Theor Appl Genet (1998) 97: 777–783

M. Wissuwa · M. Yano · N. Ae

Mapping of QTLs for phosphorus-deficiency tolerance in rice (*Oryza sativa* L.)

Received: 9 February 1998 / Accepted: 29 April 1998

Abstract Phosphorus (P) deficiency of soils is a major yield-limiting factor in rice production. Increasing the P-deficiency tolerance of rice cultivars may represent a more cost-effective solution than relying on fertilizer application. The objective of this study was to identify putative QTLs for P-deficiency tolerance in rice, using 98 backcross inbred lines derived from a *japonica* × *indica* cross and genotyped at 245 RFLP marker loci. Lines were grown on P-deficient soil and P uptake, internal P-use efficiency, dry weight, and tiller number were determined. Three QTLs were identified for dry weight and four QTLs for P uptake, together explaining 45.4% and 54.5% of the variation for the respective traits. Peaks for both traits were in good agreement which was to be expected considering the tight correlation of $r = 0.96$ between dry weight and P uptake. For both traits the QTL linked to marker C443 on chromosome 12 had a major effect. Two of the three QTLs detected for internal P-use efficiency, including the major one on chromosome 12, coincided with QTLs for P uptake; however, whereas *indica* alleles increased P uptake they reduced P-use efficiency. We concluded that this was not due to the tight linkage of two genes in repulsion but rather due to an indirect effect of P uptake on P-use efficiency. Most lines with high use efficiency were characterized by very low P uptake and dry weight and apparently experienced extreme P-deficiency stress. Their higher P-use efficiency was thus the result of highly sub-optimal tissue-P concentrations and did not represent a positive adaptation to low P availability. The number of tillers produced under P deficiency is viewed as an indirect indicator of P-deficiency tolerance in rice. In addition to the major QTL on chromosome 12 already identified for all other traits, two QTLs on chromosome 4 and 12 were identified for tiller number. Their position, however, coincided with QTLs for tiller number reported elsewhere under P-sufficient conditions and therefore appear to be not related to P-deficiency tolerance. In this study P-deficiency tolerance was mainly caused by differences in P uptake and not in P-use efficiency. Using a trait indirectly related to P-deficiency tolerance such as tiller number, we detected a major QTL but none of the minor QTLs detected for P uptake or dry weight.

Key words Rice · QTL · Phosphorus · Use efficiency · Deficiency tolerance

Communicated by K. Oono

M. Wissuwa (✉) · N. Ae
National Institute of Agro-Environmental Sciences,
3-1-1 Kannondai, Tsukuba, Ibaraki 305, Japan
Fax: +81-298-388199
E-mail: wissuwa@ss.niaes.affrc.go.jp

M. Yano
Rice Genome Research Program, National Institute of Agrobiological Resources, Tsukuba, Japan

Introduction

Low levels of plant-available phosphorus (P) in soils are a major constraint for rice (*Oryza sativa* L.) production throughout the world. While this is more pronounced in upland rice, P deficiency has been identified as a main factor in preventing the realization of high yield potentials of modern varieties in lowland rice production as well (De Datta et al. 1990). Deficiencies can be alleviated by fertilizer application, but farmers are constantly facing financial difficulties with increasing fertilizer costs, especially in developing countries. This problem is aggravated by the high P-fixing capacity of many soils commonly found in rice growing regions (Wada et al. 1990). On these soils only 10–20% of the P supplied in fertilizers is available to plants, the rest being bound in the soil, mainly to Fe and Al.

The development of cultivars with an improved ability to utilize this large but hardly plant-available P pool could offer a more sustainable solution than relying on fertilizer application alone. So far breeders have concentrated their efforts on screening existing cultivars and lines under P-deficient conditions. P-deficiency tolerance has either been measured directly as dry weight or grain yield produced on low-P soils (IRRI 1985; Fegeria 1988), or indirectly by correlated traits such as tiller number (Hung 1985) or relative tiller number (Chaubey et al. 1994). Information on the inheritance of P-deficiency tolerance and P-uptake efficiency (external efficiency) and P-use efficiency (internal efficiency) as the two parameters determining dry weight or yield produced under low-P stress in scarce. This information, in combination with a better understanding of the underlying physiological mechanisms, should be very valuable for initiating an efficient breeding program to raise P-deficiency tolerance in rice above the already present level found in some genotypes. Majumber et al. (1989) and Chaubey et al. (1994) detected significant general combining ability (gca) and specific combining ability (sca) effects in their diallel crosses of P-efficient and -inefficient rice cultivars and concluded that P-deficiency tolerance is a quantitatively inherited trait with outstanding parents being carriers of mostly additive genes.

