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QTLs for Na^+ and K^+ uptake of the shoots and roots controlling rice salt tolerance

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Abstract An F_2 and an equivalent F_3 population derived from a cross between a high salt-tolerance *indica* variety, Nona Bokra, and a susceptible elite *japonica* variety, Koshihikari, were produced. We performed QTL mapping for physiological traits related to rice salt-tolerance. Three QTLs for survival days of seedlings (SDSs) under salt stress were detected on chromosomes 1, 6 and 7, respectively, and explained 13.9% to 18.0% of the total phenotypic variance. Based on the correlations between SDSs and other physiological traits, it was considered that damage of leaves was attributed to accumulation of Na^+ in the shoot by transport of Na^+ from the root to the shoot in external high concentration. We found eight QTLs including three for three traits of the shoots, and five for four traits of the roots at five chromosomal regions, controlled complex physiological traits related to rice salt-tolerance under salt stress. Of these QTLs, the two major QTLs with the very large effect, qSNC-7 for shoot Na^+ concentration and qSKC-1 for shoot K^+ concentration, explained 48.5% and 40.1% of the total phenotypic variance, respectively. The QTLs detected between the shoots and the roots almost did not share the same map locations, suggesting that the genes controlling the transport of Na^+ and K^+ between the shoots and the roots may be different.

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Introduction

It is estimated that saline soils cover our earth's surface from 400 to 950 million hectares. Accumulation of salt in the soil causes deleterious effects and leads to a reduction in rice production as well as other crops. Improving the salt tolerance in rice is one of the most-important objectives of rice breeding-programs in coastal areas. Many trials have been performed in developing of the elite variety with a high level of salt tolerance, but to-date the endeavor was not yet a success. Breeding goals are hampered by a lack of understanding of genetic mechanisms for salt tolerance. To facilitate a development of new varieties with a high level of salinity tolerance, it will be required to understand the genetic control mechanisms for salt tolerance.

Salt tolerance of the crop is the final manifestation of several components, such as Na^+ uptake, K^+ uptake, ion balance and ion compartmentation, etc. Yeo et al. (1990) tried to dissect a complex physiological trait of salt tolerance in rice using improved methods of identifying and measuring physiological components such as shoot sodium concentration, plant survival scores and plant vigour. However, genetic analysis has not been performed. In the last decade, the development of molecular markers has made it possible to investigate the inheritance of complex traits and to tag and manipulate individual QTLs involved (Yano and Sasaki 1997). Many QTL analyses of important agronomic traits of rice have been carried out, such as yield (Lin et al. 1996a; Xiao et al. 1996) and heading date (Li et al. 1995; Lin et al. 1996b; Yano et al. 1997, 2001). The dissection of such a complex

trait by means of the QTL mapping-approach will be of great significance for breeding by enhancing the salt tolerance of rice. QTL analyses of salt tolerance of rice were carried out by using molecular markers in several groups (Zhang et al. 1995; Lin et al. 1998; Gong et al. 1999; Prasad et al. 2000; Koyama et al. 2001). Zhang et al. (1995) detected a QTL involved in salt tolerance on chromosome 7. Lin et al. (1998) mapped only one QTL with a small effect for survival days of the seedling on chromosome 5. Gong et al. (1999) and Prasad et al. (2000) also mapped a QTL for salt tolerance on chromosomes 1 and 6, respectively. Ten QTLs for five traits, such as Na^+ (one QTL) and K^+ (three QTLs) uptake, Na^+ (two QTLs) and K^+ (two QTLs) concentration, and Na^+:K^+ ratio (two QTLs) in the shoot were identified (Koyama et al. 2001). However, QTL analysis for traits related to salt tolerance in the root has not been conducted yet. As mentioned above, 14 QTLs with small effect for several traits related to salt tolerance were identified, but any QTL with a large effect was not found. Several studies indicated that some salt- and drought-induced transcripts were used as markers and were mapped on regions of QTLs detected previously (see summaries edited by Ausubel 2002). Therefore, identifications of new QTLs related to salt tolerance may contribute to characterize unknown or novel salt-induced transcripts.

In this study, to find new QTLs or major QTLs for salt tolerance with large effect, we detected QTLs for several physiological traits associated with salt tolerance in the shoot and the root of rice, using F_2 and F_3 generations derived from a cross between a high salt-tolerance variety and a sensitive variety of salt treatment. These results will provide important information for further functional analysis of salt-tolerance genes in rice. The molecular markers linked with QTLs for salt tolerance might then be useful for breeding programs in rice by marker-assisted selection.

