Mining Applicable Elite Alleles of Growth Duration, Plant Height and Panicle Number per Plant by Conditional QTL Mapping in Japonica Rice

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Abstract: Unconditional and conditional QTL mapping were conducted for growth duration (GD), plant height (PH) and effective panicle number per plant (PN) using a recombinant inbred line (RIL) population derived from a cross between two japonica rice varieties Xiushui 79 and C Bao. The RIL population consisted of 254 lines was planted in two environments, Nanjing and Sihong, Jiangsu Province, China. Results showed that additive effects were major in all of QTLs for GD, PH and PN detected by the two methods, and the epistatic effects explained a small proportion of phenotypic variation. No interactions were detected between additive QTL and environment, and between epistatic QTL pairs and environment. After growth duration was adjusted to an identical level, RM80-160bp was detected as an applicable elite allele for PN, with an additive effect of 0.71. When effective panicle number per plant was adjusted to an identical level, RM448-240bp was detected as an applicable elite allele for GD, with an additive effect of 4.64. After plant height was adjusted to an identical level, RM80-160bp was detected as an applicable elite allele for PN, with an additive effect of 0.62, and RM448-240bp was detected as an applicable elite allele for GD, with an additive effect of 3.89. These applicable elite alleles could be used to improve target traits without influencing the other two traits.

Key words: japonica rice; growth duration; plant height; effective panicle number per plant; unconditional QTL mapping; conditional QTL mapping; recombinant inbred line

After more than 40 years studies on japonica hybrid rice in China, the area of japonica hybrids planted annually is 8 280 000 hm², less than 6% of the total area of japonica rice (Deng et al, 2006; Tang et al, 2008). There are two critical reasons for the slow development of japonica hybrid rice. One is the narrow adaptive ability of a single hybrid (Tang et al, 2008), and the other is the indistinctive competition heterosis of hybrids compared with standard pure line cultivars, due to less effective panicle number per plant (Li and Hong, 2004 and 2005; Jin et al, 2005), despite of large panicle and more number of spikelets per panicle (Hua et al, 2007) in hybrids. In general, more spikelet number per panicle was negatively correlated with effective panicle number per plant (Xu et al, 2005), and grain yield per unit area was positively correlated with growth duration (Su et al, 2003). DNA molecular basis of the complicated relationship has been analyzed by large number of QTL mapping research (Li et al, 1995 and 2000; Lin et al, 1998; Maheswaran et al, 2000; Cao et al, 2001; Xing et al, 2001; Kennard et al, 2002; Yuan et al, 2003). However, most of these studies did not consider the influence of other traits on the QTL for the target trait. Therefore, the elite alleles identified by above studies may not be applicable to genetic improvement, especially elite alleles of target trait detected in genetic segregating populations derived from indica-japonica crosses. It is difficult to get expected results when elite alleles were introduced into the materials to be improved, due to the influence of the loci for plant height and growth duration, etc. To mine applicable elite alleles for adaptive ability and the related trait of effective panicle number per plant, unconditional QTL mapping and conditional QTL mapping for the traits of growth duration, plant height and effective panicle number per plant were conducted in two growth environments by using a recombinant inbred line (RIL) population.

MATERIALS AND METHODS

Rice materials

The population in this study consisted of 254 RILs
(F1:12) was derived from a cross between two rice materials Xiushui 79 (japonica cultivar) and C Bao (japonica restorer line) by single-seed descend. The female parent, Xiushui 79, was bred by Jiaxing Institute of Agricultural Sciences, Zhejiang Province, China, and the male parent, C Bao, was bred by Anhui Academy of Agricultural Sciences, Anhui Province, China.