Advances in molecular marker technology over the past decade have led to the development of detailed molecular linkage maps in rice (McCouch et al. 1988; Kurata et al. 1994; Harushima et al. 1998). These linkage maps have allowed the dissection of quantitatively expressed traits into Mendelian factors referred to as quantitative trait loci (QTLs), each linked to molecular markers of a known map position (Paterson et al. 1988). The detection of putative QTLs represents a crucial first step that could eventually lead to the identification of genes controlling P uptake and P-use efficiency or to the identification of tightly linked markers to be used in marker-assisted selection.

The objective of the study presented here was to detect and map QTLs for dry weight and tiller number as indicators of P-deficiency tolerance, as well as for P uptake and P-use efficiency as the underlying parameters. This was done in a rice population grown on a P-deficient soil containing Fe- and Al-P, which are barely soluble, as the predominant inorganic P forms.

Materials and methods

Plant material

The Japanese variety 'Nipponbare' of the *japonica* subspecies was crossed with 'Kasalath', an *indica* type landrace from Assam, India. The resulting F_1 was backcrossed to 'Nipponbare' to increase fertility in the *japonica* × *indica* hybrid. Ninety-eight backcross inbred lines (BILs) were developed by advancing BC_1F_1 lines for five generations by the single-seed descent method (Lin et al. 1998). Leaf material of the BC_1F_5 was used for DNA extraction and restriction fragment length polymorphism (RFLP) analysis, whereas phenotypic data were collected on the BC_1F_6. In addition to the BILs and both parents, 14 rice varieties differing in P-uptake ability (Ae, unpublished data) were included as standards in this study. Those varieties were 'IR26' and 'IR36' from IRRI, The Phillippines; 'Yamadanishiki' from Japan; 'Oryza Sabana-6', 'IAC 47', 'IAC 1246', and 'CT 11891-2-2-7' from CIAT, Colombia; 'Progresso', 'CNA 4143', 'CNA 4128', 'CNA 4291', and 'CNA 7013' from Brazil; 'Morogsol' from India; and 'WAB 99-84' from WARDA, West Africa.

Evaluation of plant performance under low P stress

A fiberglass container of the dimensions $11.60 \times 0.85 \times 0.22$ m (length × width × depth) was filled with topsoil (Humic haplic andosol) from a field situated at the NIAES campus in Tsukuba, Japan. This field has not received P fertilizer for at least 30 years and thus is characterized by low levels of plant-available P. The field was fertilized with the equivalent of 100 kg ha^{-1} of N and K_2O prior to topsoil removal for filling the container. Seeds of the 98 BILs, two parents, and 14 standards were soaked overnight in a Benlate (5 g l^{-1}) plus Patan (1.2 g l^{-1}) suspension, washed with distilled water, and allowed to germinate at 30°C for 48 h. Germinated seeds were planted into the low P soil in a randomized complete block design with five replications on 16 May 1997. Replications (rows) were spaced 15 cm apart; spacing within rows was 10 cm. Plants were grown under upland conditions, but drought stress was avoided by watering the plants during dry spells in summer.

In order to assess the stress intensity due to low P availability, the 14 standard varieties were furthermore grown in two sets of 10-l pots (3 plants per pot) filled with the same low P soil used in the fiberglass container. One set was fertilized as in the main experiment, and the second set was used as a plus-P control after receiving the equivalent of 60 kg P_2O_5 ha^{-1}.

On 18 September (125 days after planting) the plants were cut and their tillers counted. After oven-drying the samples at 65°C for 5 days and subsequent dry weight determination, we ground the samples in a Wiley mill to pass a 1-mm mesh. The tissue-P concentration in 1 mg of plant sample was determined colorimetrically by the phosphovanadate method (Hanson 1950) after digestion in a mixture of HNO_3, $HClO_4$, H_2SO_4 (3:1:1). Total P uptake was calculated as the product of dry weight and tissue-P concentration, and P-use efficiency was expressed in g dry weight mg^{-1} P taken up.