Materials and methods

Plant materials

The parental line, Nona Bokra, was a well-known high salt-tolerance *indica* variety, and the other parental line, Koshihikari was a salt-susceptible elite *japonica* variety. An F_2 population derived from a cross between Nona Bokra and Koshihikari was constructed. F_3 lines were developed with each line originating from a different F_2 plant.

Evaluation of physiological traits for salt tolerance

The parents, Nona Bokra and Koshihikari, and 133 F_3 lines (16 plants in each line) were used to evaluate the salt tolerance. The seeds were placed at 45°C for 1 week to break any possible dormancy, then germinated at 35°C for 48 h; finally, the most-uniform germinated seeds were sown in holes of thin styrofoam board with a nylon net bottom, which floated on water for 3 days, then transferred to floating on Yoshida's cultural solution (Yoshida et al. 1976). At 8 days after sowing, the seedlings were transferred to cultural solution containing 140 mM of NaCl. Survival days of seedlings (SDSs) were recorded for each individual plant in days from seeding to death. The seedlings were grown in a growth chamber with a 13-h light/11-h dark photoperiod at 26°C. The solution was changed by a fresh one every 2 days and the pH was maintained at 5.8.

To observe physiological traits, such as Na^+ and K^+ concentration, and Na^+ and K^+ total quantity in the shoots and the roots, the second experiment was performed. The procedure and management of the experiment was the same as the above-mentioned experiment. At 10 days after treating by NaCl, the shoots and the roots were harvested, respectively, and the roots were rinsed with distilled water. Shoots and roots were dried, weighed and extracted in acetic acid (100 mM) at 90°C for 2 h, respectively. The extraction was divided into three groups, and sodium and potassium in each group was determined by the atomic absorption spectrophotometer (AA-680, Shimadzu, Japan). The concentration and the quantity of two ions in the shoots and the roots were calculated, respectively, using the data determined.

Construction of an RFLP linkage map

One hundred and thirty three plants of the F_2 population were used to construct a linkage map. RFLP analysis was carried out following the procedure described by Harushima et al. (1998). A total of 161 RFLP markers, which covered the whole rice genome and revealed polymorphisms between the parents, were used to determine RFLP genotypes of each plant in the F_2 population.

An RFLP linkage map was established using the program MAPMAKER/EXP 3.0 (Lander et al. 1987; Stephen et al. 1990) based on the genotype data of the F_2 population. Map distances between marker loci were presented in centiMorgans (cM) derived using the Kosambi function of the program. A LOD score of 3.0 was used to determine both the linkage groups and the order of markers.

QTL analysis

The MAPMAKER/QTL program (Lander and Botstein 1989; Lincoln et al. 1993) was used to identify QTLs affecting salt tolerance on the basis of interval analysis. A LOD score of 3.0 was used to declare the presence of putative QTLs in a given genomic region. The percentages of total phenotypic variation explained by each QTL, and the additive effect, were estimated by MAPMAKER/QTL.

Results

Phenotypic variation

Under the 140 mM NaCl condition, the distribution of the survival days of seedlings (SDSs) from the 133 F_3 lines was illustrated in Fig. 1. It was normally distributed ranging from 22 to 36 days, indicating polygenic segregation.

Four physiological traits in the shoots or the roots were measured (Table 1). The distributions of phenotypic data for these traits in the shoots or the roots treated by 140 mM NaCl for 10 days were shown, respectively, (Fig. 1). For all traits, the F_2 population showed continuous segregation. The SNTQ, SKC, RNC and RKC showed significant transgressive segregations with values either larger or smaller than those of the parents.

