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Genetic dissection of silicon uptake ability in rice (*Oryza sativa* L.)

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Abstract

The adequate presence of silicon (Si) in rice plants can enhance their yield and improve their tolerance to various biotic and abiotic stresses. In this study Si uptake abilities were compared between the japonica rice cultivar (cv.) Kinmaze and the indica rice cv. DV85 under three Si concentrations (0.16, 0.4, and 1.6 mM) at different time points from 1 to 12 h. The results showed that the phenotypic values of two traits—Si uptake by individual plants (SP, Si uptake by all roots of a plant) and Si uptake per unit root dry weight (SR = SP/root dry weight)—of Kinmaze were significantly higher than those of DV85 ($P < 0.01$). Meanwhile, a kinetic study indicated that the Si transporters in Kinmaze and DV85 had the same affinity for silicic acid, but with different V_{max} values, indicating that Kinmaze had more Si transporters in the roots than DV85. This may be the main reason for the difference in Si uptake ability between Kinmaze and DV85. In addition, a mapping population consisting of 81 recombinant inbred lines (RILs) derived from the cross between Kinmaze and DV85 was used to detect quantitative trait loci (QTLs) underlying SP and SR. The RILs follow a continuous one-peak distribution and show transgressive segregation in both directions for SP, SR, and root dry weight (RDW). Three QTLs for SP, four for SR, and three for RDW were detected. This can explain 7.16–17.15% of the phenotypic variation (PVE). Thus, the results obtained in this study provide a better understanding of the mechanism of rice Si uptake ability and the basis for fine-mapping the genes involved.

Keywords: Rice (*Oryza Sativa* L.); Si uptake; Recombinant inbred lines (RILs); Quantitative trait locus (QTL)

1. Introduction

Silicon in rice plants can increase photosynthesis, decrease susceptibility to disease and insect damage, prevent lodging, and alleviate water and various mineral stresses [1–5]. Most beneficial effects from Si are realized through the formation of silica gel, which is deposited on the surface of leaves, stems and other organs of plants [4]. Without Si, the growth of rice is negatively affected, and the productivity decreases greatly due to reduced fertility [6,7].

Ma and Takshashi [5] found that Si accumulation in shoots varied considerably among plant species. Among higher plants, only Gramineae and Cyperacea showed a high Si accumulation. Cucurbitales, Urticales, and Commelinaceae have an intermediate Si accumulation, whereas most other plant species have low Si accumulation. The differences in Si accumulation have been attributed to the Si absorbing ability of the roots. Three Si uptake modes have been proposed: active, passive, and rejective uptakes, which are responsible for high, medium, and low Si accumulation in the plants, respectively [8]. Since most important crops are unable to take up Si actively via the roots, they therefore fail to attain high Si levels in the shoots and cannot benefit from Si. However, the foliar application of Si has been reported to be effective in inhibiting powdery mildew development on cucumber, muskmelon, and grape leaves [9,10]. A possible reason may be that Si applied to leaves could deposit on the surface of leaves and play a similar role to Si absorbed by the roots. Nevertheless, the most effective strategy to improve Si uptake capacity is the utilization of the best plant genotype to increase the Si uptake genetically in cultivars. In this case the beneficial effects of Si would be consistent from plant to plant.

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Rice is a typical Si-accumulating plant. Si accumulation in rice plant may exceed 10% of the shoot dry weight [5]. High Si accumulation in rice originates from the Si-uptake capacity of root [8,11]. A proteinaceous transporter mediates Si uptake in rice roots [12]. A higher density of the transporter SIT1 for radial transport and the presence of the SIT2 transporter for xylem loading are responsible for the higher Si accumulation in rice [13]. The gene *SIT2*, encoding the Si transporter SIT2 for xylem loading, has been mapped to chromosome 2 by using an F_2 population derived from the cross between a rice mutant and the indica rice cv. Kasalath [14].

In addition, Deren et al. [15], Winslow [16,17], and Ma and Takshashi [5] found that japonica rice had a higher Si concentration than indica rice in Si-deficient soil condition. Genotypic differences in Si concentration was associated with ecotype (subspecies), implying that the Si uptake ability might be different between japonica and indica. Majumder et al. [18] showed that phenotypic differences in Si concentrations of rice were controlled by polygenes. Recently, Dai et al. [19] identified a total of 10 QTLs with additive effects and 14 digenic interactions with additive-by-additive epistatic effects for the silicon concentration in different organs in rice.

Most research concerning the comparison of root Si uptake ability in different rice cultivars is conjectural from testing the Si content in shoots. There is no study directly using the Si uptake from the roots. Because roots are the uptake organ for Si, a systematic analysis of Si uptake directly from roots is necessary. In addition, a genetic analysis of high Si uptake cultivars of rice will also be a valuable tool for dissecting the mechanism of rice high Si uptake. The objectives of this study were (i) to compare Si uptake ability between the japonica cv. Kinmaze and the indica cv. DV85, and (ii) to identify QTLs controlling Si uptake in rice.

2. Materials and methods

2.1. Plant materials and growth environment

A total of 81 RILs were derived by single-seed descent from a cross between Kinmaze and DV85. The RIL population was previously genotyped using 137 restriction fragment length polymorphism (RFLP) markers, which were distributed evenly on the 12 rice chromosomes [20]. This linkage map extends 1386.2 cM with an average marker interval of 10.1 cM.