RFLP mapping and QTL detection

A linkage map of the 245 RFLP makers used for QTL detection was obtained from the Rice Genome Project, Japan, as previously described by Lin et al. (1998). Data for tiller number and plant P content were log-transformed prior to analysis. QTL analysis was performed using the composite interval mapping (CIM) method proposed by Zeng (1994). Computations were done with the software package PLABQTL (Utz and Melchinger 1996), which uses a multiple regression approach as suggested by Haley and Knott (1992). Because a specific model for BILs was not available, we analyzed our data as an F_2 backcross and treated heterozygous markers as missing data. In a first step, simple interval mapping was performed and cofactors selected. For cofactor selection F-to-enter and F-to-drop thresholds were set at 6.0 to avoid selecting multiple markers linked to one QTL as cofactors. Using these cofactors to reduce the residual variation. We could detect QTLs with CIM. A LOD score >2.80 was considered significant for QTL detection. Support intervals were determined using a LOD fall-off of 1.0.

Results

Phenotypic response

The P availability of the soil used in this study was low at 1.0 mg P kg^{-1} (Truog-P) or 4.5 mg P kg^{-1} (Bray2-P) (Otani and Ae 1996). Al- and Fe-P were the predominant inorganic P forms, the more plant-available Ca-P was only detected in traces. Low P availability was clearly the growth-limiting factor of the P-deficient soil as shown by a 50.4% reduction in dry weight and a 46.7% reduction in tiller number relative to P-fertilized conditions (Table 1). These reductions were caused by a 61% decrease in P uptake that could not be compensated by increases in P-use efficiency.

For all of the traits studied transgressive variation was observed towards the negative side with only P-use efficiency showing positive transgression (Fig. 1). 'Kasalath' was far more P-deficiency tolerant than any of the BILs in terms of P uptake and dry matter production and was among the top three entries for tiller number. The high P-deficiency tolerance of 'Kasalath' was confirmed in comparisons with the 14 standard cultivars that had been chosen based on their exceptionally high or low P uptake as determined in earlier experiments (Ae, unpublished data). Only 'Morogsol', like 'Kasalath' an *indica* type landrace from India, had significantly higher dry weight and P uptake; all other cultivars were significantly lower than 'Kasalath' (data not shown). The P-use efficiency of 'Kasalath' and other genotypes with high P uptake was low and negatively correlated with dry weight and P uptake (Table 2). 'Nipponbare' showed average P-use efficiency and was slightly below average for the other three parameters. Variability among the 98 BILs was highest for P uptake with a CV of 64%, followed by dry weight, tiller number, and P-use efficiency with CVs of 54%, 51%, and 17%, respectively.

QTL detection

RFLP and linkage analysis of the BILs has been described in detail by Lin et al. (1998). The average distance between the 245 RFLP markers used in QTL mapping was 4.8 cM. Percentage heterozygocity (4.6%) was not significantly different from the expected value of 3.1%, and segregation ratios followed the expected Mendelian ratio of 3 : 1 for most markers.

Four putative QTLs were detected P uptake on chromosomes 2, 6, 10, and 12 (Fig. 2, Table 3). Together they explained 54.5% of the variation for P uptake observed among the BILs. One of these QTLs, linked to marker C443 on chromosome 12, had a major effect and accounted for half of the explained variation. For three of the four QTLs, including the major one, the positive allele came from 'Kasalath'. Of the three QTLs mapped for dry weight, the ones on chromosome 6 and 12 coincided with QTLs for P uptake (Fig. 2). Again the QTL linked to marker C443 had a major effect, explaining 26.5% of the variation for dry weight compared to 27.9% for P uptake. No QTL for dry weight was mapped on chromosomes 2 and 10, but peaks at the same intervals as for P uptake were detected, albeit with sub-significant LOD scores of 2.30 in the case of the interval G222-C365 on chromosome 2 and 2.19 for the interval R1629-R2447 on chromosome 10. Similarly, the QTL for dry weight on chromosome 3 coincided with a visible but not significant peak for P uptake (LOD score of 2.24).

