Inheritance and QTL Mapping of Salt Tolerance in Rice

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Abstract: An F2 population derived from the cross between Jiucaiqing (japonica) and IR36 (indica) was used to analyze the inheritance of salt tolerance in rice by genetic model of major-genes plus polygenes, and to map the corresponding QTLs by SSR molecular markers. Rice plants of P1, P2, F1 and F2 at 5- to 6- leaf stage were treated under 140 mmol/L NaCl for 10 days. Three indices representing the ability of salt tolerance of rice seedlings were measured, including salt tolerance rating (STR), Na+/K+ ratio in roots and dry matter weight of shoots (DWS). STR, Na+/K+ and DWS were all controlled by two major genes with modification by polygenes. Heritability of these traits from major genes was 17.8, 53.3 and 52.3%, respectively. The linkage map constructed by 62 SSR molecular markers covered a total length of about 1 142 cM. There were three QTLs detected for STR located on chromosome 1, 5 and 9, two QTLs for DWS on chromosomes 8 and 9, and two QTLs for Na+/K+ on chromosomes 2 and 6, one on each chromosome respectively. Single QTL accounted for 6.7 to 19.3% of phenotypic variation. Identification method of salt tolerance in rice and breeding of rice varieties with salt tolerance based on molecular markers assisted selection had been discussed.

Key words: rice (Oryza sativa); salt tolerance; inheritance; quantitative trait locus; molecular marker

Salinity in soils is a major constraint to plant growth and development in the coastal area worldwide. Many research efforts have been made to screen plant germplasm tolerant to salt stress and to understand genetic mechanism of plant salt-tolerance. Most of studies suggested that salt tolerance in crops was controlled mainly by polygenes with additive and dominant effects, while some ascribed the tolerance to major genes [1, 2]. Generally, the oligogenes or polygenes governing salt tolerance are difficult to be detected by classical methods of quantitative genetics due to environmental influence. Limited knowledge on genetic mechanism of salt tolerance had resulted in slower progress in crop improvement for salt tolerance. However, mixed genetic models have been recently developed to characterize the inheritance of either agronomic or physiological traits controlled by major genes and polygenes, and to estimate their genetic effects and heritability [3]. In addition, with the development of DNA markers and construction of saturated genetic maps of some crops like rice, it has become possible to analyze and manipulate the quantitative trait locus (QTL), especially those associated with phenotypic traits. Therefore, the genes governing salt tolerance could be independently traced in a segregation population and pyramided via molecular marker assisted selection (MAS) in the breeding of new varieties with strong tolerance to salt stress.

Improvement of salt stress tolerance in commercial varieties would not only increase grain yield of rice under slight salt-stress condition, but also may extend rice growing to the region with moderate salt content in soils. In our previous research it was found that a japonica landrace Jiucaiqing, from the Taihu Valley of Jiangsu Province, had strong tolerance to salt stress and showed a high yield potential under 250 mmol/L NaCl condition. In this research we studied the inheritance of salt tolerance at the seedling stage in Jiucaiqing using genetic models of major-genes plus polygenes, and mapped some QTLs controlling the salt tolerance by SSR molecular markers based on an F2 population from the cross between Jiucaiqing and IR36.

MATERIALS AND METHODS

Plant materials

Two parent rice varieties Jiucaiqing (JCQ, P1) and IR36 (P2) were used in this experiment. The former is a japonica landrace with strong salt tolerance, and the latter is an indica variety sensitive
to salt stress. The cross between JCQ and IR36 was
made in Nanjing in the summer of 2000, and F2
population was developed in Hainan during the winter
of the same year. P1, P2, F1 and F2 were grown in the
experimental field at Nanjing in the summer, 2001, and
their tolerance to salt stress was identified. Rice
seeds were germinated and sown in seed-tray
according to the method of Wang et al [7]. Ten
seedlings of each P1, P2 and F1 and 250 seedlings of F2
were planted.

