
<th>Chr.</th>
<th>Peak marker</th>
<th>SPA LOG PV(%)</th>
<th>Add</th>
<th>IM LOG PV(%)</th>
<th>Add</th>
<th>SPA LOG PV(%)</th>
<th>Add</th>
<th>IM LOG PV(%)</th>
<th>Add</th>
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<td></td>
<td></td>
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<td></td>
<td>SPA</td>
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<td>IM</td>
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<td>SPA</td>
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<td>IM</td>
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<td>LOG PV(%)</td>
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<td>LOG PV(%)</td>
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<td>LOG PV(%)</td>
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<td>Panicle per plant</td>
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<tr>
<td>ppl1.1</td>
<td>1</td>
<td>RM490</td>
<td>RM490-RM1201</td>
<td>2.34</td>
<td>3</td>
<td>0.48</td>
<td>2.61</td>
<td>0.86</td>
<td>3.35</td>
<td>0.43</td>
<td>4.61</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>RM262</td>
<td>RM341-RM3874</td>
<td>4.11</td>
<td>5</td>
<td>0.80</td>
<td>2.44</td>
<td>0.75</td>
<td>3.14</td>
<td>0.45</td>
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<td>Spikelets per panicle</td>
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<td>spp1.1</td>
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<td></td>
<td>3</td>
<td>RM231</td>
<td>RM22-RM231</td>
<td>1.90</td>
<td>2</td>
<td>10.81</td>
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<td>12.46</td>
<td>2.27</td>
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<td>-1.71</td>
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<td>Percentage seed set</td>
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<td>pss12.1</td>
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<td>2.43</td>
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<td>2.20</td>
<td>1.44</td>
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<td>2.39</td>
<td>-4.28</td>
<td>2.26</td>
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</tbody>
</table>

* QTL detected at an experiment-wise $P < 0.005$ (SPA LOD > 2.06, IM LOD > 2.20) unless otherwise indicated. * Bold LOD scores were significant at an experiment-wise $P < 0.001$ (SPA LOD > 2.78, IM LOD > 3.34). * Underlined LOD scores were significant in two generations, BC4F2 and BC4F4. * Italized LOD scores were just below the experiment-wise significance level for SPA but at or above that for IM.
Grain yield per plant

Four QTLs for grain yield per plant were identified in both generations. At one QTL, yld1.1, near the maker RM104 on chromosome 1, the O. rufipogon-derived alleles can increase grain yield per plant in the 93-11 background, with the additive effect of 2.43/3.15 g and 1.44/1.99 g in two generations, respectively.

Comparison with other QTL studies across the O. rufipogon

The results of QTL analysis using the accession of O. rufipogon (IRGC 105491) as a donor parent and four different elite cultivar varieties as the recurrent parents have been compared by Septiningsih et al. (2003a), who indicated that some of QTLs exhibited same effects in different genetic backgrounds and environments while other QTLs were not. Our study supported this viewpoint by comparing to the results of Tan et al. (2007) using another plant of the wild rice from the same habitat as the donor in the indica cultivar Teqing background. In this study, a total of eight (30.8%) QTLs were also detected in the study of Tan et al. (2007), for example, the kgw4.1 locus was detected in both generations in this study, and qKGW4 in the similar region was reported by Tan et al. (2007), and the QTL of O. rufipogon-derived alleles decreased 1,000-grain weight in both different genetic backgrounds. In addition, other six QTLs related to panicles per plant (ppl2.1 and ppl7.1), spikelets per panicle (spp7.1), grains per panicle (gpp3.1 and gpp7.1) and 1,000-grain weight (kgw7.1) were also mapped on the similar regions of chromosomes and showed similar effects in the two different backgrounds. Otherwise, one QTL for grain yield per plant (yld1.1) was mapped on the similar regions of chromosomes and but showed effect contrarily in two different backgrounds. Other 18 (69.2%) of 26 QTLs identified in this study were not detected in the study of Tan et al. (2007) (Table 4).