**Field experiments**

In 2009, the RILs and the two parents were grown in paddy fields at the Jiangpu Experimental Station, Nanjing Agricultural University (E1) and Foundation Seed Production Farm in Sihong County in Jiangsu Province (E2), China, respectively. E1, located in the northern bank of the Yangtze River (118°35′ E and 32°05′ N). The soil in E1 is very sticky when it is wet and becomes very hard when it is dried, classified into the paste and heavy-bodied soil type. During the rice-growing season, sunshine is sufficient. The germinated seeds retention water is poor. During the rice-growing season, sunshine is sufficient. The germinated seeds were sown in a seedling bed on 8 May, 2009 in E1 and 10 May, 2009 in E2, respectively. Seedlings of 35-day-old were transplanted to a paddy field, with a single plant per hill. In each environment, the parents and RILs were planted in two replications and each line was planted in three rows with seven seedlings per row, in a density of 17 cm × 25 cm. Regular field management was carried out.

**Phenotypic measurements**

Growth duration (GD), plant height (PH) and effective panicle number per plant (PN) were recorded in five central plants in the second lines. GD means the days from sowing to heading, and the heading date was recorded as the first panicle emerged 1 cm from the flag leaf collar in the selected individual plant. PH was the distance between the soil surface and the tip of the highest panicle (exclude awns). A panicle with at least five filled grains was recorded as a productive panicle. The trait mean of five sampled plants from each plot was used in the data analysis, and the means of the two replications were used for QTL analysis.

**Genetic linkage map construction**

For the RIL population, a genetic map consisting of 91 SSR markers on 19 linkage groups was constructed in our previous report (Guo and Hong, 2010). The genetic map spanned 969 cM, with an average distance of 10.6 cM between adjacent markers.

**Statistical analysis**

The phenotypic values for GD, PH and PN of the k-th RIL line in environment h were partitioned according to the following mixed linear model:

\[
y_{hk} = \mu + a_i x_{Ak} + a_j x_{Aj} + a_{ij} x_{A_{ij}} + u_{Ehk} e_{hk} + u_{A_{ik}E} e_{A_{ik}E} + u_{A_{ij}E} e_{A_{ij}E} + \sum_{j} (u_{M_{ik}(h)} e^M_{M_{ik}(h)} + u_{M_{ij}(h)} e^M_{M_{ij}(h)} + u_{M_{ij}(h)} e^M_{M_{ij}(h)}
\]

Where \(\mu\) is the mean value of the population; \(a_i\) and \(a_j\) are the additive main effects (fixed effects) of the two putative \(Q_i\) and \(Q_j\), respectively; \(a_{ij}\) is the additive × additive epistatic effect (fixed effect) between \(Q_i\) and \(Q_j\); \(x_{Ak}\), \(x_{Aj}\) and \(x_{A_{ij}}\) are the coefficients of these genetic main effects; \(e_{hk}\) is the random effect of environment \(h\), with the coefficient of \(U_{Ehk}\); \(e_{A_{ik}E}\) (or \(U_{A_{ik}E}\)) is the random additive × environment interaction effect, with the coefficient of \(U_{A_{ik}E}\) (or \(U_{A_{ij}E}\)) for \(Q_i\) (or \(Q_j\)); \(e_{A_{ij}E}\) is the random epistasis × environment interaction effect, with the coefficient of \(U_{A_{ij}E}\); \(e_{M_{ij}(h)}\) is the random effect of the \(l\)-th marker × marker interaction nested within the \(h\)-th environment, with the coefficient of \(U_{M_{ij}(h)}\); and \(e_{hk}\) is the residual random effect. Marker factors \(e_{M_{ij}(h)}\) in the model were used to absorb additive and epistatic effects of background QTLs for controlling noise.