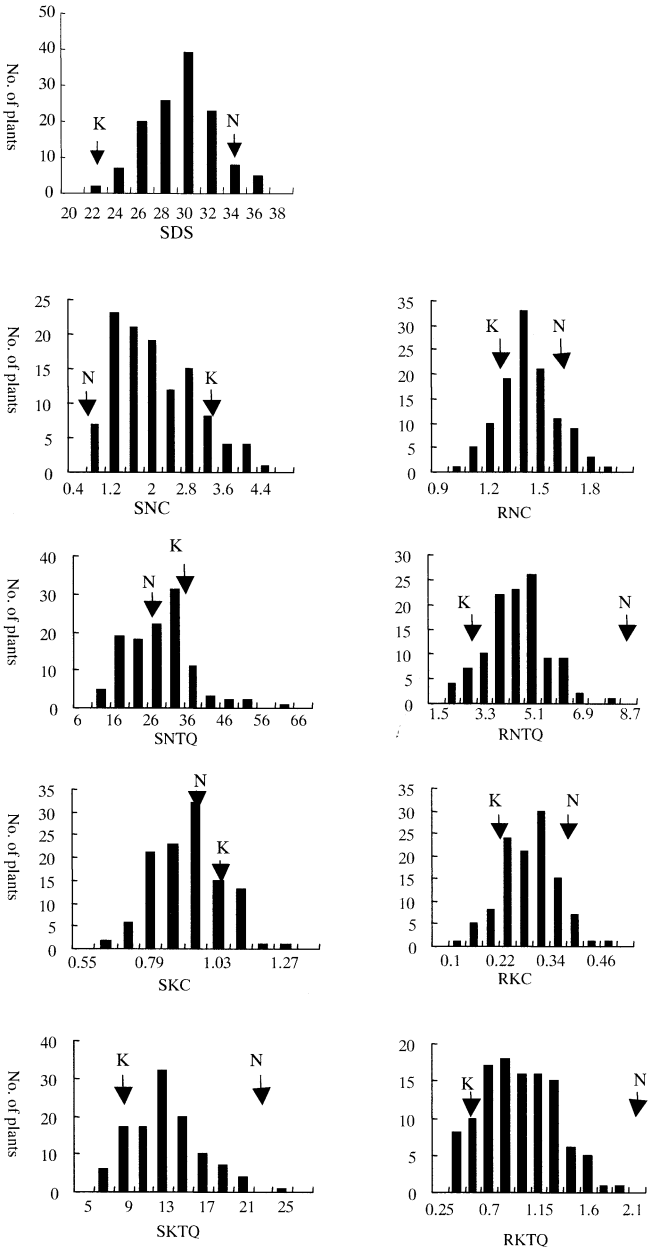

Fig. 1 Frequency distribution of survival days of seedlings (SDSs) under salt stress and four physiological traits of the shoots and the roots under salt stress for 10 days in the 133 F_3 lines. *Arrows* indicate the mean of traits for two parents. *K* and *N* indicate Koshihikari and Nona Bokra, respectively

Table 2 Correlation coefficients between SDS and four traits of the shoots of seedlings, and among four traits of the shoots of seedlings under salt stress

Trait	SDS	SNC	SNTQ	SKC
SNC	−0.422**			
SNTQ	−0.364**	0.794**		
SKC	0.125	−0.266**	−0.307**	
SKTQ	0.153	−0.627**	−0.169	0.461**

** Indicates significant difference at the 0.01 level

Table 3 Correlation coefficients between SDS and four traits of the roots of seedlings, and among four traits of the roots of seedlings under salt stress

Trait	SDS	RNC	RNTQ	RKC
RNC	−0.134			
RNTQ	−0.021	0.460**		
RKC	0.181	0.271**	0.398**	
RKTQ	0.121	0.160	0.792**	0.760**

** Indicates significant difference at the 0.01 level

Correlation among physiological traits

The correlation coefficients between SDS and four physiological traits in the shoots and in the roots of seedlings under salt stress, were presented in Tables 2 and 3, respectively. SDS was only negatively correlated with two Na^+ traits in the shoots, SNC and SNTQ, respectively.

The correlation coefficients among four physiological traits of the shoots of seedlings in salt stress were shown in Table 2. Of six combinations among four traits, five pairs showed significant correlations. SNC was positively correlated with SNTQ and negatively correlated with both SKC and SKTQ. SNTQ was negatively correlated with SKC. SKC was positively correlated with SKTQ. Among four traits of the roots of seedlings, the positive correlations between RNC and RNTQ or RKC, between RNTQ and RKC or RKTQ and between RKC and RKTQ were observed (Table 3).

