

# The candidate QTLs affecting phosphorus absorption efficiency and root weight in maize (*Zea mays* L.)

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**Abstract** A maize  $F_2$  population was first used to construct a genetic linkage map of Chromosome 6 covering 117.6 cM with an average interval of 3.68 cM between adjacent markers. Based on composite interval mapping (CIM), the quantitative trait loci (QTL) for phosphorus absorption efficiency (PAE) and root-related traits was detected in four environments, i.e., Kaixian County under deficient phosphorus (KXDP), Kaixian County under normal phosphorus (KXNP), SUDP1, and SUDP2. QTLs affecting root weight (RW) were detected simultaneously at the *dupssr15* locus region (bin 6.06) on Chromosome 6 in the four environments, while QTL affecting taproot length and fiber number was only detected in one or two environments. The result suggested that taproot length and fiber number were more easily affected by the environment than PAE and RW. The alleles originating from 082 increased PAE and RW on Chromosome 6. The QTL on bin 6.06 explained 4%–10% and 4%–8% of the total phenotypic variance of PAE and RW, respectively, and the estimates of the genetic effects presented dominance and overdominance. The QTL for RW in the *dupssr15* locus is the minor QTLs environment interactive effects, which should be particularly useful in MAS manipulation of breeding maize.

**Keywords** maize, QTL analysis, candidate QTLs, phosphorus absorption efficiency, root-related traits, four environments

## Introduction

Phosphorus is an essential nutrient for plant production, and the phosphorus deficiency is one of the most common and serious environmental constraints in tropic regions, reducing maize mean yields. As a result, improving the adaptation and/or tolerance of maize to phosphorus deficiency is an important objective in most regions (Helentjaris et al., 1986; Hinsinger and Gilkes, 1996; Hinsinger, 2001). Plants can actively improve their acquisition of P in several ways. Access to total soil P resources might be improved by increasing the absorbing area of the root system, through increased root length and root fiber number (Zuber et al., 1968; Guingo et al., 1998; Tuberosa et al., 2003; Zhu et al., 2005).

Great progress has been made on detecting QTLs in rice, cotton, *Brassica napus*, and maize in recent years, with QTLs

mapped of yield and agronomic and quality traits in tetraploid potato (Tuberosa et al., 1998a, 1998b, 2002). QTLs of agronomic and fiber traits in cotton have been detected by AFLP marker (Wu et al., 2007). QTLs for morphological and physiologic traits related to rice stress tolerance have been studied. QTLs associated with root morphology, crop yield, and stress resistance have been mapped in rice, maize, and soybean (Chen et al., 2008, 2009, Chen and Xu, 2011; Chen et al., 2011). QTLs have also been researched in the maximum root length of maize, total root number of maize, leaf water potential of cotton, osmosis, and osmotic adjustment (Zhu et al., 2005; Chen et al., 2008). Marker-assisted selection (MAS) based on QTL has been used in the genetic improvement of yield in maize, common bean, barley, and rice. Moreover, some achievements have been made in molecular marker-assisted breeding (Tuberosa et al., 1998a; Yan et al., 2004; Zhu et al., 2005; Chen et al., 2009).

QTL mapping provides a means to detect complex genetic characters, such as QTL of plant in response to phosphorus deficiency and allows the identification of molecular markers linked to desirable QTLs that can be directly used to improve

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PAE and root-related traits through MAS. In maize, the QTLs for root number in Polj17  $\times$  F-2 and root volume in B73  $\times$  Mo17 (Kaeppeler et al., 2000) have been described. Tuberosa et al. (2002) reported QTL regions influencing root diameter and root length in hydroponics, while Guingo et al. (1998) identified the QTL for root weight. Moreover, recently, Guingo et al. (1998) and Tuberosa et al. (2002) have described the QTL for root pulling force in hydroponics. The QTLs of root hair length and lateral branch length in hydroponics were studied, and a QTL flanked by np1409-nc007 for root hair length was mapped on Chromosome 5 (Zhu and Lynch, 2004).

The previous studies in QTLs for root traits were in hydroponics under unnatural environment for plant growth with a small number of QTLs, a short linkage map for QTLs, and a comparatively large distance between markers. Furthermore, the QTL for the same root trait in different environments has not been studied so far.