Adjusted genetic effects were estimated by the conditional mapping method for GD, PH and PN (Zhu, 1995; Ye et al, 2009). As with the Eq.(1), the conditional value \(y_{hk|(T_1|T_2)}\) could be partitioned as:

\[
y_{hk|(T_1|T_2)} = y_{h|(T_1|T_2)} + a_{i h|(T_1|T_2)} x_{A_{ik}} + a_{j h|(T_1|T_2)} x_{Aj} + a_{ij h|(T_1|T_2)} x_{A_{ij}} + u_{E(h|(T_1|T_2))} e_{hk} + u_{A_{ih}(h|(T_1|T_2))} e_{A_{ih}(h|(T_1|T_2))} + u_{A_{ijh}(h|(T_1|T_2))} e_{A_{ijh}(h|(T_1|T_2))} + \sum_{j} (u_{M_{ih}(h|(T_1|T_2))} e^M_{M_{ih}(h|(T_1|T_2))} + u_{M_{ijh}(h|(T_1|T_2))} e^M_{M_{ijh}(h|(T_1|T_2))}
\]

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\]

Where \(\mu\) is the mean value of the population; \(a_i\) and \(a_j\) are the additive main effects (fixed effects) of the two putative \(Q_i\) and \(Q_j\), respectively; \(a_{ij}\) is the additive × additive epistatic effect (fixed effect) between \(Q_i\) and \(Q_j\); \(x_{Ak}\), \(x_{Aj}\) and \(x_{A_{ij}}\) are the coefficients of these genetic main effects; \(e_{hk}\) is the random effect of environment \(h\), with the coefficient of \(U_{Ehk}\); \(e_{A_{ik}E}\) (or \(U_{A_{ik}E}\)) is the random additive × environment interaction effect, with the coefficient of \(U_{A_{ik}E}\) (or \(U_{A_{ij}E}\)) for \(Q_i\) (or \(Q_j\)); \(e_{A_{ij}E}\) is the random epistasis × environment interaction effect, with the coefficient of \(U_{A_{ij}E}\); \(e_{M_{ij}(h)}\) is the random effect of the \(l\)-th marker × marker interaction nested within the \(h\)-th environment, with the coefficient of \(U_{M_{ij}(h)}\); and \(e_{hk}\) is the residual random effect. Marker factors \(e_{M_{ij}(h)}\) in the model were used to absorb additive and epistatic effects of background QTLs for controlling noise.

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\]
Where $T_1|T_2$ denotes trait 1 conditioned on trait 2, which means eliminating the phenotypic variation of trait 2. For example, $PH|GD$ means the performance of $PH$ when $GD$ is adjusted to an identical level, or $PN|PH$ means the performance of $PN$ when $PH$ is adjusted to an identical level. All parameters were defined as conditional effects as in the Eq. (1). Such as, $a_{i1|T_1}$ was the adjusted additive main effect of putative $Q_i$.

The trait measurement averaged over the two replications in each environment was used for QTL mapping. Unconditional QTL mapping (namely conventional QTL mapping) was conducted for $GD$, $PH$ and $PN$ by the method of mixed liner model and computer program QTLNetwork 2.0 (Yang et al., 2007). The remaining two traits were conducted by a conditional QTL mapping method when one of the traits was adjusted to an identical level. A threshold probability of $P=0.005$ was used to detect additive QTLs, additive × additive QTL pairs and QTL × environment (Q × E) interactions. QTL nomenclature followed that of McCouch et al (1997).

Applicable elite alleles indicate elite alleles that were detected by unconditional and conditional QTL mapping methods at the same time, and accounted for 7% or more of the phenotypic variation.

RESULTS

Trait performance

The heading date of Xiushui 79 was 20 August in the two environments, and the heading dates of C Bao were 21 August in E1 and 22 August in E2. The heading dates of the RIL population ranged from 4 August to 19 September in E1 and 8 August to 22 September in E2, respectively. Both $PH$ and $PN$ showed significant differences between parents in the two environments. The plant height of Xiushui 79 in E1 was higher than that in E2, and the case was similar for C Bao. Meanwhile, the plant height of C Bao was higher than that of Xiushui 79, which was consistence across two environments. The effective panicle number per plant of Xiushui 79 was more than that of C Bao across two environments, and the difference between environments was not significant.