More than 20 seeds from each of the two parents and 81 RILs were surface sterilized in 0.5% (v/v) NaOCl for 10 min, then rinsed and soaked in deionized water at 30 °C for 1 day. Seeds were germinated in a dark growth chamber at 30 °C for 2 days. Ten uniformly-germinated seedlings from each line were transplanted to plastic sieves with pores of approximately 2.9 mm (just less than the size of rice seeds). The plastic sieves were then put into plastic pots (length, 31.5 cm; width, 24.5 cm; height, 12.5 cm) containing 4.5 l of one-half-strength of Kinmura B nutrient solution (pH 5.6, no silicon added); the seeds on sieves were just immersed into the nutrient solution, which was renewed every 2 days. The plants grew in a controlled-environment growth chamber at 26/22 °C (14 h light/10 h dark).

2.2. Time course study of Si uptake between Kinmaze and DV85

Five 20-day uniform seedlings from Kinmaze and DV85 were selected for the Si uptake study. These plants were placed into 50 ml plastic bottles containing one-half concentration of Kimura B solution complemented with 0.16, 0.4, and 1.6 mM Si, respectively. Each bottle was wrapped with opaque plastic membrane. At 1, 3, 6, 9, and 12 h after the Si treatment, 0.9 ml liquid of the uptake solution was taken from each bottle for the determination of Si concentration. Transpiration was also measured by evaluating water loss at each sampling time. After the uptake experiment, the roots were harvested and dried in an oven at 60 °C for 2 days, and the dry weights were recorded.

Potassium metasilicate (K_2SiO_3) was used as the source of silicon. The pH of the nutrient solution was adjusted to 5.6 by using 0.1 mM HCl. The amount of Si uptake was calculated from the depletion of Si in the uptake solutions. Si uptake per plant (SP) was calculated according to the following formula:

$$SP = NW_b \times CS_b - (NW_b - WW) \times CS_f$$

where NW_b is the amount of nutrient at the beginning of experiment; CS_b and CS_f are the Si concentrations at the beginning and the end of the experiment, respectively, and WW is the amount of water loss. Si uptake per unit root dry weight (SR) was calculated as:

$$SR = SP/RDW$$

where RDW is the root dry weight per plant. The Si concentration in the solution was determined by using the colorimetric molybdenum blue method as described by Okuda and Takahashi [21] and Ma et al. [22].

2.3. Kinetic study of Si uptake between Kinmaze and DV85

The 20-day seedlings of Kinmaze and DV85 were prepared as described in Section 2.1. The seedlings were allowed to take up Si in the nutrient solution (1/2 Kimura B, pH 5.6) containing silicic acid at a series of concentrations (0.1, 0.2, 0.3, 0.4, 0.8, 1.3, 1.6, and 2.0 mM) in a 50 ml plastic bottle. Each of the two parents was repetitively analyzed for three replicate plants after the uptake period of 9 h.

2.4. Si uptake of the RILs

The seedlings of the 20-day plants from each of the 81 RILs and the parents were allowed to absorb Si in the nutrient solution (1/2 Kimura B, pH 5.6) containing 0.4 mM silicic acid. Each line had five replicate plants, and the uptake period was 9 h. This experiment was repeated two or three times per line depending on the reproducibility of the phenotype data collected.

2.5. QTL analysis

Composite interval mapping (CIM) was conducted by using Win QTL Cart 2.0 at a LOD threshold of 2.0 [23]. The naming of QTL followed the rule formulated by McCouch et al. [24].

3. Results

3.1. Comparison of Si uptake ability between Kinmaze and DV85

Si uptake increased with time in both cultivars at the three levels of Si concentrations: low (0.16 mM), medium (0.4 mM), and high (1.6 mM) (Fig. 1). In the low Si nutrient, the SP and SR of Kinmaze at 6 h were 86.15 μg plant^{-1} and 12.14 mg g^{-1} root dry weight (Fig. 1A and B), respectively. These values were significantly higher than those of DV85, with a SP and SR of 63.38 μg plant^{-1} and 9.16 mg g^{-1} root dry weight, respectively. The same tendency was observed at 9 and 12 h (Fig. 1A and B), and in the 0.4 mM (Fig. 1C and D) and 1.6 mM Si concentration nutrients (Fig. 1E and F). However, no significant difference was observed in the transpiration rate between the two cultivars (data not shown). The results showed that the Si uptake ability represented by either SP or SR in Kinmaze was significantly higher than that in DV85 from 3 to 12 h. Additionally, no difference was observed in the root dry weight between Kinmaze and DV8, indicating that the difference of SP between the two cultivars resulted from SR.

3.2. Kinetics of the Si uptake in Kinmaze and DV85

When the Si concentration in the nutrient solution was low, the Si uptake by the roots of both Kinmaze and DV85 was enhanced with increasing external Si concentration (Fig. 2). However, the Si uptake was saturated at a concentration of approximately 0.8 mM. This is consistent with the result reported by Tamai and Ma [12], namely, that Si uptake by rice is mediated by a kind of proteinaceous transporter. When the Si concentration became high, significant differences were observed between the two rice cultivars. The V_{max} value was