The genotypic responses to phosphorus deficiency are different and genotype  $\times$  environment interaction well known in many quantitative trait locus (QTL), which severely limits practices in plant breeding by using marker-assisted selection (MAS) (Tuberosa et al., 2002, Tuberosa et al., 2003; Yan et al., 2004). Only the identification of stable QTL responsible for phosphorus absorption efficiency and root-related traits across P levels, different environments, and different growth stages might be used in MAS.

The objectives of this study were to identify the QTLs for phosphorus absorption efficiency and root-related traits in field conditions and the stable QTL and analyze the common regions of QTLs for multitraits under the four environments including different P levels, different sites, and different growth stages, which may be useful for improving phosphorus efficiency by means of marker-assisted selection.

## Materials and methods

### Plant materials

The mapping population included 241  $F_{2:3}$  families derived from a corresponding number of randomly chosen  $F_2$  plants of the cross between inbred 082 (P deficiency tolerant) and Ye107 (P deficiency susceptible), which differed in phosphorus efficiency and root traits. The  $F_2$  families were reproduced from October 2006 to February 2007 in Hainan, China. The  $F_{2:3}$  families were reproduced in March–July, 2007 in Xiema, Beibei, China.

### Field experiment

The experiment was designed as a split plot experiment with three replications at Kaixian County (KX), with P as main environment,  $F_{2:3}$  families along with  $F_1$  and both parents

lines as vice environment. The field experiment was conducted at a randomized block design with three replications at the South-west University (SU).  $F_{2:3}$  families along with  $F_1$  and both parents lines were sowed. A set of experiments were conducted at Kaixian County (KX) (31°11'N latitude, 98°58'E longitude; 1000 m altitude) and South-west University (SU) (29°48'N latitude, 106°33'E longitude; 150 m altitude) during September to October in 2007. In Kaixian soil, the contents of total N, P, K, and available N, P, K were 0.236 g/kg, 0.395 g/kg, 18.9 g/kg, 14.7 mg/kg, 2.0 mg/kg, and 117 mg/kg, respectively; the organic matter was 2.99 g/kg, and the pH was 8.2. In South-West University soil, the contents of total N, P, K, and available N, P, and K were 0.259 g/kg, 0.602 g/kg, 17.8 g/kg, 14.1 mg/kg, 2.6 mg/kg, 121 mg/kg, respectively, the organic matter was 3.43 g/kg, and the pH was 7.9. Fertilizers were applied before sowing at rates of 120 kg N and 50 kg P per hectare under normal P application (KXNP), but only applied at a rate of 120 kg N under deficient P application at Kaixian (KXDP), while fertilizers were applied before sowing at rates of 120 kg N per hectare at the South-West University (SUDP). The area per split plot was 2.5 m<sup>2</sup> with 10 plants. Cultivation was carried out according to standard practices.

### Measurement of biologic traits

The plants were harvested at the 21st day after emergence of seedling at Kaixian (KX), while they were collected at the 21st (SUDP1) and 35th (SUDP2) day at the South-West University (SU). The fibrous root number (FN) and taproot length (RL) was recorded. The above-ground biomass weight and the root dry weight (RW) were determined after plants were deactivated at 105°C for 30 min and dried at 80°C for 72 h. The plant weight was the sum of the above-ground biomass weight and the root dry weight.

### Analysis of plant phosphorus content

Plants were dried at 60°C for 72 h, ground, and burned to ash at 500°C for 12 h after being weighed. The ash was dissolved by adding 8 mL of 100 mM HCl to each sample. The dissolved samples were analyzed for phosphorus concentration by means of spectroscopic methodology. The phosphorus absorption efficiency (PAE) was calculated by plant weight  $\times$  plant phosphorus concentration.

### Statistical analysis of data

Arithmetic means of three replicates was calculated for each trait of each  $F_{2:3}$  family. The transgressive segregation was performed for genotypes, which had traits with values beyond the two parents (i.e., larger than 082 or smaller than Ye107) in four environments. The heritability of traits for the  $F_{2:3}$  families was estimated by the following formula:

$$h_b^2(\%) = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \hat{\sigma}_E^2} \times 100,$$

where  $\hat{\sigma}_G^2$  and  $\hat{\sigma}_E^2$  are the estimates of genetic variance and environment variance, respectively.