The phenotypic values of $GD$, $PH$ and $PN$ of the RIL population and its parents over two environments are presented in Table 1. $GD$, $PH$ and $PN$ of the RIL population segregated continuously and both skewness and kurtosis values were less than 1.0 except the kurtosis value of $GD$ in E2. The segregation of $GD$, $PH$ and $PN$ in the RIL population showed a normal distribution and transgressive segregations were observed (Table 1). Therefore, the data were suitable for QTL analysis.

Unconditional QTL analyses of $GD$, $PH$ and $PN$

A total of 14 additive QTLs for $GD$, $PH$ and $PN$ were identified by the unconditional QTL mapping method in the two environments. Five QTLs were for $GD$, five for $PH$ and four for $PN$, respectively. QTL × environment interactions were not significant for additive QTLs (Table 2). Eight pairs of additive × additive QTL interaction were detected for the three traits totally, including three interactions between main effect loci, four interactions between two loci having no main effect and one interaction between main effect loci and no main effect loci. QTL × environment interactions were not significant for additive × additive QTL pairs (Table 3).

Five additive QTLs detected for $GD$, $qGD-2-1$, $qGD-3-1$, $qGD-8-1$, $qGD-10-1$ and $qGD-11-1$ explained 5.67%, 11.79%, 6.17%, 1.12% and 1.93% of the phenotypic variation. The alleles from C Bao at these five loci showed positive effects (Table 2). One pair of additive × additive QTL interaction between main effect

<table>
<thead>
<tr>
<th>Environment</th>
<th>Trait</th>
<th>Parent</th>
<th>RIL population</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Xiushui 79</td>
<td>C Bao</td>
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<tr>
<td>Nanjing (E1)</td>
<td>$GD$ (d)</td>
<td>108.0</td>
<td>109.0</td>
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<td></td>
<td>$PH$ (cm)</td>
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<td>$PN$</td>
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<td>Sihong (E2)</td>
<td>$GD$ (d)</td>
<td>108.0</td>
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<td></td>
<td>$PH$ (cm)</td>
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<td>90.3</td>
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<td></td>
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<td>11.5</td>
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GD, Growth duration; PH, Plant height; PN, Effective panicle number per plant; GD|PH, Growth duration after plant height was adjusted to an identical level; PH|GD, Plant height after growth duration was adjusted to an identical level. The same for Table 3.

The alleles from C Bao at these three loci showed positive effects. One pair of additive × additive QTL interaction between main effect loci and no main effect loci and two interactions between two loci having no main effect were detected for PH, accounting for 9.58% of the total phenotypic variation in the population. One interaction (6-5/7-3) had negative effects on PH, while the remaining two interactions had positive effects on PH.

Among the five additive QTLs detected for PH, qPH-1-1 and qPH-8-2 explained 19.15% and 7.31% of the phenotypic variation, respectively. The alleles from Xiushui 79 at these two loci showed positive effects. One pair of additive × additive QTL interaction between main effect loci and no main effect loci and two interactions between two loci having no main effect were detected for PH, accounting for 9.58% of the total phenotypic variation in the population. One interaction (6-5/7-3) had negative effects on PH, while the remaining two interactions had positive effects on PH.

Among the four additive QTLs detected for PN, qPN-1-1 and qPN-8-1 explained 3.75% and 1.21% of the phenotypic variation, respectively. The alleles from C Bao at these two loci showed positive effects.
qPN-2-1 and qPN-8-2 explained 5.05% and 9.04% of the phenotypic variation, respectively. The alleles from C Bao at these two loci showed positive effects. Two pairs of additive × additive QTL interaction between main effect loci and one interaction between two loci having no main effect were detected for PN, accounting for 7.22% of the total phenotypic variation in the population. One main effect loci interaction (qPN-2-1/qPN-8-2) had positive effects on PH, while the other two interactions had negative effects on PN.