Table 4
Comparison of QTLs with other studies of wild rice

<table>
<thead>
<tr>
<th>Chr. Marker interval</th>
<th>QTLs in this study</th>
<th>QTLs identified in O. rufipogon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spy, IM b, ANOVA</td>
<td></td>
</tr>
<tr>
<td>1 RM1-RM243</td>
<td>ppl1.1, kgw1.1</td>
<td>qPN1-1, qGWP1</td>
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<tr>
<td>RM5-RM1232</td>
<td>kgw1.2</td>
<td></td>
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<tr>
<td>RM1183-RM5362</td>
<td>spp1.1, ppl1.1, yld1.1</td>
<td>qPN7-1</td>
</tr>
<tr>
<td>2 RM341-RM6318</td>
<td>ppl2.1, kgw2.1</td>
<td>np2.2, gw2.2, qPPL2</td>
</tr>
<tr>
<td>3 RM22-RM251</td>
<td>spp3.1, gpp3.1</td>
<td>qGP3</td>
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<tr>
<td>RM282-RM16</td>
<td>kgw3.1</td>
<td>gw3.1, gqGW3-3</td>
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<tr>
<td>RM55-RM1352</td>
<td>gw3.2</td>
<td>gw3.2</td>
</tr>
<tr>
<td>4 RM303-RM348</td>
<td>kgw4.1</td>
<td></td>
</tr>
<tr>
<td>7 RM4098-RM1135</td>
<td>ppl7.1, spp7.1, gpp7.1, kgw7.1</td>
<td>qPN7-1</td>
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<td>8 RM210-RM447</td>
<td>yld8.1</td>
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<td>11 RM6335-RM332</td>
<td>kgw11.1</td>
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<tr>
<td>RM21-RM254</td>
<td>ppl11.1, kgw11.2</td>
<td>qPN11-1</td>
</tr>
<tr>
<td>12 RM7003-RM277</td>
<td>gpp12.1, ppl12.1, yld12.1</td>
<td>qFG12-2</td>
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</table>

*Underlined QTLs indicate the previous QTLs reported showing same effects with the QTLs detected in this study, while QTLs in bold were opposite effects. *QTL mapping method: SPA, single-point analysis; IM, interval mapping; CIM, composite interval mapping; ANOVA standard analysis of variance. *The origin of O. rufipogon.
These parallel studies enable comparisons to be made to identify O. rufipogon-derived alleles that are expressed by G × G or G × E interaction in different environments and genetic backgrounds. In this study, we also compared the results with those previously reported by other researchers on similar traits in different cross combinations and different environments. It is possible to compare the accessions from different regions, with C21 used in this study, including C4, a different plant collected from same site with C21 (Tan et al., 2007, 2008), IRGC 105491 (Xiao et al., 1998; Moncada et al., 2001; Septiningsih et al., 2003a; Thomson et al., 2003), 94W1, a Dongxiang wild rice strain of China, (Li et al., 2002), and IC22015 from India (Marri et al., 2005). As the results, 13 of 26 QTLs for yield-related traits identified in this study have been reported and mapped on the similar regions of chromosomes and expressed similarly in indica or japonica background (Table 4). These alleles with similar effect from wild rice of the different types or different regions imply that parallel variance might have occurred during rice domestication. In addition, eight of 26 QTLs for yield-related traits were detected in the similar chromosomal regions of different types of wild rice, but the genetic effects are completely different. Interestingly, all nine QTLs for 1,000-grain weight were identified in similar chromosome regions of different types of wild rice, of them, seven QTLs showed similar effects in indica or japonica background, while other two QTLs, kgw11.1 and kgw11.2, the genetic effects are opposite with QTLs detected in other O. rufipogon strains. This fact may suggest that the same O. rufipogon allele is superior to one cultivated allele, but inferior to another one, on the other word, the different genetic backgrounds may interact with the O. rufipogon allele in two different ways.

Genomic regions of genes or QTL clusters

Three regions with several significant QTLs for yield-related traits were detected on chromosome 1 (RM212-RM5362), 7 (RM125-RM1135) and 12 (RM7003-RM277). Of the three clusters of QTL, three QTLs including spikelets per panicle, grains per panicle and grain weight per plant were detected at the region flanking RM212 and RM5362 on the long arm of chromosome 1, and three QTLs including spikelets per panicle and grains per panicle detected at the region flanking the markers RM125-RM1135 on short arm of chromosome 7, three QTLs decreasing grains per panicle, percentage seed set and grains yield per plant were involved in the region flanking the marker RM7003 and RM277 on middle part of chromosome 12.

Discussion

Favorable O. rufipogon-derived QTLs for yield improvement

Common wild rice (O. rufipogon) is the wild ancestor of cultivated rice (Second, 1982; Oka, 1988; Wang et al., 1992). During the course of domestication from wild rice to cultivated rice, only 60% of the numbers of alleles of wild rice were remained in cultivated rice (Sun et al., 2001). To broaden the genetic variation and overcome the yield plateaus, exploitation and utilization of the favorable alleles of wild rice which have been lost or weakened in cultivated rice has become more important and urgent in modern breeding programs. Until now, a number of positive QTLs for yield and its components were identified from low-yielding common wild rice strains collected from Malaysia and China (Xiao et al., 1996, 1998; Moncada et al., 2001; Li et al., 2002; Thomson et al., 2003; Septiningsih et al., 2003a; Tian et al., 2006; Tan et al., 2008), and positive QTLs have been fine mapped (He et al., 2006).