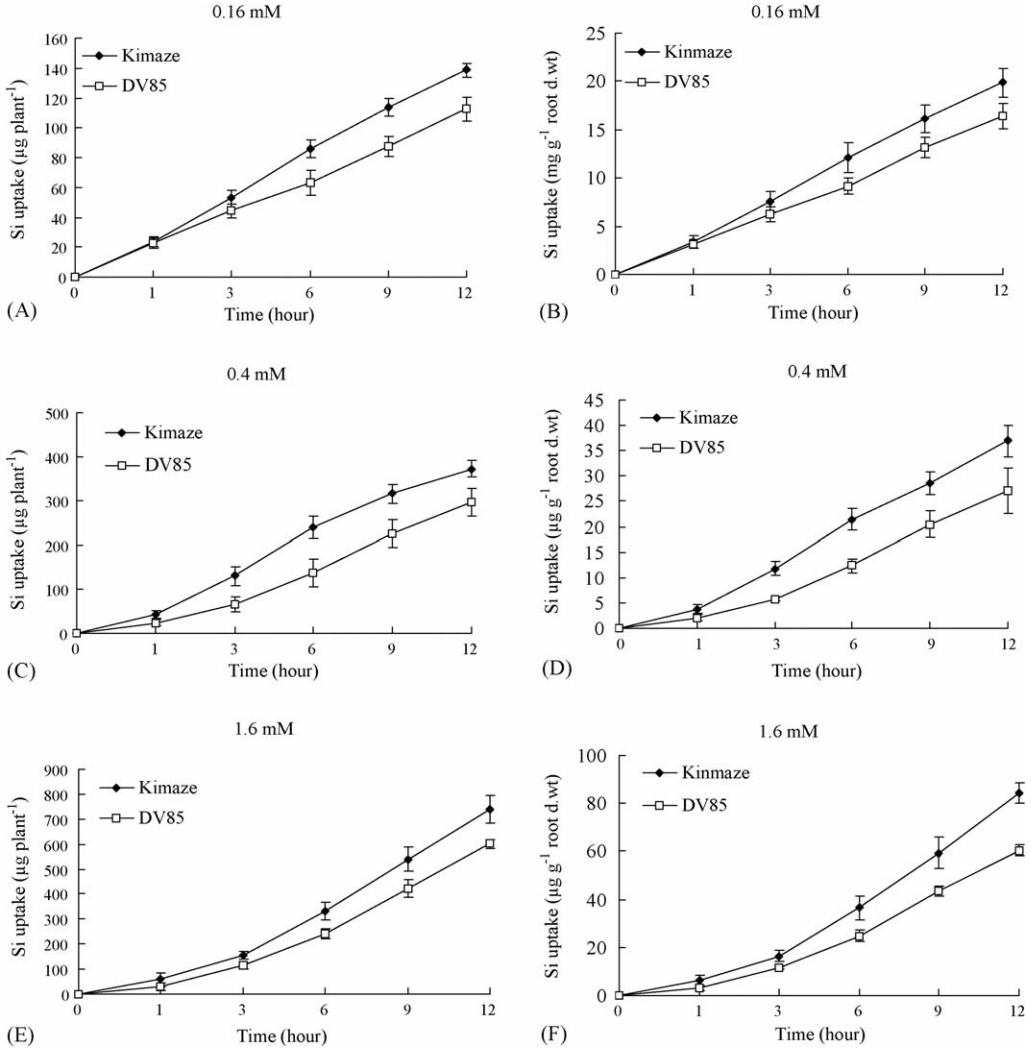

Fig. 1. Si uptake in the japonica cv. Kinmaze and the indica cv. DV85. Twenty-day-old seedlings were placed in a nutrient solution containing 0.16 mM (A, B), 0.4 mM (C, D) and 1.6 mM (E, F) Si, respectively. Left: Si uptake per plant; right: Si uptake per unit root dry weight. Data shown are means ± S.D. of five replicates.

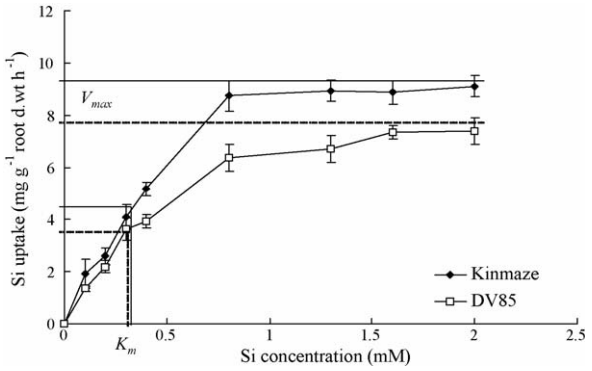

Fig. 2. Silicon uptake by roots of Kinmaze and DV85 with various Si concentrations. The seedlings were cultured for 9 h. Data shown are means ± S.D. of three replicates.

estimated as 9.3 mg g^{-1} root dry weight h^{-1} for Kinmaze and 7.5 mg g^{-1} root dry weight h^{-1} for DV85. However, based on the curve, the half saturation value (K_m) was estimated at 0.28–0.34 mM for Kinmaze and DV85. This result indicated that the transporters of the two cultivars have a similar affinity for silica acid. The V_{max} of Kinmaze was significantly higher than that of DV85, indicating that the density of the Si transporter in the root differs between the two cultivars. Kinmaze has a higher density of Si transporter than DV85 resulting in the different SR in the two cultivars.