### Conditional QTL analyses of GD, PH and PN

Four additive QTLs for PN were detected when GD was adjusted to an identical level (Table 2), and qPN-1-1, qPN-2-1 and qPN-8-2 were detected by the unconditional mapping method also. This indicated that differential expression of alleles at these three loci was not influenced by GD. In other words, if we substituted the allele linked to RM495-130bp for the allele linked to RM495-145bp from C Bao on rice chromosome 1, it will increase PN by 0.45, but not affect the GD of substituted material. Similarly, RM145-180bp and RM80-160bp were also elite alleles for increasing PN. The conditional QTL-qPN-8-3 was not detected by the unconditional QTL mapping method, indicating differential expression of the alleles at this locus was influenced by GD. Meanwhile, the unconditional QTL-qPN-8-1 was not detected by the conditional QTL mapping method, indicating that qPN-8-1 was a false positive locus, and the discrepancy of PN might due to the difference of GD. Two elite alleles of RM490-110bp and RM80-180bp for PH were detected when GD was adjusted to an identical level. And if the allele linked to RM490-105bp was substituted by the allele linked to RM490-110bp, the plant height would increase 7.93 cm.

Four additive QTLs for GD were detected when PH was adjusted to an identical level (Table 2), and qGD-3-1 and qGD-10-1 were detected by the unconditional mapping method also. This indicated...
that the differential expression of alleles at these two loci was not influenced by PH, which meant that if the allele linked to RM448-245bp was substituted by the allele linked to RM448-240bp, the growth duration would shorten 3.89 d, and if RM171-155bp was substituted by RM171-150bp, the growth duration would shorten 1.58 d, without affecting the PH of the improved material. When PH was adjusted to an identical level, three elite alleles for PN, i.e. RM495-130bp, RM145-180bp and RM80-160bp, were detected. And if we substituted the allele linked to RM80-180bp for the allele linked to RM80-160bp, effective panicle number per plant would increase 0.62.

Six additive QTLs for GD were detected when PN was adjusted to an identical level (Table 2), and $q_{GD-2-1}$, $q_{GD-3-1}$, $q_{GD-8-1}$, $q_{GD-10-1}$ and $q_{GD-11-1}$ were detected by the unconditional mapping method also, which suggested that the differential expressions of alleles at the five loci were not influenced by PN. The five elite alleles at the five loci were RM1358-190bp, RM448-240bp, RM22899-160bp, RM171-150bp and RM287-150bp, respectively. If the allele linked to RM448-245bp was substituted by the allele linked to RM448-240bp, the growth duration would shorten 4.64 d. After PN was adjusted to an identical level, four additive QTLs were detected for PH. The elite alleles of the four loci were RM490-110b, RM448-245bp, RM22899-175bp and RM257-150bp, respectively. If we substituted the alleles linked to RM490-105bp and RM257-160bp for the alleles linked to RM490-110bp and RM257-150bp, respectively, the plant height would increase 8.43 cm and 8.06 cm, respectively.

QTL×environment interactions were not significant for all additive loci mentioned above.

Twenty pairs of additive × additive QTL interactions were detected by the conditional mapping method, explained 0.74%−6.38% of the phenotypic variation. Among the 20 pairs of additive × additive QTL interactions, 6 interactions occurred between main effect loci, 10 interactions between two loci having no main effect and 4 interactions between main effect loci and no main effect loci (Table 3). Interactions between additive × additive QTL pairs and environment were not significant.