Identification of salt tolerance

When plants had developed three tillers with 3 to
4 leaves, all tillers were separated from main stem and
cultured in the nutritional solution for the evaluation
of tolerance to salt stress. The tillers from each plant
were randomly rooted in 1.5 cm thick foam board
with a spacing of 5 cm×6 cm, then the board was
placed in plastic boxes (25 cm×35 cm×9 cm) filled
with nutrition solution prepared according to Yashida
et al [5]. Seven days later, the nutrition solution was
replaced by fresh one with additional 140 mmol/L
NaCl, and again 5 days later, the practice was repeated.
The solution pH value was maintained at 5.6. The
average temperature was (22.2±3.5) °C / (30.6±2.8)
°C (night/day) during the period of salt treatment. At
10 d of salt treatment, measurement was done for the
salinity tolerance rating (STR), dry matter weight of
shoot (DWS) and Na+/K+ in roots (Na+/K+). STR was
ranked from 1 to 5 according to the standard by
Gregorio et al [6]. Tiller plant samples were rinsed
with distilled water and separated into shoots and
roots, then dried for weighing. The content of Na+, K+
in roots was measured as described by Wang et al [7].

Co-segregation analysis of P1, F1, P2 and F2

A co-segregation genetic analysis was performed
by mixed genetic model of major-genes and polygenes
using P1, F1, P2 and F2 population, according to Zhang
et al [3]. The likelihood function of samples is as follows:

\[ L(x; \theta) = \prod_{i=1}^{n_1} f(x_i; \mu_1, \sigma_1^2) \prod_{i=1}^{n_2} f(x_i; \mu_2, \sigma_2^2) \prod_{i=1}^{n_3} f(x_i; \mu_3, \sigma_3^2) \prod_{i=1}^{n_4} f(x_i; \mu_4, \sigma_4^2) \]

Where \( f(x; \mu, \sigma^2) \) is density function of normal
distribution \( N(\mu, \sigma^2) \), and \( n_1-n_4 \) indicate numbers of
P1, F1, P2 and F2 plants, respectively, \( K \) represents
component distribution number of F2, and \( \theta \) is error
variance of observation values of homogeneity
population.

Firstly, five groups and twenty four types of
genetic models including one-major-gene model,
two-major-gene model, polygenes model, mixed
model of one-major-gene plus polygenes and that of
two-major-genes plus polygenes were constructed.
Secondly, the parameters of component distribution
were estimated through IECM algorithm. Then the
best-fitting genetic model was chosen according to
Akaike’s Information Criterion (AIC), a likelihood-
ratio test and tests for goodness of fit. Finally the
genetic parameters as well as genetic effects, genetic
variance and heritability were estimated.

SSR analysis and QTL detection

Leaves from the main stem of each plant
examined were sampled, and genomic DNA was
extracted according to Dellaporta et al [8]. A total of
319 SSR primer pairs were surveyed based on their
polymorphism between two parents, and the primers
exhibiting polymorphism were used to amplify the
DNA of each plant of F2 population. PCR reaction
was carried out in a total volume of 10 µL containing
10 ng of template DNA, 4 µmol/L of each primer, 2.5
mmol/L of each dNTP, 1.5 mmol/L MgCl2, 0.5 unit of
Taq polymerase, 1 µL of 10 × buffer. PCR
amplification was performed on a PTC100 (MJ
research) Thermal Cycler under the following
conditions: predenaturing at 95°C for 5 min, followed
by 35 cycles of denaturing at 94°C for 45 s, annealing
at 55°C for 30 s, extension at 72°C for 1 min; and a
final extension at 72°C for 7 min. The amplification
products were electrophoresed for 2 h on 10%
polyacrylamide gels and detected by silver staining as
described by Panaud et al [9].

A SSR linkage map of F2 population was
constructed using Mapmaker 3.0 [10], and the genetic
distances (cM) were calculated from recombination
values using Kosambi function [11]. The linkage
between single marker and salt-tolerance traits was
detected by single-way ANOVA [12]. QTLs affecting
relative parameters were sought with interval mapping
using Cartographer 1.0 [13, 14], and a threshold of
LOD>2.0 was used per test to claim the presence of QTL. The parameters such as additive effects and variance explained were also estimated. QTL nomenclature was followed according to McCouch et al[15].

RESULTS

Inheritance of salt tolerance

The variance analysis showed that the variability of STR, DWS and Na⁺/K⁺ among the tillers from different F₂ plants were significantly higher than that of among the three tillers from a single plant (Table 1). In general, the variance in salt-tolerance among three tillers from one F₂ plant might be attributed to the experimental error caused by the difference in growing condition, but the variance among tillers from different F₂ plants was mainly due to the genetic segregation in F₂ population.