3.3. Variation of Si uptake ability and root dry weight in the RIL population

The Kinmaze/DV85 RIL population showed considerable transgressive segregation for both SP and SR (Fig. 3). Approximately three- and four-fold increases in variation for the SP and SR in the RIL population existed compared with the difference between the parents. A 325 μg $plant^{-1}$ difference in SP and a 39 mg g^{-1} root dry weight difference in SR were observed between the two extreme RILs, indicating larger variation occurs among the 81 RILs. The SP and SR of the population ranged from 125 to 450 μg $plant^{-1}$, and from 27 to 66 mg g^{-1} root dry weight, with a mean of 256.13 μg $plant^{-1}$ and 38.66 mg g^{-1} root dry weight, respectively. Additionally, transgressive segregation for the RDW was also observed in the RILs though there was less difference in the RDW between the parents (Fig. 3C). The phenotypic values of RDW ranged from 2.87 to 12.65 mg, with a mean of 6.84 mg. Therefore, the phenotypic normal distribution and transgressive segregation in the RIL population indicated the polygenic inheritance of the SP, SR, and RDW.

In addition, although a low correlation was observed between the SP and SR, the highly significant correlation between the SP and WR ($r = 0.8087^{**}$) suggested that SP was much more affected by WR than by SR. Thus, root biomass may play an important role in Si uptake per plant. Also, a negative correlation ($r = -0.4489^{**}$) between the SR and WR existed, indicating that the increased amount of the Si transporter in the roots was not equal to that of the biomass. This implied that the higher density of Si transporter in Kinmaze might be a result of higher transportation speed in Kinmaze than in DV85 controlled by the unknown Si transporter gene.

3.4. QTL analysis for Si uptake and root dry weight in rice

Three QTLs flanked by *R1440-XNpb379*, *G187-R1963*, and *C701-C148* on chromosomes 7, 8, and 10 were identified for SP with PVEs of 13.15, 10.99, and 11.46%, respectively (Table 1).

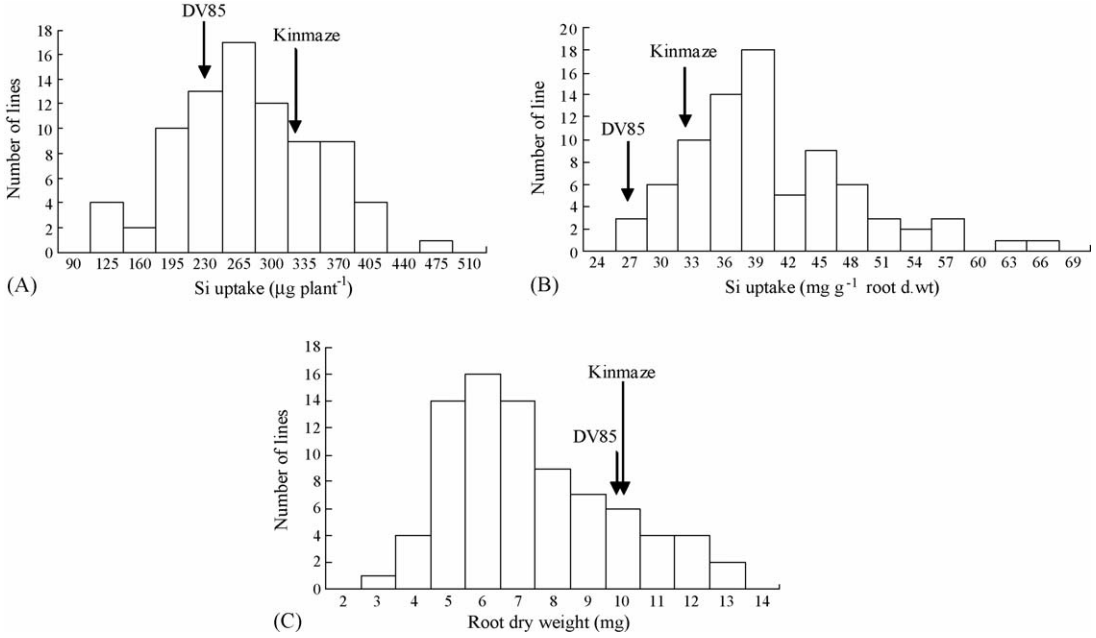

Fig. 3. Frequency distributions of the phenotypic values of Si uptake per plant (A), Si uptake per unit root dry weight (B), and root dry weight (C) among the 81 RI lines and two parents.

Table 1
Chromosome locations and genetics effects of QTLs for Si uptake ability per plant (SP) in the Kinmaze/DV85 RIL population

Locus	Chromosome	Marker interval	LOD score	Additive effect (μg plant^{-1})	Variance explained (%)
qSILp-7	7	*R1440-XNpb379*	3.31	26.61	13.15
qSILp-8	8	*G187-R1963*	3.03	−24.45	10.99
qSILp-10	10	*C701-C148*	2.36	−25.67	11.46

Table 2
Chromosome locations and genetic effects of QTLs for Si uptake ability per unit root dry weight (SR) in the Kinmaze/DV85 RIL population

Locus	Chromosome	Marker interval	LOD score	Additive effect (mg g^{-1} root dry weight)	Variance explained (%)
qSILr-1	1	*R1485-XNpb343*	3.39	2.87	11.65
qSILr-3	3	*XNpb182-XNpb74*	2.06	2.18	7.16
qSILr-9	9	*C609-XNpb108*	3.65	3.25	15.14
qSILr-11	11	*C410-XNpb44*	3.39	2.89	12.21

Table 3
Chromosome locations and genetic effects of QTLs for root dry weight (RDW) in the Kinmaze/DV85 RIL population