For GD trait, eight pairs of additive × additive QTL interactions were detected among the 20 pairs of interactions. Out of the eight interactions, only one interaction between $q_{GD-2-1}$ and $q_{GD-10-1}$ was detected by both unconditional and conditional QTL mapping that PN was adjusted to an identical level. Interaction between $q_{GD-2-1}$ and $q_{GD-10-1}$ will shorten 2.12 d of GD. Nine pairs of additive × additive QTL interactions were detected for PH. Among them, five pairs of additive × additive QTL interactions were detected when GD was adjusted to an identical level. Two pairs of interactions between 1-2 and 2-1, and between 6-5 and 7-3 were also detected by the unconditional mapping method. The interaction between 1-2 and 2-1 would increase 3.63 cm of PH, whereas the interaction between 6-5 and 7-3 would reduce 4.11 cm of PH. In the event that PN was adjusted to an identical level, four pairs of additive × additive QTL interactions were detected for PH, and only one pair of interaction (between $q_{PN-9-1}$ and 11-1) was also detected by the unconditional mapping method. The interaction will increase 3.52 cm of PH. Three pairs of additive × additive QTL interactions were detected for PN. These three interaction pairs were all detected when GD or PH were adjusted to an identical level. Additionally, they were also detected by the unconditional mapping method, which indicated that these interaction pairs for PN were not affected by GD or PH. Among the three interactions, the interaction between $q_{PN-1-1}$ and $q_{PN-8-2}$ could reduce 0.25 of PN, the interaction between 3-8 and 6-5, could reduce 0.48 of PN, and the interaction between $q_{PN-2-1}$ and $q_{PN-8-2}$ could increase 0.45 of PN.

**DISCUSSION**

QTL mapping for GD, PH and PN were conducted by using unconditional and conditional QTL mapping in japonica rice in this study. Results showed that some loci or pairs for the three traits were genetically independently and some were influenced by the other two traits as well. Additive effects were principal in all of the QTLs for GD, PH and PN in japonica rice, and epistatic effects explained a small proportion of phenotypic variation. No interactions were detected between additive QTL (epistatic QTL pairs) and environment. Loci or pairs detected only by the unconditional QTL mapping method might be
false positive.

Growth duration is a major constraint for wide adaptive ability of a single japonica hybrid rice. Hybrids with high-yielding potential in southern Jiangsu could not mature safely when planted in middle and northern Jiangsu Province in China. High-yielding hybrids in northern Jiangsu could be planted in middle and southern Jiangsu and matured naturally, but the yield per unit area decreased and heterosis disappeared due to shortened growth duration. According to the results obtained by the unconditional and conditional QTL mapping, we found that if the allele linked to RM448-240bp on chromosome 3 were pyramided with the allele linked to RM171-150bp on chromosome 10, growth duration would shorten 5.5 d, and PN and PH of the improved material were not influenced. If alleles linked to RM1358-190bp, RM448-240bp, RM22899-160bp, RM171-150bp and RM287-150bp were pyramided, growth duration would shorten 14 d, and PN of the improved material was not influenced.

It is reported that there were significantly negative correlations between PN and PH, and between PN and GD (Cui et al, 2004). In this study, however, by using unconditional and conditional QTL mapping, some of loci for PN were correlated with GD and PH, and most of loci for PN inherited independently, without affecting GD and PH. Meanwhile, all pairs of additive × additive interactions between loci detected in this study were independent of the other two traits. Three elite alleles for PN, i.e. RM495-145bp, RM145-180bp and RM80-160bp, were detected when GD was adjusted to an identical level. Therefore, we can pyramid the allele linked to RM495-145bp on chromosome 1 and the allele linked to RM145-180bp on chromosome 2, and make PN increase by 1.3. Also, GD was not influenced by this accumulation. The effective panicle number per plant would increase by 2 if we pyramid the allele linked to RM145-180bp on chromosome 3 and change the allele linked to RM80-160bp in chromosome 8, due to the interaction between these two loci. However, the three elite alleles cannot be pyramided simultaneously because the accumulation of the allele linked to RM495-145bp and the allele linked to RM80-160bp will decrease PN by 0.25. Similarly, the three elite alleles designated as RM495-130bp, RM145-180bp and RM80-160bp for PN were detected when PH was adjusted to an identical level. If we pyramid the allele linked to RM145-180bp and the allele linked to RM80-160bp, the effective panicle number per plant would increase by 2, and GD and PH were not affected by the pyramiding.

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