There was a remarkable discrepancy in STR, DWS and Na⁺/K⁺ ratio between the two parents, and JCQ was more tolerant to salt stress than IR36. The F₁ plant showed transgressive inheritance in STR and DWS, and some transgressive plants were observed in F₂ population (Fig. 1).

The results showed that inheritance of STR and Na⁺/K⁺ ratio could be explained with genetic model E-6 of equal dominance major-genes plus polygenes, and the dominant effects by two major genes were equal to additive effects (Table 2, Table 3). However, inheritance of DWS could be explained with genetic model E-1 of additive-dominance-epistasis major-genes plus polygenes, its two major genes represented not only additive and dominant effects but also epistatic effects (Table 2, Table 3).

According to analysis by the selected genetic model, the traits representing salt tolerance in rice

<table>
<thead>
<tr>
<th>Trait</th>
<th>df</th>
<th>MS₁</th>
<th>MS₂</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>197</td>
<td>1.07</td>
<td>0.38</td>
<td>2.79**</td>
</tr>
<tr>
<td>DWS</td>
<td>197</td>
<td>0.51</td>
<td>0.04</td>
<td>12.40**</td>
</tr>
<tr>
<td>Na⁺/K⁺ ratio</td>
<td>192</td>
<td>14.32</td>
<td>0.26</td>
<td>55.28**</td>
</tr>
</tbody>
</table>

df: Degree of freedom; MS₁: Squares among tillers from different plants; MS₂: Squares among tillers from the same plant; F, MS₁ / MS₂; **Significance at the level of 1%.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Model</th>
<th>Max-likelihood value</th>
<th>Min-AIC value</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>E-6</td>
<td>-197.12</td>
<td>398.24</td>
</tr>
<tr>
<td>Na⁺/K⁺</td>
<td>E-6</td>
<td>-455.05</td>
<td>914.09</td>
</tr>
<tr>
<td>DWS</td>
<td>E-1</td>
<td>-135.23</td>
<td>288.46</td>
</tr>
</tbody>
</table>
seedling were all controlled by two major genes with modification of polygenes. The total heritability of STR, Na+/K+ ratio and DWS were 74.08, 81.04 and 80.5%, respectively. However, the heritability of major genes for STR was significantly lower than those for Na+/K+ ratio and DWS (Table 4).

### QTL analysis of salt tolerance in rice seedling

Of the 319 SSR primer pairs tested, 147 produced polymorphic bands between the genomic DNAs of parents and 69 primer pairs amplified clear and scorable bands for F2 individuals. A linkage map based on F2 population was constructed, which covered a total of 1142.3 cM with an average two-locus interval of 20.0 cM. The position of most SSR markers on chromosomes was identical with the previously reported [16].

Single-way ANOVA was employed to determine whether those molecular markers were significantly related to STR, Na+/K+ ratio and DWS. Thirteen markers scattered on chromosomes 1, 3, 5, 6, 8 and 9 were found to be associated with the traits of salt tolerance. Among them, four, six and three markers were linked to the traits STR, Na+/K+ ratio and DWS, respectively (Table 5). Interestingly, either three markers on the chromosomes 1 and 6 were found associated with STR, Na+/K+ ratio or DWS, respectively, and either two markers on chromosomes 8 and 9 were also related to the STR and DWS, respectively.

Interval mapping method was further used to detect the position of QTLs and estimate their genetic effects. Seven QTLs associated with salt tolerance were detected (Table 6). Among them, three QTLs for STR were located on chromosomes 1, 5 and 9, two