Three putative QTLs were detected for P-use efficiency, together explaining 42.1% of the variation. The major QTL on chromosome 12 and the minor one on chromosome 2 coincided with QTLs for P uptake (Fig. 2), however, 'Nipponbare' alleles increased P-use efficiency, whereas 'Kasalath' alleles increased P uptake. The putative QTL on chromosome 4 did not correspond to peaks for any of the other traits. The same was true for two of the three putative QTLs for tiller number. For all three, together explaining 40.3% of the variation, 'Kasalath' alleles increased tiller number. Again the major portion of the variation was due to the QTL linked to marker C443 on chromosome 12.

Significant two-way interactions involving markers flanking a putative QTL were only detected for tiller number on chromosome 12 (C901). Lines with 'Kasalath' alleles at loci C901 and C701 (on chromosome 10) had 7.0 tillers on average, whereas lines with 'Kasalath' alleles on C901 alone only had 4.0 tillers and lines without a Kasalath alleles at C901 had 3.5 tillers.

Table 1 Effect of P-deficiency stress (− P) relative to P-fertilized (+ P) conditions on the performance of 14 rice cultivars

	+P[a]	−P[b]	Reduction (%)	Range (reduction) (%)
P uptake (mg $plant^{-1}$)	8.95	3.48	61.0	28.9–96.5
Tissue P concentration (mg P g^{-1})	0.86	0.67	22.9	6.8–40.4
Dry weight (g $plant^{-1}$)	10.45	5.19	50.4	5.3–94.1
Tiller number	9.37	5.00	46.7	15.4–87.5

[a] Pots received the equivalent of 60 kg P_2O_5 ha^{-1}

[b] Plants grown on soil deficient in available P (1.0 mg P kg^{-1} soil, Truog-P; 4.5 mg P kg^{-1} soil, Bray2-P)

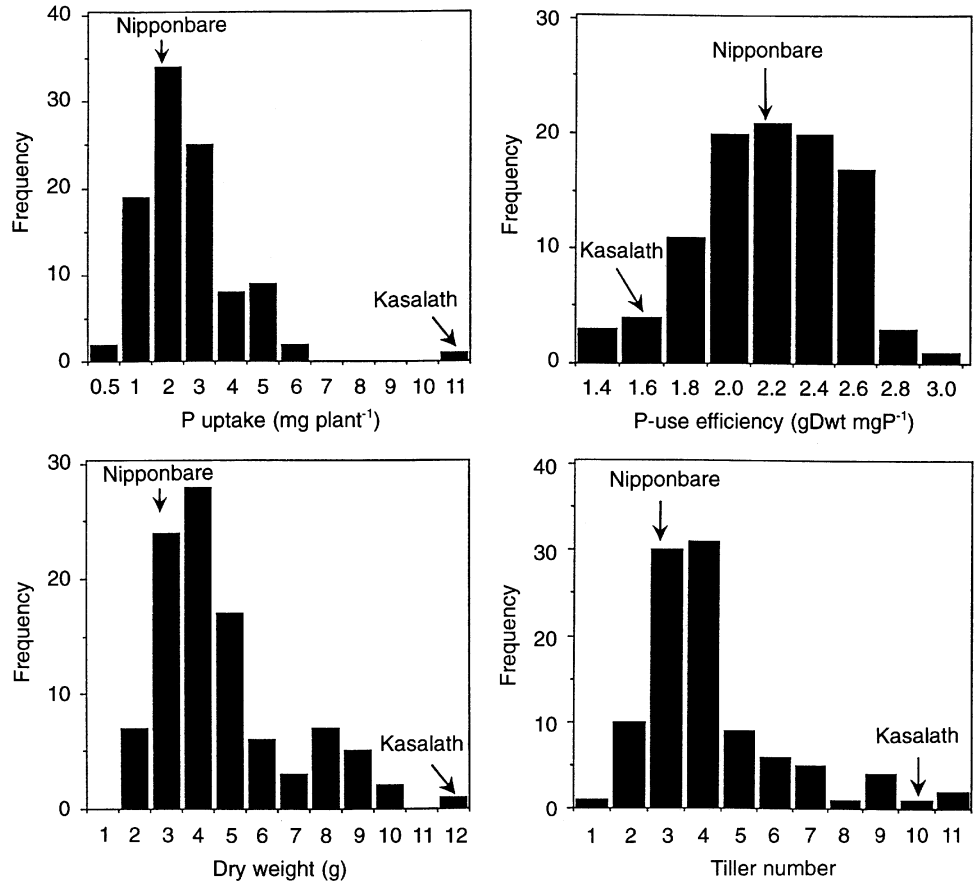

Fig. 1 Frequency distribution of 98 backcross inbred lines and their parents 'Kasalath' and 'Nipponbare' for the traits dry weight, P uptake, P-use efficiency, and tiller number