In this study, we used Yuanjiang common wild rice, C21, a different plant from report of Tan et al. (2007, 2008), and 26 putative QTLs affecting six yield-related traits were detected in both two different generations of BC2F2 and BC3F2. Of these QTLs, the alleles of 10 (38.5%) QTLs originating from O. rufipogon had a positive effect for yield and its components in the 93-11 background. The percentage of favorable alleles from wild rice was lower than that reported in previous studies in which O. rufipogon alleles accounted for 51%, 56% and 53% of the beneficial alleles, respectively (Xiao et al., 1998; Moncada et al., 2001; and Thomson et al., 2003), and similar to that reported with beneficial QTLs detected using a BC3F2 population derived from another accession of Yuanjiang common wild rice, C4, in the indica cultivar Teqing genetic background (40.5%; Tan et al., 2008) and that reported the beneficial QTLs identified using a BC2 population derived from the indica variety IR64 and O. rufipogon...
shown), and this effect may be explained by the QTL linked with a negative QTL increase plant height (data not shown). In addition, other potentially useful materials for breeding efforts on condition that the disadvantage linkage drag could be broken through careful selection in the improvement. In this study, five (19.2%) out of 26 QTLs for yield-related traits were reported for the first time, indicating potentially novel alleles from Yuanjiang common wild rice (Table 4). Of the five QTLs, two of the alleles derived from YJCWR showed positive effects. For instance, the positive QTLs (ssp3.1, gpp3.1) for spikelets per panicle and grains per panicle were mapped near the SSR marker RM231 on the short arm of chromosome 3. It is suggested that the wild rice from different regions might carry different alleles in yield-related traits. It will be of great interest to identify the specific genes in the different types of wild rice and explore their molecular mechanisms during rice evolution through fine-mapping and positional cloning.

Ragot et al. (1995) and Tanksley et al. (1996) have reported that wild-QTL alleles that are favorable for some traits are often associated with deleterious effects on other traits. The positive QTLs from O. rufipogon represent potentially useful materials for breeding efforts on condition that the disadvantage linkage drag could be broken through careful selection in the improvement. In this study, O. rufipogon alleles at ppl2.1 and ppl11.1 contributed positively to panicle per plant, but decreasing the 1,000-grain weight (Fig. 1 and Table 3). In addition, other potentially beneficial QTLs of yield-related traits are also linked to the QTLs conferring negative traits, for example, gpp1.1 and ydl1.1 which have increasing effect were closely linked with a negative QTL increase plant height (data not shown), and this effect may be explained by the QTL closely linked to sd1 locus (Cho et al., 1994).

Genomic regions of genes or QTL clusters as genomic hotspots

Recently, the observation of clustering of functionally related genes has been of great interest in many species. For example, Cai et al. (2002) reported that QTLs for domestication-related traits of rice tended to be clustered on particular regions of chromosomes 3, 6, 8, 9, 11 and 12. Thomson et al. (2003) found morphological traits related to the domestication process and/or weedy characteristics, including plant height, shattering, tiller type and awns, clustered on chromosomes 1 and 4. In addition, using annual type of O. rufipogon also called as O. nivara, Li et al. (2006) that the most striking co-localization was located on chromosome 7 for five of six morphological traits and chromosome 4 that positively affects all seven morphological traits except taller number. The cluster distribution was also founded in yield-related traits, for instance, Brondani et al. (2002) detected that specific marker regions strongly associated with more than one trait were observed for yield-related traits including panicle number, spikelets per panicle, percentage of filled grains per panicle, 100-grain weight, grain yield per plant, filled grain number per panicle and grain yield per panicle.

QTL for significantly correlated traits usually had same chromosome location (Brondani et al., 2002; Hittalmani et al., 2003; Tian et al., 2006). In this study, the yield-related QTLs were detected at same regions on chromosome 1 (RM212-RM5362), 7 (RM125-RM1135) and 12 (RM7003-RM277). Of the three clusters of QTL, one of the most interesting region flanked RM212 and RM5362 on the long arm of chromosome 1, in this region, the QTL cluster was also found in the three of four populations constructed using the accession of O. rufipogon (IRGC 105491) as a donor parent in different indica or japonica backgrounds and environments (Xiao et al., 1998; Septiningsih et al., 2003a; Thomson et al., 2003). Although the cytoplasm of our population and that of Moncada et al. (2001) were both from the wild rice, above QTL cluster on chromosome 1 was not founded in the latter population. The congruence of the QTLs on the chromosome for various traits may be due to either linkage of genes or pleiotropism of a single locus. Although it is not possible to make conclusions about pleiotropy or gene linkage in these QTL regions now, with the developing of molecular marker technology and the complete sequencing of the rice genome, it could be concentrated on such regions to identify and to clone putative
Fig. 1. Molecular linkage map with positions of QTL for six yield and its components in both generations of BC$_1$F$_2$ and BC$_5$F$_6$. 
genes or QTLs that control those traits by developing further generations of near-isogenic lines containing finely mapped QTL. It will be helpful to identify close relationships and discern between pleiotropy and tight linkage or overlapping genes.

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References