Locus	Chromosome	Marker interval	LOD score	Additive effect (mg)	Variance explained (%)
qRDW-2	2	*R418-C560*	3.68	0.97	17.15
qRDW-3	3	*XNpb144-XNpb249*	2.29	−0.86	13.52
qRDW-7	7	*R2394-XNpb379*	2.25	0.67	8.08

The allele from Kinmaze at *qSILp-7* increased SP, but the Kinmaze alleles at *qSILp-8* and *qSILp-10* decreased SP. Four QTLs located at *R1485-XNpb343*, *XNpb182-XNpb74*, *C609-XNpb108*, *C410-XNpb44* were detected for SR on chromosomes 1, 3, 9, and 11, with PVEs of 11.65, 7.16, 15.14, and 12.21%, respectively (Table 2). Four alleles from Kinmaze at these four loci increased the phenotypic values of SR by 2.87, 2.18, 3.25, and 2.89 mg g^{-1} root dry weight, respectively.

Three QTLs defined by *R418-C560*, *XNpb144-X249*, and *R2394-XNpb379* were identified for RDW on chromosomes 2, 3, and 7, explaining the 17.15, 13.52, and 8.08% of phenotypic variance, respectively. The positive alleles for increasing RDW at *qRDW-2* and *qRDW-7* were from Kinmaze, while the positive effect of *qRDW-3* was contributed by the allele from DV85.

This co-localization of the QTLs *qSILp-7* and *qRDW-7* (Tables 2 and 3) may theoretically result from the pleiotropic effects of the same locus or the physical linkage of two loci. It was highly probable, however, that *qSILp-7* and *RDW-7* are the same locus in this study. The main reasons included: (1) this genomic region had a positive additive effect for both SP and RDW, (2) the positive effects of the two QTLs were both distributed by the allele Kinmaze, and (3) the correlation of SP and SR was considerably higher in the RILs population ($r = 0.8087^{**}$), implying that this QTL may increase SP by increasing the root biomass.

4. Discussion

Si absorbed by roots is in the form of silicic acid as an undissociated molecule [25]. Si is then immediately transported to the shoot, together with the transpiration stream, and polymerized and accumulated on the cell surface of the rice leaf [26]. The amount of Si in roots is about 2% of the total Si accumulation of whole plants [27]. Hence, the Si concentration in shoots is mainly determined by two factors: (1) the Si absorbed by the whole root system (SP: the amount of Si uptake by an individual plant) and (2) the shoots' biomass growth (WS: the weight of all the macronutrients and micronutrients accumulated in shoots such as O, H, C, Si, N, P, K, Ca and Mg, etc.). The Si concentration in the whole shoot can be calculated as SP/WS. It may be more reasonable to choose SP when conferring the Si concentration in shoots. On the other hand, nutrient uptake per unit weight (or length) of roots reflected the uptake ability by roots, and properties of transporters in roots could be also illuminated through the research on Si uptake per unit root weight (or length) [12,28]. So, in the present study, Si uptake per plant (SP) and Si uptake per unit dry root weight (SR) were both used to investigate the Si uptake ability. Otherwise, SP might be affected by the amount of rice roots, so that root dry weight (RDW) was also considered in whether RDW has a significant effect on SP in this study.

Since the average Si concentration in soil solution is 0.1–0.6 mM [29], the concentrations of 0.16 mM and 0.4 mM Si used in this study represented the low and common values of the soil solution. The results obtained from these two concentrations of Si should reflect the true differences of Si uptake in the two cultivars under field conditions. Similarly, these results from the analysis of the RILs at the Si concentration of 0.4 mM should be valuable in rice breeding.

The conclusion that the phenotypic values of the SP and SR of Kinmaze (japonica) were significantly higher than those of DV85 (indica) in the three concentrations ($P < 0.01$) (Fig. 1), was consistent with results reported by Deren et al. [15],