Construction of the linkage map

Of the 161 RFLP markers, genotypes of the F_2 population were tested, and 154 marker loci were mapped on the

Table 1 Traits analyzed

Trait abbreviation	Trait description
SDS	Survival days of seedling
SNC	Shoot Na^+ concentration (Î¼mol mg^{-1} of shoot dry weight)
SNTQ	Shoot Na^+ total quantity (Î¼mol/plant)
SKC	Shoot K^+ concentration (Î¼mol mg^{-1} of shoot dry weight)
SKTQ	Shoot K^+ total quantity (Î¼mol/plant)
RNC	Root Na^+ concentration (Î¼mol mg^{-1} of root dry weight)
RNTQ	Root Na^+ total quantity (Î¼mol/plant)
RKC	Root K^+ concentration (Î¼mol mg^{-1} of root dry weight)
RKTQ	Root K^+ total quantity (Î¼mol/plant)

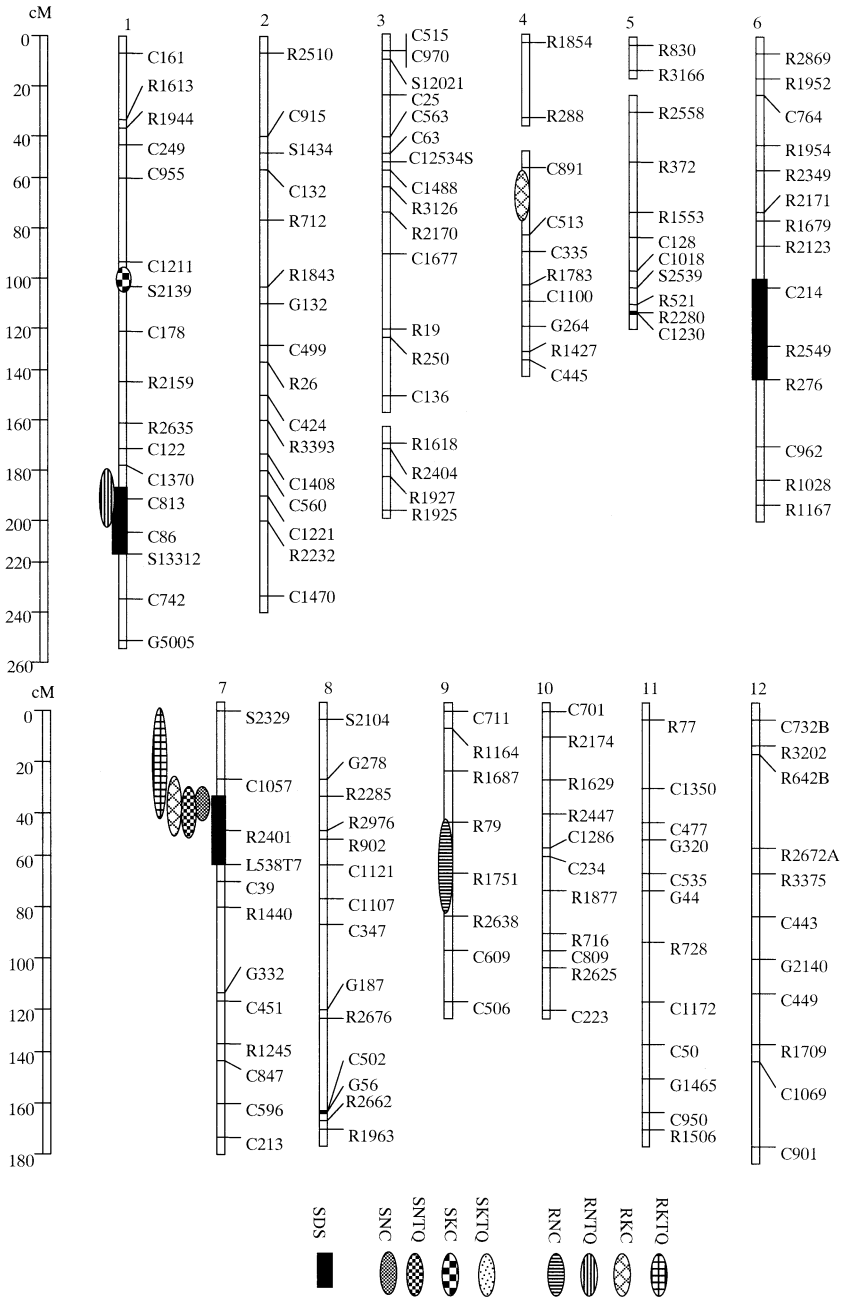

Fig. 2 Genetic linkage map showing the location of QTLs for survival days of seedlings (SDSs) and four physiological traits of the shoots and the roots under salt stress (140 mM of NaCl) in the Nona Bokra / Koshihikari F_2 population. Distances are in Kosambi centi-Morgans. The *boxes* or the *ellipses* on the chromosomes represent putative regions of QTLs. A reduction of a one LOD value from LOD peaks was used to define left and right borders of the confidence interval for QTLs