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### Table 3. Estimations for genetic parameters of three indices for rice salt-tolerance.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Model</th>
<th>m</th>
<th>d_a</th>
<th>d_b</th>
<th>h_a</th>
<th>h_b</th>
<th>i</th>
<th>j_a</th>
<th>j_b</th>
<th>[d]</th>
<th>[h]</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>E-6</td>
<td>3.18</td>
<td>-0.22</td>
<td>-0.22</td>
<td>-0.22</td>
<td>-0.22</td>
<td>-0.22</td>
<td>-0.06</td>
<td>-0.51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Na'/K⁺ ratio</td>
<td>E-6</td>
<td>9.11</td>
<td>-1.43</td>
<td>-1.43</td>
<td>-1.43</td>
<td>-1.43</td>
<td>-1.43</td>
<td>0.93</td>
<td>3.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DWS</td>
<td>E-1</td>
<td>0.77</td>
<td>0.17</td>
<td>0.16</td>
<td>-0.44</td>
<td>-0.23</td>
<td>0.48</td>
<td>0.08</td>
<td>0.21</td>
<td>0.02</td>
<td>1.46</td>
</tr>
</tbody>
</table>

- m, Means of F2 population; d_a & d_b, additive effect of major genes; h_a & h_b, dominance effect of major genes; i, Effect of dominance × dominance; j_a & j_b, Effect of additive × additive; [d], Additive effect of polygenes; [h], Dominance effect of polygenes.

### Table 4. Genetic variance and heritability of salt tolerance of rice in the seedling.

<table>
<thead>
<tr>
<th>Trait</th>
<th>GV_mg</th>
<th>GV_pg</th>
<th>h_mg(%)</th>
<th>h_pg(%)</th>
<th>h_mg+h_pg(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>0.072</td>
<td>0.228</td>
<td>17.78</td>
<td>56.30</td>
<td>74.08</td>
</tr>
<tr>
<td>Na'/K⁺ ratio</td>
<td>3.074</td>
<td>1.598</td>
<td>53.32</td>
<td>27.72</td>
<td>81.04</td>
</tr>
<tr>
<td>DWS</td>
<td>0.126</td>
<td>0.068</td>
<td>52.28</td>
<td>28.22</td>
<td>80.50</td>
</tr>
</tbody>
</table>

**GV_mg, Genetic variance of major genes; GV_pg, Genetic variance of polygenes; h_mg, Heritability of major genes; h_pg, Heritability of polygenes.**

### Table 5. The QTL of salt-tolerant traits detected by single-way ANOVA.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Marker</th>
<th>Chromosome</th>
<th>Mean square between group</th>
<th>Mean square within group</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>RM9</td>
<td>1</td>
<td>1.74</td>
<td>0.32</td>
<td>5.35**</td>
</tr>
<tr>
<td></td>
<td>RM7</td>
<td>3</td>
<td>1.59</td>
<td>0.35</td>
<td>4.51†</td>
</tr>
<tr>
<td></td>
<td>RM161</td>
<td>5</td>
<td>1.92</td>
<td>0.35</td>
<td>5.51†</td>
</tr>
<tr>
<td></td>
<td>RM136</td>
<td>6</td>
<td>1.29</td>
<td>0.34</td>
<td>3.75†</td>
</tr>
<tr>
<td></td>
<td>RM223</td>
<td>8</td>
<td>1.25</td>
<td>0.36</td>
<td>3.51†</td>
</tr>
<tr>
<td></td>
<td>RM215</td>
<td>9</td>
<td>1.72</td>
<td>0.35</td>
<td>4.92**</td>
</tr>
<tr>
<td>Na'/K⁺ ratio</td>
<td>RM104</td>
<td>1</td>
<td>11.20</td>
<td>3.62</td>
<td>3.10†</td>
</tr>
<tr>
<td></td>
<td>RM13</td>
<td>5</td>
<td>12.76</td>
<td>3.65</td>
<td>3.49†</td>
</tr>
<tr>
<td></td>
<td>RM136</td>
<td>6</td>
<td>14.14</td>
<td>3.56</td>
<td>3.98†</td>
</tr>
<tr>
<td></td>
<td>RM345</td>
<td>6</td>
<td>14.76</td>
<td>3.56</td>
<td>4.15†</td>
</tr>
<tr>
<td>DWS</td>
<td>RM265</td>
<td>1</td>
<td>0.98</td>
<td>0.22</td>
<td>4.32†</td>
</tr>
<tr>
<td></td>
<td>RM223</td>
<td>8</td>
<td>1.20</td>
<td>0.21</td>
<td>5.85**</td>
</tr>
<tr>
<td></td>
<td>RM215</td>
<td>9</td>
<td>0.78</td>
<td>0.21</td>
<td>3.69†</td>
</tr>
</tbody>
</table>