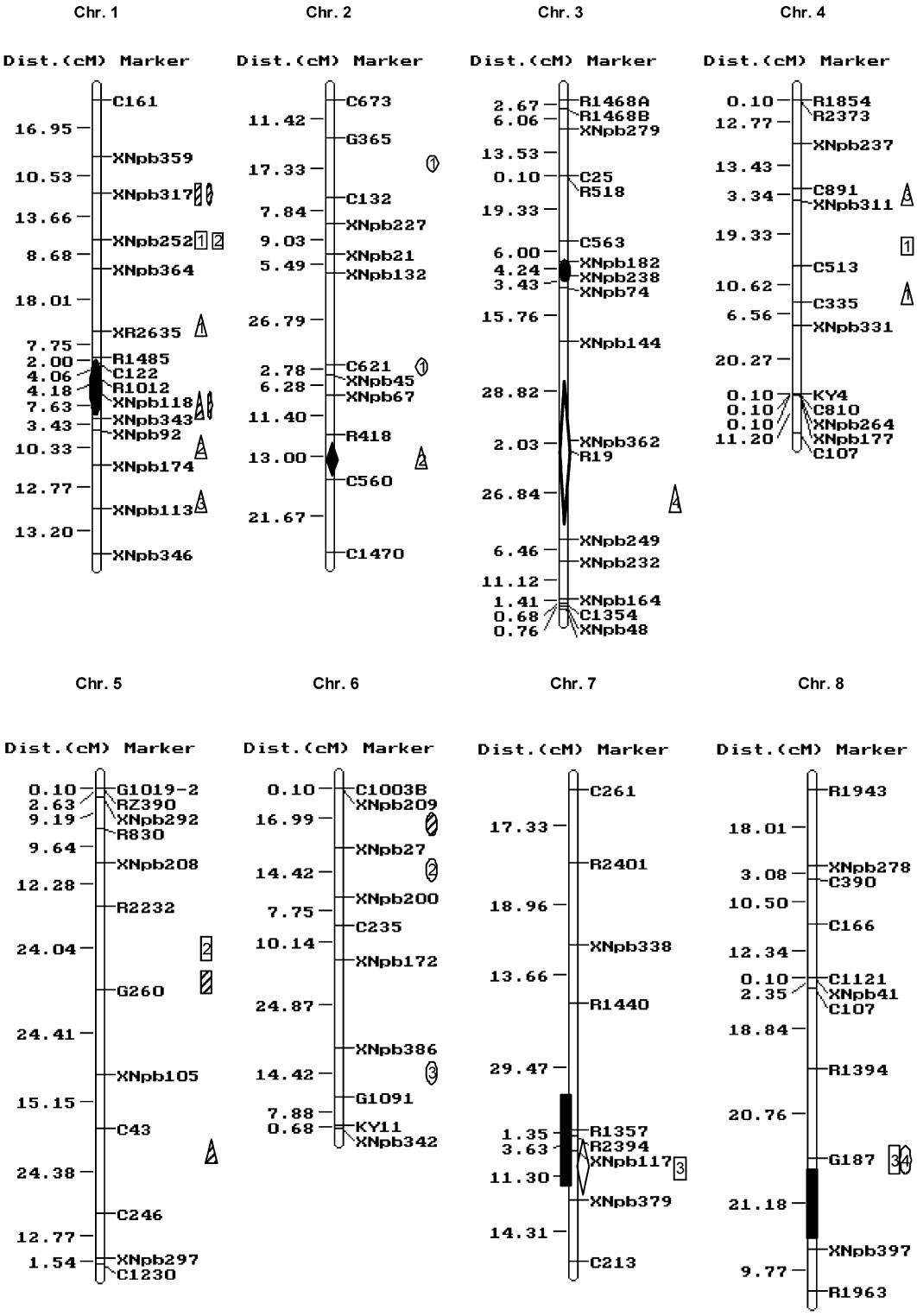

Fig. 4. Chromosomal locations of QTLs associated with Si uptake and QTLs associated with the root dry weight in the Kinmaze/DV85 RIL population and chromosomal locations of the QTLs associated with the Si content in rice organs detected by Dai et al. (2005).

Winslow [16,17], and Ma and Takshashi [5], namely, that japonica rice could accumulate more Si than indica rice when grown on Si-deficient soil. However, our results from both the kinetic study and the time-course experiments showed that the Si uptake ability of the japonica rice Kinmaze was significantly higher than that of indica rice DV85 regardless of the Si concentration. This disagreement with the observations of Winslow [16,17] and Ma and Takshashi [5], namely that no Si concentration differences between the japonica and indica rice were found in Si-rich soil, might result from different responses to Si supply based on the genotypes used in Winslow and Ma. In other words, the indica rice used in their research might have a