linkage map (Fig. 2). The linkage map covered 12 chromosomes and spanned 1,704.4 cM of the rice genome with an average interval of 12.3 cM between marker loci. There were gaps on chromosomes 3, 4 and 5. It was found that most markers on the map were located on the expected chromosome in the expected orders by comparing with the map of Harushima et al. (1998).

QTL mapping

QTLs for survival days of seedlings (SDSs)

Three QTLs were detected on chromosomes 1, 6 and 7, respectively (Table 4 and Fig. 2). qSDS-1 with the largest effect explained 18.0% of the total phenotypic variance, and the additive effect of the Nona Bokra allele increased SDS by 1.92 days. The other two QTLs, qSDS-6 and qSDS-7, explained 17.0% and 13.9% of the total phenotypic variance, respectively, and the Nona Bokra allele at these QTLs increased SDS.

Table 4 Putative QTLs for salt tolerance in the F_2 population derived from Nona Bokra and Koshihikari

Traits	QTL[a]	Chr.	Markers bordering QTL	Peak LOD	a[b]	PVE[c]	DPE[d]
SDS	qSDS-1	1	C813-C86	4.88	1.92	18.0	N
	qSDS-6	6	C214-R2549	3.63	1.73	17.0	N
	qSDS-7	7	R2401-L538T7	3.32	1.22	13.9	N
SNC	qSNC-7	7	C1057-R2401	7.66	–0.51	48.5	K
SNTQ	qSNTQ-7	7	C1057-R2401	4.26	–2.76	16.1	K
SKC	qSKC-1	1	C1211-S2139	11.74	0.11	40.1	N
RNC	qRNC-9	9	R1751-R2638	3.25	0.07	16.7	N
RNTQ	qRNTQ-1	1	C813-C86	3.25	0.61	12.4	N
RKC	qRKC-4	4	C891-C513	4.28	0.04	21.6	N
	qRKC-7	7	C1057-R2401	3.48	0.03	17.8	N
RKTQ	qRKTQ-7	7	C1057-R2401	3.82	0.15	17.3	N

[a] QTLs are named by abbreviations plus chromosomal number
[b] Additive effect on the Nona Bokra allele
[c] Percentage of total phenotypic variance explained by the QTL
[d] Direction of phenotypic effect; *K* and *N* indicate Koshihikari and Nona Bokra, respectively

Shoot Na^+ concentration (SNC)

Under salt stress, only one QTL with a very large effect for SNC was found within the C1057-R2401 region on chromosome 7 (Table 4 and Fig. 2). The qSNC-7 explained 48.5% of the total phenotypic variance, and the additive effect of the Nona Bokra (salt tolerance variety) allele reduced SNC by 0.51 μmol mg^{-1}.

Shoot Na^+ total quantity (SNTQ)

One QTL for SNTQ was also mapped within the C1057-R2401 region on chromosome 7 under salt stress. The QTL explained 16.1% of the total phenotypic variance, and had an additive effect of 2.76 μmol for reducing SNTQ from the Nona Bokra allele.

Shoot K^+ concentration (SKC)

One QTL for SKC with a very large effect was detected under salt stress. This QTL was located within the C1211-S2139 region on chromosome 1 (Table 4 and Fig. 2). The qSKC-1(LOD=11.74) accounted for 40.1% of the total phenotypic variance, and the Nona Bokra allele for qSKC-1 had an additive effect of 0.11 μmol mg^{-1} for increased SKC.

Shoot K^+ total quantity (SKTQ)

No QTL for SKTQ was detected under salt stress.

Root Na^+ concentration (RNC)

One QTL affecting RNC, qRNC-9, was identified on chromosome 9 (Table 4 and Fig. 2). This QTL had a relatively small effect, which explained 16.7% of the total phenotypic variance and had the additive effects of 0.07 μmol mg^{-1} for increased RNC.