Table 2 Correlation coefficients for traits related to P-deficiency tolerance measured on 98 backcross inbred lines

	P-use efficiency	Dry weight	Tiller number
P uptake (mg plant^{-1})	−0.72[a]	0.96	0.75
P-use efficiency (g Dwt mg^{-1} P)		−0.60	−0.52
Dry weight (g plant^{-1})			0.74

[a] All correlation coefficients were significant at $P < 0.01$

Two-way interactions involving two putative QTLs were not detected.

Discussion

The ideal P-deficiency-tolerant genotype would combine high P uptake with efficient internal P use. We detected two common QTLs for uptake and use efficiency on chromosomes 2 and 12. For both QTLs 'Kasalath' alleles increased uptake but reduced use efficiency. This could be due to either the presence of two loci within the significant intervals, both tightly linked in repulsion, or to only one loci per interval but with opposite effects on P uptake and use efficiency. Selecting for positive 'Kasalath' alleles to improve P uptake would at the same time reduce use efficiency, making it difficult/impossible to improve both parameters simultaneously. This, however, would not effect progress in increasing tolerance to P deficiency because P uptake was the parameter of principal importance in our study, whereas use efficiency had little effect in increasing tolerance to low P availability. That P uptake was the more influential of the two parameters is implied by its tight correlation of $r = 0.96$ with dry weight (Table 2), while P-use efficiency was negatively correlated ($r = -0.60$) to dry weight and not positively as expected. The majority of plants growing well on the P-deficient soil (producing above average dry matter) were characterized by high P uptake but relatively little dry matter produced per unit of P taken up. Among the plants in the top third in terms of P-use efficiency, on the other hand, only two had above average dry weight. It can therefore be assumed that the high P-use efficiency of some plants is not a positive adaptation worth exploiting by plant breeders but rather the result of inefficient P uptake, which then led to severe P deficiency and slightly higher dry matter per unit P but low total dry matter production.