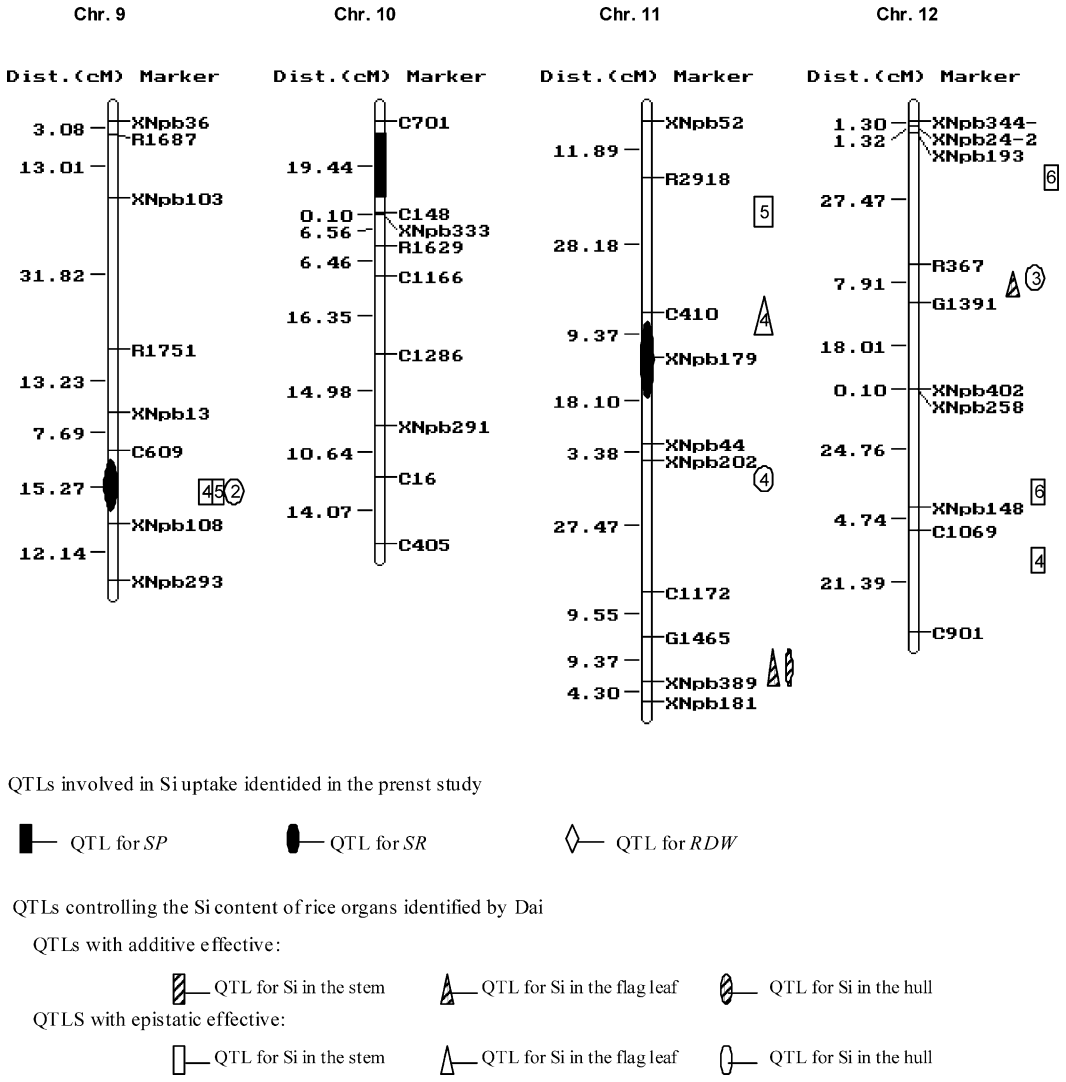

Fig. 4. (*Continued*).

greater increase in the vegetative growth of roots than japonica in a long term Si-rich soil culture. As a result of that, indica rice could uptake larger amounts of Si through its larger root system as compared with japonica rice.

Significant phenotypic variations were observed for SP, SR, and RDW in the Kinmaze/DV85 mapping population, and a total of 10 genomic regions affecting SP, SR, and RDW were identified. However, no co-location between SR and SP was found in this study. The uptake kinetic curves had the same tendencies between the cultivars, and the affinity of transporters for Si showed no difference between the two cultivars (Fig. 4). The difference in Si uptake per unit root dry weight (SR) between the two cultivars mainly came from the density of the transporter when the two cultivars were compared in the same Si concentration. In this case, SR could represent the density of Si transporter in roots, while SP reflects the total amount of Si transporter in the roots of an individual plant. Meanwhile, a higher correlation was found between the SP and root dry weight, but a lower correlation was between the SP and SR in the RIL population. The SP was little affected by SR; they should be two different traits involving in Si uptake and be controlled by two different genetic factors with low correlation. Based on the above analysis, we speculated that the SR affects Si concentration in the xylem flow in root, while the SP controls the total amount of Si uptake by the whole root of an individual plant.

Silicon localization in rice tissues is related to transpiration, and heavy deposits of silica are often observed where water movement terminates [30]. Dai et al. [19] identified QTLs controlling the Si concentration in different organs of rice, but so far no QTLs controlling the Si concentration of whole rice shoot have been reported. Nevertheless, when compared with the results reported by Dai, two of the three QTLs controlling the SP and three of the four QTLs affecting the SR were found to be overlapping or near to the genomic regions where QTLs with additive effects or digenic interactions with additive-by-additive epistatic effects were detected for Si content in different organs (the comparison of the QTL locations between the two studies was performed according to the web-accessible data resource for comparative genome analysis in the grasses:

http://www.gramene.org/). For example, QTLs *qSILp-7*, *qSILp-8*, *qSILr-1*, *qSILr-9*, and *qSILr-11* were overlapping or near to the genomic regions of *RZ395-RM18B*, *R1394-RM210*, *RG570-RM107*, *RM246-RG101* and *RG118-RM202* affecting the Si content in stem, stem, leaf, stem and leaf, respectively. In addition, *qSILp-7* had a similar location to QTLs conditioning stem diameter on rice chromosome 7 identified by Kashiwagi and Ishimaru [31]. This co-localization may be explained by using the result reported by Shimoyama , namely, that Si could increase the thickness of the culm wall and the size of the vascular bundles [32]. However, the *SIT2* gene mapped on chromosome 2 by Ma et al. [14] was not detected in this study, possibly because the two cultivars have the same affinity for the silica acid associated with the *SIT2* gene.

These QTLs identified in our study will provide the genetic basis for further research on Si uptake ability in rice. Comparisons will be further made to evaluate the consistency of QTL detection for Si uptake in various genetic backgrounds and to identify some novel major QTLs not observed in this study, since similar genetic analyses are ongoing using other mapping populations in our lab. These efforts highlight the value of molecular quantitative genetic approaches for exploring the molecular mechanism of Si uptake in rice.