Root Na^+ total quantity (RNTQ)

One QTL was found on chromosome 1. The QTL explained 12.4% of the total phenotypic variance and the Nona Bokra allele increased RNTQ.

Root K^+ concentration (RKC)

Two QTLs affecting RKC were identified on chromosomes 4 and 7. The percentages of phenotypic variance explained by these QTLs were 21.6% and 17.8%, respectively, and the additive effects were 0.04 and 0.03 μmol mg^{-1}, respectively. The Nona Bokra alleles at both QTLs resulted in an increment of RKC.

Root K^+ total quantity (RKTQ)

One QTL affecting RKTQ was detected and mapped to the same chromosomal location as the QTL for RKC on chromosome 7. The QTL explained 17.3% of the trait variance, and had a positive additive effect of 0.15 μmol.

Discussion

Comparison between QTLs detected in this study and those in previous reports

In the present study, we found 11 QTLs including three for SDS, three for three traits of the shoots, and five for four traits of the roots at six chromosomal regions controlled complex physiological traits related to rice salt-tolerance under salt stress (Table 4, and Fig. 2). There have been several other reports on QTL analysis of rice salt-tolerance (Zhang et al. 1995; Lin et al. 1998; Gong et al. 1999; Koyama et al. 2001). Most of these QTL analyses were conducted by using RFLP markers developed at the Cornell University (Causse et al. 1994) except for the study of Koyama et al. (2001), which used an AFLP linkage map which anchored few Microsatellites

and few RFLP markers of Cornell University. However, RFLP markers of the Japanese Rice Genome Research Program (RGP) were used in the present study. Therefore, it is difficult to directly compare the chromosomal location of QTLs detected in this study and the previous report. However, recently, a RFLP linkage map of RGP (Harushima et al. 1998) and one the Cornell University (Causse et al. 1994) were integrated (http://www.gramene.org/). It allowed us to roughly compare the QTLs detected in different groups. The chromosomal position of qSKC-1 for the shoot K^+ concentration detected in this study is similar to that of the *K^+1 conc* reported by Koyama et al. (2001). However, qSKC-1 as a major QTL with a very large effect explained 40.1% of the total phenotypic variance, while *K^+1 conc* with a small effect only explained 10.6% of the variance for this trait. The comparison between the chromosomal positions of the two QTLs is difficult to determine; whether both QTLs are at the same loci or are different tightly linked loci. Further analysis, including the fine mapping of both QTLs using common markers, and cloning and the sequence comparison of these QTLs, will be required to answer these questions. Only one QTL for salt tolerance was detected in three other studies (Zhang et al. 1995; Lin et al. 1998; Gong et al. 1999), respectively; however, these three QTLs were not located on the same or the similar regions corresponding to the QTLs detected in this study. Based on the comparison of this study and previous studies, qSNC-7 as a major QTL for shoot Na^+ concentration, which had a large effect and explained 48.5% of the total phenotypic variation, was newly identified on chromosome 7. No detection of this QTL in previous studies may due to the fact there is no variation between the two parents for this QTL.

Trait correlations and the clustering of QTLs

QTLs for traits correlated were often mapped in the same chromosomal regions (Abler et al. 1991; Paterson et al. 1991; Vedboom et al. 1994). This trend was observed in this study. For example, SDS and SNC were correlated and had two QTLs, qSDS-7 and qSNC-7, which were found at approximately the same map locations in chromosome 7 (Table 2 and Fig. 2). SDS and SNTQ also showed a high correlation, and had two QTLs, qSDS-7 and qSNTQ-7, in similar location on chromosome 7 (Table 2 and Fig. 2). In these cases, the directions of the correlations were consistent with that of the effects of the QTLs on the traits (Table 2 and Table 4). These results supported the fact that the trait correlation may be attributed to the effect of pleiotropy or to the very close linkage of genes.