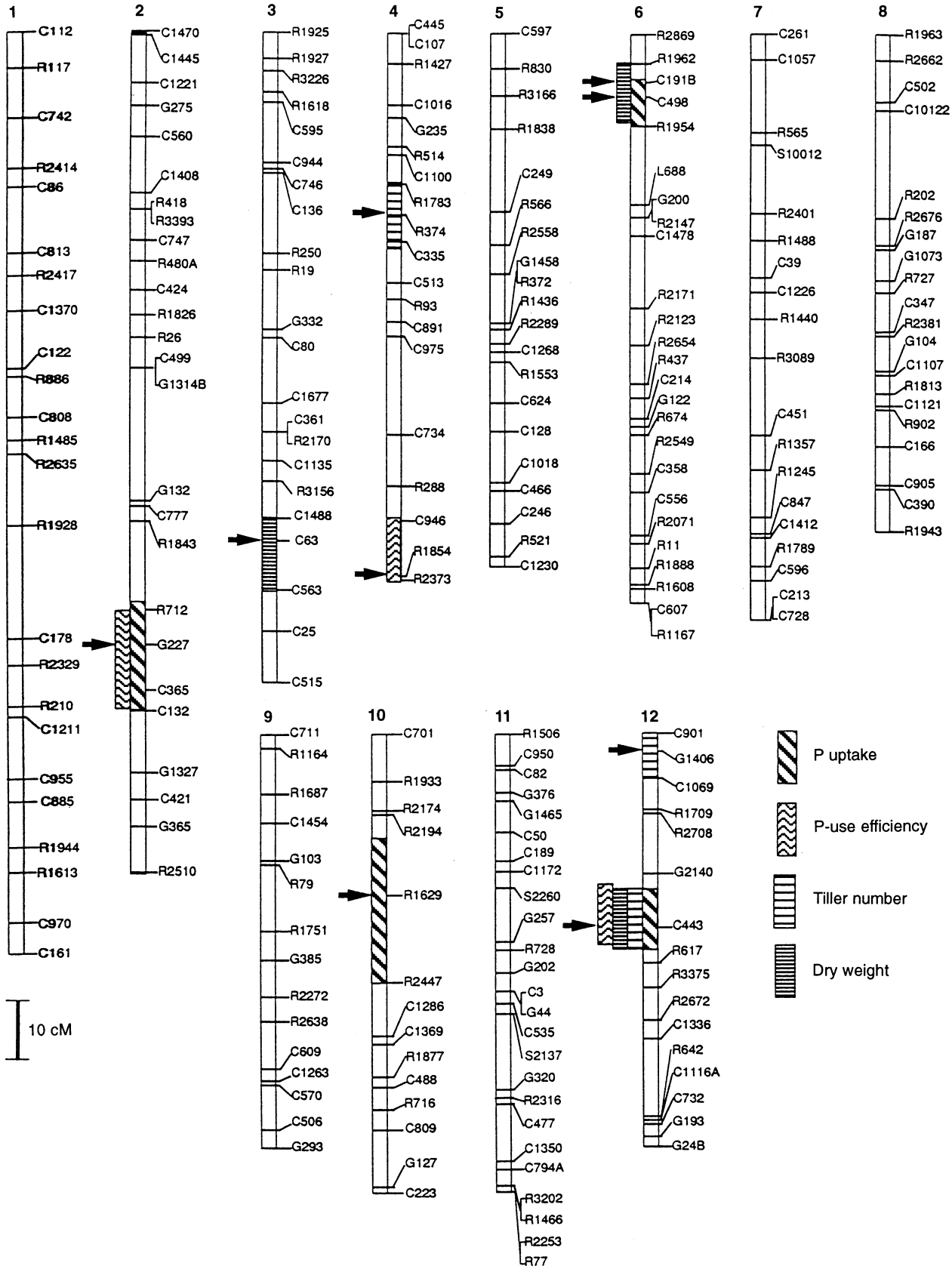

Fig. 2 Linkage map and positions of putative QTLs exceeding the LOD threshold of 2.80 for the traits dry weight, P uptake, P-use efficiency, and tiller number. A LOD fall-off of 1.0 was used to define the borders of the confidence intervals for QTLs. *Arrows* indicate the nearest marker locus to the QTL

Table 3 Putative QTLs for P uptake, P-use efficiency, dry weight, and tiller number under low-P stress

	Marker interval[a]	Chromosome	Position[b]	Distance[c]	LOD	% Variation[d]	Substitution effect[e]	Positive allele[f]
P uptake	G227-C365	2	106	+3	2.82	5.8	+971	K
	C498-R1954	6	13	+2	3.52	9.8	+705	K
	R1629-R2447	10	32	+6	4.70	7.7	−621	N
	G2140-C443	12	30	−3	10.74	27.9	+1938	K
				Total[g]	16.25	54.5		
P-use efficiency	G227-C365	2	106	+3	5.22	9.8	−0.346	N
	C946-R1854	4	86	−4	4.35	9.4	+0.303	K
	G2140-C443	12	28	−4	6.57	19.1	−0.465	N
				Total[g]	11.40	32.1		
Dry weight	C1488-C63	3	86	−1	3.08	6.4	−992	N
	C191-C498	6	10	+1	4.71	9.7	+1560	K
	G2140-C443	12	30	−3	10.50	26.5	+3193	K
				Total[g]	12.89	45.4		
Tiller number	R374-C335	4	32	+2	4.37	9.8	+1.84	K
	C901-G1406	12	2	−1	3.90	9.5	+1.54	K
	G2140-C443	12	30	−3	7.87	20.6	+1.86	K
				Total[g]	10.97	40.3		

[a] Marker nearest to QTL is underlined
[b] Position on chromosome in centiMorgans
[c] Distance from nearest marker in centiMorgans
[d] Portion of phenotypic variation explained by QTL using a single-QTL model
[e] Effect of substituting both 'Nipponbare' alleles by 'Kasalath' alleles, calculated for untransformed data
[f] Allele increasing phenotype from 'Kasalath' (K) or 'Nipponbare' (N)
[g] Estimated using a multiple-QTL model including all putative QTLs