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References

[1] G.H. Korndorfer, I. Lepsch, Effect of silicon on plant growth and crop yield, in: L.E. Datonoff, G.H. Korndorfer, G.H. Synder (Eds.), Silicon in Agriculture, Elsevier Science, New York, 2001, pp. 133–147.
[2] E. Epstein, Silicon, Annu. Rev. Plant Physiol. Plant Mol. Biol. 50 (1999) 641–664.
[3] N.K. Savant, G.H. Snyder, L.E. Datnoff, Silicon management and sustainable rice production, Adv. Agron. 58 (1997) 151–199.
[4] J.F. Ma, Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses, Soil Sci. Plant Nutr. 50 (2004) 11–18.
[5] J.F. Ma, E. Takashashi, Soil, Fertilizer, and Plant Silicon Research in Japan, Elsevier science, Amsterdam, 2002.
[6] J.F. Ma, K. Nishimura, E. Takahashi, Effect of silicon on the growth of rice plant at different growth stages, Soil Sci. Plant Nutr. 35 (1989) 347–356.
[7] J.F. Ma, Function of silicon in higher plants, in: W.E.G. Muller (Ed.), Silicon Biomineralization, Springer, Berlin, 2003, pp. 127–147.
[8] E. Takahashi, J.F. Ma, Y. Miyake, The possibility of silicon as an essential element for higher plants, Comments Agric. Food Chem. 2 (1990) 99–122.
[9] P.A. Bowen, J.G. Menzies, D.L. Ethret, L. Samuels, A.M.D. Glass, Soluble silicon sprays inhibit powdery mildew development on grape leaves, J. Am. Soc. Hortic. Sci. 117 (1992) 906–912.
[10] J.G. Menzies, P.A. Bowen, D.L. Ethret, A.M.D. Glass, Foliar applications of potassium silicate reduce severity of powdery mildew on cucumber, muskmelon, and zucchini squash, J. Am. Soc. Hortic. Sci. 117 (1992) 902–905.
[11] K. Richmond, M. Sussman, Got silicon? The non-essential beneficial plant nutrient, Curr. Opin. Plant Biol. 6 (2003) 268–272.
[12] K. Tamai, J.F. Ma, Characterization of silicon uptake by rice roots, New Phytol. 158 (2003) 431–436.
[13] N. Mitani, J.F. Ma, Uptake system of silicon in different plant species, J. Exp. Bot. 414 (2005) 1255–1261.
[14] J.F. Ma, N. Mitani, S. Nagao, S. Konishi, K. Tamai, T. Iwashita, Characterization of the silicon uptake system and molecular mapping of the silicon transporter gene in rice, Plant Physiol. 136 (2004) 3284–3289.
[15] C.W. Deren, L.E. Datnoff, G.N. Snyder, Variable silicon content of rice cultivars grown on Everglades Histosols, J. Plant Nutr. 15 (1992) 2363–2368.
[16] M.D. Winslow, K. Okada, C.V. Fedrnando, Silicon deficiency and the adaptation of tropical rice ecotypes, Plant Soil 188 (1997) 239–248.
[17] M.D. Winslow, Silicon, disease resistance, and yield of rice genotypes under upland cultural conditions, Crops Sci. 32 (1992) 1208–1213.
[18] N.D. Majumder, S.C. Rakahit, D.N. Borthankur, Genetics of silica uptake in selected genotypes of rice, Plant Soil 88 (1985) 449–453.
[19] W.M. Dai, K.Q. Zhang, B.W. Duan, K.L. Zheng, J.Y. Zhuang, C. Run, Genetic dissection of silicon content in different organs of rice, Crops Sci. 45 (2005) 1345–1352.
[20] K. Ikeda, J.K. Lei, H. Tsunematsu, Y. Aida, H. Yasui, A. Yoshimura, Rice QTL analysis for days to heading using different RI (recombinant inbred) lines, Breed. Sci. 48 (Suppl. 1) (1998) 72 (in Japanese).
[21] A. Okuda, E. Takahashi, Studies on the physiological role of silicon in crop plants. I. Discussion on the silicon deficient culture method, Jpn. J. Soil Sci. Manure 32 (1961) 475–480 (in Japanese).
[22] J.F. Ma, A. Higashitani, K. Sato, K. Takeda, Genotypic variation in silicon concentration of barley grain, Plant Soil 249 (2003) 383–387.
[23] Z.B. Zeng, Precision mapping of quantitative trait loci, Genetics 136 (1994) 1457–1468.
[24] S.R. McCouch, Y.G. Cho, M. Yano, E. Paul, M. Blinstrub, H. Morishima, T. Kinoshita, Report on QTL nomenclature, Rice Genet. Newsl. 14 (1997) 11–13.
[25] E. Takahashi, K. Hino, Silica uptake by plant with special reference to the forms of dissolved silica, Jpn. J. Soil Sci. Manure 49 (1978) 357–360.
[26] S. Yoshida, Chemical aspects of the role of silicon in physiology of the rice plant, Bull. Natl. Inst. Agric. Sci. B 15 (1965) 1–58.
[27] L.H.P. Jones, K.A. Handreck, Silica in soils, plants and animals, Adv. Agron. 19 (1967) 107–149.
[28] E. Epstein, D.W. Rains, O.E. Elzam, Resolution of dual mechanisms of potassium absorption by barley roots, Proc. Natl. Acad. Sci. U.S.A. 49 (1963) 684–692.
[29] E. Epstein, The anomaly of silicon in plant biology, in: Proceedings of the National Academy of Science, vol. 91, 1994, pp. 11–17.
[30] S. Yoshida, Y. Ohnishi, K. Kitagishi, Histochemistry of silicon in rice plant, Soil Sci. Plant Nutr. 8 (1962) 36–41.
[31] T. Kashiwagi, K. Ishimaru, Identification and functional analysis of a locus for improvement of lodging resistance in rice, Plant Physiol. 134 (2004) 676–683.
[32] S. Shimoyama, Effect of calcium silicate application to rice plants on the alleviation of lodging and damage from strong gales. Studies in the improvement of ultimate yields of crops by the application of silicate materials, Jpn. Assoc. Adv. Sci. (1958) 57–99.