Phenotypic resistance of salinity is expressed as the ability to survive and grow in a salinised medium (Yeo et al. 1990). The survival day of seedlings (SDSs) is a final criterion that measured salt tolerance of the plant in a salinised medium. However, SDS is complex physiological trait related to ion concentration or quantity and to osmosis. Salinity affects almost all processes of the plant, because of the osmotic effects by high ionic concentrations, and because of competitive interference with nutrient uptake and of toxic effects within the plant tissue (Yeo and Flowers 1989). In this study, SDS was correlated with shoot Na^+ concentration (SNC) and shoot Na^+ total quantity (SNTQ), respectively, but not with root Na^+ concentration (RNC) and root Na^+ total quantity (RNTQ) under salt stress (Tables 2 and 3). It was suggested that internal Na^+ concentration or the quantity of the shoot was increased by transport of Na^+ from the root to the shoot (leaf) in external high concentration (140 mM NaCl), and the build up of salt in the leaves, which subsequently led to the fact that the leaves were ultimately damaged, because re-translocation from shoot to root is trivial than that from root to shoot (Yeo and Flowers 1982). This suggestion supports the notion that excess Na^+ was the primary cause of salt sensitivity in non-halophytes (Greenway and Munns 1980). On the other hand, the concentration or quantity of K^+ in both shoot and root was not correlated with SDS (Tables 2 and 3). These results suggested that the high concentration of K^+ did not directly damage leaves.

QTL pyramiding

QTL pyramiding is the process that assemble many genes that work well together and, for a specific trait, assemble the alleles with similar effects from different loci (Xu 1997). This process can create the superior genotype to improve the variety. In this study of 133 F_3 lines, three lines showed the largest surviving days of the seedlings (35 to 35.8 days), i.e. high salt tolerance. Actually, the alleles of several QTLs from the high salt-tolerance variety Nona Bokra were pyramided in these three lines, respectively. In the three lines, the Nona Bokra alleles of five QTLs (qSDS-1, qSDS-7, qSNC-7, qSKC-1 and qRNC-9), three QTLs (qSDS-1, qSDS-7 and qSNC-7) and three QTLs (qSDS-7, qSNC-7 and qSKC-1) were assembled, respectively. These results indicated that breeding methods of QTLs pyramiding by using marker-assisted selection is very useful for the development of new varieties with a high level of salt tolerance.

Relationship between Na^+ and K^+

Based on several studies, the processes of Na^+ and K^+ uptake in rice were considered to be independent under salt stress (Yeo et al. 1987, 1988; Garcia et al. 1997; Yadav et al. 1997). Koyama et al. (2001) also pointed out that the uptake of Na^+ and K^+ maybe be independent, due to the major pathways of Na^+ and K^+ uptake in rice occur in parallel and not directly in competition. However, based on data in Table 2 of this study, there was a negative correlation between SKC and SNC, suggesting that a competition between Na^+ and K^+ occurred in terms of uptake in the shoots.

K^+ is critical for Na^+ tolerance due to the fact that K^+ and Na^+ are chemically very similar. Zhu et al. (1998) reported that SOS (for salt overly sensitive) genes, *SOS1*, *SOS2* and *SOS3* in *Arabidopsis*, were postulated to encode regulatory components controlling plant K^+ nutrition which in turn was essential for salt tolerance, and considered that K^+ nutrition correlated closely with salt tolerance in salt stress. We found that one major QTL controlling shoot K^+ concentration, qSKC-1, which the allele of the high salt-tolerant variety Nona Bokra at this locus increased K^+ concentration in the shoot (Table 4), and indicated that qSKC-1 maybe plays important roles in rice salt tolerance under salt stress. We are progressing with map-based cloning of qSKC-1 to understand its function.

The difference of QTLs for salt tolerance between the shoots and the roots of seedlings

There have not been reports on QTLs for salt tolerance of the roots in previous studies. However, such QTLs are also important for understanding the mechanisms involved in the salt tolerance of rice. In the current study, we detected five QTLs for four traits associated with salt tolerance in the roots, and also identified three QTLs for three traits of the shoots. However, QTLs detected between the shoots and the roots of seedlings were quite different. Between the QTL for SNC and the QTL for RNC, and between the QTL for SNTQ and the QTL for RNTQ, these were not the same map locations, (Table 4, Fig. 2). One QTL for SKC and two for RKC were detected on different chromosomes, respectively. It was suggested that the genes controlling the transport of the two ions, Na^+ and K^+, between the shoots and the roots of seedling, may be different or induced incoordinately by salt stress. Guo et al. (2001) have analyzed the expression of *PKS2* to *PKS8* in shoots and in roots, and their regulation by salt stress; they also found that some were expressed at a higher level in the root than in the shoot. This observation supported our suggestion.

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