In this study, dry weight 125 days after sowing was used as an indicator of P-deficiency tolerance instead of grain yield because the BILs differed in maturity and grains could not be harvested at the same time for all lines. Dry weight production under P-deficient conditions largely depended on P uptake, but reports on the dependence of grain yield on P uptake are less conclusive. Fageria et al. (1988) did not detect a significant correlation between these two parameters, but the stress intensity in their study was low. They found that grain yield was only reduced by 14% relative to P fertilization and that tissue-P concentrations remained well above 1 mg P g^{-1} dry weight, which is considered the deficiency threshold for rice at the tillering stage. In a study conducted at IRRI (1994) a significant correlation between P uptake and grain yield of $r = 0.40$ was detected, and Koyama (1973) reported that grain yield highly depended on P uptake, with this dependence increasing with increasing stress intensity. Dry weight had a tighter correlation with P uptake than grain yield in all of these studies, and the discrepancy could be explained by genotypic differences in the efficiency of retranslocation of P from vegetative to generative tissues. This efficiency largely depends on differences in the harvest index (HI) and should therefore be independent of P uptake, unlike tissue-P-use efficiency. Based on our results it seems appropriate for breeders trying to develop genotypes with increased tolerance to P deficiency to combine high P uptake ability with high HI, rather than to concentrate on P-use efficiency. Increasing P-use efficiency is further limited by the negative effects that low seed-P concentrations may have on seed quality. Under low P availability Hedley et al. (1994) showed that the P content in seeds had large effects on seedling establishment and early root growth, which ultimately affected P uptake.

Absolute and relative tiller numbers have been suggested as indirect indicators of P-deficiency tolerance in rice (Hung 1985; Chaubey et al. 1994). They have the advantage of being easily determined nondestructively during the growth period unlike dry weight or P uptake. Of the three QTLs for tiller number detected here, one coincided with the major QTL (C443) for P uptake and dry weight. The other two QTLs did not even coincide with insignificant but apparent peaks for P uptake or dry weight and therefore appear to be unrelated to both traits. A potential shortcoming in using an indirect trait such as tiller number to detect QTLs for a related property is that the detected QTLs may represent genotypic differences only related to the indirect trait (tiller number) without significance for the target trait. In the case of tiller number the danger of confounding general tillering ability with sensitivity to P deficiency is particularly high if absolute tiller numbers are used, as in this study, rather than tiller number relative to non-stress conditions. We therefore compared our results with putative QTLs for tiller number published elsewhere. The QTLs for tiller number at

position 32 cM on chromosome 4 and 2 cM on chromosome 12 were located within significant intervals affecting tiller number under non-stress conditions as published by Ray et al. (1996). The major QTL on chromosome 12 (C443) was not associated with either tillers (Ray et al. 1996) or number of panicles (Lin et al. 1996). Using the indirect trait tiller number therefore enabled us to identify a major QTL for P-deficiency tolerance, but we failed to detect any of the other putative QTLs with minor effects on P uptake or dry weight.

The ability to extract P from soils with low P availability is likely to depend on root properties. In an attempt to explain how the putative QTL exerted their influence on P-deficiency tolerance we screened the literature for previously described QTLs related to root characteristics. Only the position of the QTL on chromosome 6 (C498, 13 cM) overlapped with a QTL of potential importance for P uptake (Ray et al. 1996). That QTL explained 10% of the variation for total root number in an *indica* × *japonica* cross, and as in our study, the *indica* allele had the positive effect. For the other putative QTLs detected in our study no match was found.

The results of this study could be used to develop near-isogenic lines (NILs) that would ideally differ only for one of the chromosomal regions containing putative QTLs for P uptake. QTLs on chromosome 2, 6, and 12 are good candidates because the positive allele in each case comes from 'Kasalath', the parent with the by far superior P-deficiency tolerance. These NILs could be used to confirm the presence of putative QTLs, to fine-map their position, and to conduct physiological studies aimed at investigating the potential mechanisms leading to superior P uptake (Yano and Sasaki 1997). Breeders could then use these QTLs in marker-aided selection to transfer the superior P-uptake ability from landraces like 'Kasalath' into elite breeding material with a higher harvest index to increase productivity under P deficiency above present levels.