†, ** Significant at the levels of 5% and 1%, respectively.
QTLs for Na+/K+ ratio on chromosome 2 and 6, and two QTLs for DWS on chromosome 8 and 9, one on each chromosome respectively. The explanation for phenotypic variations by a single QTL varied from 6.7 to 19.3%. The genetic effects of these QTLs were different, \( q_{STR-1} \), \( q_{NAK-2} \) and \( q_{NAK-6} \) being dominant, and \( q_{STR-5} \), \( q_{STR-9} \) and \( q_{DWS-8} \), \( q_{DWS-9} \) being super-dominant. Fig. 5 showed the relative position of QTLs for traits representing salt tolerance in rice seedling. Only \( q_{STR-9} \) and \( q_{DWS-9} \) might be very close positioned or even overlapped, and the others scattered on the different chromosomes.

According to additive effect of each QTL (Table 6), majority of alleles enhancing salt tolerance, such as \( q_{STR-1} \), \( q_{STR-9} \), \( q_{NAK-2} \) and \( q_{DWS-8} \), were derived from salt-tolerant parent JCQ, and the rest from the salt sensitive parent IR36.

### DISCUSSION

\( F_2 \) population is commonly utilized to research the inheritance of phenotypic traits for crops. Unlike DH or RIL population, it is a segregation population, and \( F_2 \) individuals differ in their genetic background with each other. In order to identify variation for salt-tolerance among the plants of \( F_2 \) population, several tillers separated from one plant were treated independently with salt stress in this experiment. It was found that variance of salt-tolerance among tillers from the same parental plant was much lower than that from the same \( F_2 \) individual. Therefore, more replications could contribute to a better estimation of salt tolerance in the segregation population [17].

The previous research showed that salt tolerance in rice was controlled by polygenes with the additive

### Table 6. QTL of salt-tolerant traits detected by IMM and their genetic effects.

<table>
<thead>
<tr>
<th>Trait</th>
<th>QTL</th>
<th>Marker interval</th>
<th>Chromosome</th>
<th>Peak position</th>
<th>LOD</th>
<th>Additive effect</th>
<th>D/a</th>
<th>Variance explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>STR</td>
<td>( q_{STR-1} )</td>
<td>RM9–RM128</td>
<td>1</td>
<td>0.0</td>
<td>2.06</td>
<td>-0.17</td>
<td>0.82</td>
<td>6.7</td>
</tr>
<tr>
<td></td>
<td>( q_{STR-5} )</td>
<td>RM161–RM13</td>
<td>5</td>
<td>6.0</td>
<td>2.72</td>
<td>0.32</td>
<td>1.37</td>
<td>14.3</td>
</tr>
<tr>
<td></td>
<td>( q_{STR-9} )</td>
<td>RM278–M215</td>
<td>9</td>
<td>20.0</td>
<td>2.06</td>
<td>-0.08</td>
<td>3.62</td>
<td>7.0</td>
</tr>
<tr>
<td>Root Na+/K+</td>
<td>( q_{NAK-2} )</td>
<td>RM318–RM262</td>
<td>2</td>
<td>26.0</td>
<td>2.73</td>
<td>1.27</td>
<td>0.38</td>
<td>19.3</td>
</tr>
<tr>
<td></td>
<td>( q_{NAK-6} )</td>
<td>RM176–RM345</td>
<td>6</td>
<td>9.9</td>
<td>2.03</td>
<td>-0.71</td>
<td>0.86</td>
<td>7.9</td>
</tr>
<tr>
<td>DWS</td>
<td>( q_{DWS-8} )</td>
<td>RM223–RM152</td>
<td>8</td>
<td>0.0</td>
<td>2.47</td>
<td>0.06</td>
<td>4.33</td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td>( q_{DWS-9} )</td>
<td>RM278–RM215</td>
<td>9</td>
<td>14.0</td>
<td>2.31</td>
<td>-0.04</td>
<td>7.5</td>
<td>11.5</td>
</tr>
</tbody>
</table>