Acknowledgments The authors declare that all experiments were conducted in compliance with the current laws of Japan.

References

Chaubey CN, Senadhira D, Gregorio GB (1994) Genetic analysis of tolerance for phosphorus deficiency in rice (*Oryza sativa* L.). Theor Appl Genet 89:313–317

De Datta SK, Biswas TK, Charoenchamratcheep C (1990) Phosphorus requirements and management for lowland rice. In: Proceedings of a symposium, 6–10 March 1989, IRRI. The Philippines Phosphorus Requirements Sustainable Agric Asia Oceania. IRRI, The Philippines, pp 307–323

Fageria NK, Morais OP, Baligar VC, Wright RJ (1988) Response of rice cultivars to phosphorus supply on an oxisol. Fert Res 16:195–206

Haley CS, Knott SA (1992) A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. Heredity 69:315–324

Hanson WC (1950) The photometric determination of phosphorus in fertilizers using the phosphovanado-molybdate complex. J Sci Food Agric 1:172–173

Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush GS, Sasaki T (1998) A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics 148:479–494

Hedly MJ, Kirk GJD, Santos MB (1994) Phosphorus efficiency and the forms of soil phosphorus utilized by poland rice cultivars. Plant Soil 158:53–62

Hung HH (1985) Studies on tillering ability of rice under phosphorus stress. PhD thesis, A and M University, Texas

IRRI (1985) IRRI annual report for 1984. International Rice Research Institute, Manila, The Philippines

IRRI (1994) program report for 1993. International Rice Research Institute, Manila, The Philippines

Koyama T, Chammek C, Snitwonge P (1973) Varietal differences of Thai rice in the resistance to phosphorus deficiency. Trop Agric Res Cent Jpn Tech Bull 4

Kurata N, Nagamura Y, Yamamoto K, Harushima Y, Sue N, Wu J, Antonio BA, Shomura A, Shimizu T, Lin S-Y, Inoue T, Fukuda A, Shimano T, Kuboki Y, Toyama T, Miyamoto Y, Krihara T, Hayasaka K, Miyao A, Monna L, Zhong HS, Tamura Y, Wang Z-X, Momma T, Umehara Y, Yano M, Sasaki T, Monibe Y (1994) A 300 kilobase interval genetic map of rice including 883 expressed sequences. Nat Genet 8:365–372

Lin HX, Qian HR, Zhuang JY, Lu J, Min SK, Xiong ZM, Huang N, Zheng KL (1996) RFLP mapping of QTLs for yield and related characters in rice (*Oryza sativa* L.). Theor Appl Genet 92:920–927

Lin SY, Sasaki T, Yano M (1998) Mapping quantitative trait loci controlling seed dormancy and heading date in rice, *Oryza sativa* L. using backcross inbred lines. Theor Appl Genet 96:997–1003

Majumder ND, Borthakur DN, Rakshit SC (1989) Heterosis in rice under phosphorus stress. Indian J Genet 49:231–235

McCouch SR, Kochert G, Yu ZH, Khush GS, Coffman WR, Tanskley SD (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829

Otani T, Ae N (1986) Sensitivity of phosphorus uptake to changes in root length and soil volume. Agron J 88:371–375

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726

Ray JD, Yu L, McCouch SR, Champoux MC (1996) Mapping quantitative trait loci associated with root penetration ability in rice (*Oryza sativa* L.). Theor Appl Genet 92:627–636

Utz HF, Melchinger AE (1996) PLABQTL: a program for composite interval mapping of QTL. J Quant Trait Loci http://probe.nalusda.gov.8000/otherdocs/jqtl

Wada K, Xue-Yuan L, Moody PW (1990) Chemistry of adverse upland soils. In: Proceedings of a symposium, 6–10 March 1989, IRRI. The Philippines Phosphorus requirements Sustainable Agric Asia Oceania. IRRI, The Philippines, pp 243–253

Yano M, Sasaki T (1997) Genetic and molecular dissection of quantitative traits in rice. Plant Mol Biol 35:145–153

Zeng ZB (1994) Precision mapping of quantitative trait loci. Genetics 136:1457–1468