IMM, Interval mapping method.
and dominant effects, the former playing a major role [2, 6, 18]. Akbar et al [1] reported that the dry matter weight of rice seedling under salt stress was affected by at least two groups of genes with additive effect, and no epistatic effect was detected. Gregorio et al [6] observed that there were two groups of genes involved in the sodium and potassium uptake in rice, one group for sodium exclusion and the other for potassium absorption. In this study three indices STR, DWS and Na\(^+/\)K\(^+\) ratio in root representing salt-tolerance of plant were used to analyze the inheritance of rice salt-tolerance based on the genetic models of major-genes plus polygenes. It was found that the inheritance of both STR and Na\(^+/\)K\(^+\) ratio in root under the salt stress fitted into the genetic model E-6, with dominant effects of two major genes same and equal to additive effects, and the inheritance of DWS followed genetic model E-1 of additive-dominance-epistasis major-genes plus polygenes, not only with the additive and dominant effects by two major genes but also with epistatic effects. All of the three indices had higher heritability (Table 5). The heritability for Na\(^+/\)K\(^+\) ratio in root of rice was reported over 40% [19].

Physiological traits associated with salt tolerance in rice were complex and controlled by a few major QTLs [20]. The smaller the effect of QTLs, the more difficult for it is to be detected [21]. Several hundreds of pairs of rice SSR markers have been developed. The cross between JCQ and IR36 was inter-subspecific with more polymorphism at molecular level. Based on a 1142.3 cM linkage map constructed with 69 markers distributed on 12 rice chromosomes, 13 markers were found linked with the three indices of salt tolerance. Some markers on chromosome 1 were linked with STR, DWS and Na\(^+/\)K\(^+\) ratio in roots. The results were consistent with those of the previous reports [22, 23]. Yet it is unclear whether they were the same as the QTLs previously reported. Koyama et al [24] have identified some QTLs associated with Na\(^+/\)K\(^+\) ratio on chromosomes 1 and 4. In this study, only one QTL on chromosome 1 for STR was found probably due to the low density of SSR linkage map; two QTLs related to Na\(^+/\)K\(^+\) ratio were found, one each on chromosome 2 and 6. The \textit{Kna} gene related to salt tolerance in wheat (controlling Na\(^+/\)K\(^+\) discrimination) has been mapped to chromosome arm 4DL [25] and this region is probably equivalent to the tip of chromosome 3S in rice. However, no QTLs associated with Na\(^+/\)K\(^+\) ratio were detected in this region. This may be due to different mechanisms between wheat and rice.

Gu et al [26] detected three QTLs for STR on chromosome 5 and 9. Here we explored that QTLs associated with STR were located on chromosomes 1, 5 and 9. Gong et al [21] and Lin et al [27] have reported some QTLs for surviving days of rice seedling on chromosome 1 and 5, respectively. QTLs related to biomass dry matter have been mapped on chromosome 6 [24, 28]. However, QTLs for DWS were found to be located on chromosomes 8 and 9 in this study. The QTL associated with DWS in the region of RM278-RM215 on chromosome 9 was close to the QTL for STR. It is concluded that there is a relationship between DWS and STR, which may be controlled by the same gene or linked.

The numbers of major QTLs for each trait related to salt tolerance detected by molecular marker were very close to those from co-segregation analysis based on P\(_1\), F\(_1\), P\(_2\) and F\(_2\). All results indicated that each trait related to salt tolerance was controlled by at least two major QTLs. The phenotype of salt tolerance in rice is a general expression of some physiological factors. Genes governing salt tolerance are scattered among different rice varieties due to lack of pressure of salt stress during long evolutionary period [29]. This study revealed that alleles of QTL enhancing salt tolerance were not only from salt-tolerant parent but from salt sensitive parent also (Table 6), which supported other report [26]. Transgressive segregation was found in F\(_2\) population from the cross between JCQ and IR36, which might be attributed to the gathering of some QTLs associated with salt tolerance. Therefore, transgressive breeding for salt tolerance in rice could be achieved via molecular marker assisted-selection. However, precise detection of QTLs for salt tolerance remained a problem due to less SSR markers and low density linkage map. It is estimated that there have 5 700–10 000 SSRs in rice genome [30], and thus it is suggested that further study should be performed with more SSR markers and perpetual mapping population.
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