### QTL analysis

The procedure of composite interval mapping was used to identify QTLs and estimate their effects. QTL mapping was performed with the software program Windows QTL Cartographer version 2.5. Parameters for forward regression analysis were a window size of 10 cM, a walk speed of 2 cM, five background control markers, and probability thresholds of 0.05 each for the partial *F* test for both marker inclusion and exclusion (Kosambi, 1944). The significance threshold for QTL detection was calculated by 1000 random permutations of the phenotypic data at 5% level, and LOD thresholds were set at 2.48 for all traits. QTL positions were assigned at the point of maximum LOD score in the regions under consideration. Gene action mode of each significant QTL (d/a) was estimated according to the additive (a) and dominant (d) effects, which was classified to four parts of additive (0 to 0.20), partial dominant (0.21 to 0.80), dominant (0.81 to 1.20), and over dominant (> 1.20), according to Stuber and Sisco (1992) and Tuberosa et al. (1998a).

## Results

### Variation of phenotypic traits among F<sub>2:3</sub> families

In four environments, the two parental genotypes, 082 and Ye107, differed significantly in PAE, RW, RL, and FN.

The former had higher values than the later for these traits (Table 1). All traits were continuously segregated and approximately normally distributed with absolute values of skewness and kurtosis less than 1.0, which indicated that all traits were suitable for QTL mapping.

Analysis of variance (ANOVA) was employed to estimate genetic variance ( $\hat{\sigma}_G^2$ ), environment variance ( $\hat{\sigma}_E^2$ ), and subsequently broad-sense heritability ( $h_b^2$ ). The  $h_b^2$  for different traits varied from 73.8% to 91.8% (Table 1), and the heritability of the other traits was generally high (> 70%).

The analysis of variance for PAE, RW, RL, and FN tested on the F<sub>2:3</sub> families in the four environments, i.e., KXDP, KXNP, SUDP1, and SUDP2, and was summarized in Table 2. The significant variances of genotype and environment indicated that the PAE, RW, RL, and FN might be affected by both the genotypes and environments.

### Correlation among traits at the two sites

The correlation coefficient among traits was shown in Table 3. All traits were highly positive correlated ( $r > 0.70$ ).

### QTL analysis

In the four environments, KXDP, KXNP, SUDP1, and SUDP2. One QTL was detected to influence PAE, which was located in the interval dupssr15–P1M7/a (bins 6.06) on Chromosome 6 (Table 4 and Fig. 1). The QTL on Chromosome 6 explained 4%–10% of total phenotypic variance of PAE. The alleles from the QTL on Chromosome 6, which contributes to increasing the PAE, were from the higher phosphorus efficiency parental genotype 082(P1) and estimates of the genetic effects presented partial dominance.

**Table 1** Estimates of genetic variance ( $\hat{\sigma}_G^2$ ) and environment variance ( $\hat{\sigma}_E^2$ ) among 241 F<sub>2:3</sub> families from the cross of 082 × Ye107

Environments	Traits	Parents			F <sub>2:3</sub> families				
		082	Ye107	Difference	Mean	Range	$\hat{\sigma}_G^2$	$\hat{\sigma}_E^2$	$h_b^2(\%)$
<b>KXNP</b>	PAE-KXNP	4.32	2.11	2.21**	3.06	1.35–4.88	0.603	0.0861	87.5
	RW-KXNP	5.02	2.35	2.67**	3.68	1.85–5.32	0.4438	0.1208	78.6
	RL-KXNP	20.54	12.85	7.69*	16.71	8.84–22.17	5.0552	1.2402	80.3
	FN-KXNP	254	175	79*	201.64	104–277	811.9733	241.1698	77.1
<b>KXDP</b>	PAE-KXDP	3.23	1.2	2.03**	2.24	0.84–4.07	0.647	0.065	90.9
	RW-KXDP	4.12	1.85	2.27**	3.28	1.67–4.67	0.3291	0.0802	80.4
	RL-KXDP	17.65	10.12	7.53**	15.26	8.00–20.65	4.6061	1.2392	78.8
	FN-KXDP	221	124	97*	185	96–259	718	232	75.6
<b>SUDP1</b>	PAE-SUDP1	3.4	1.26	2.14**	2.29	0.86–4.15	0.688	0.062	91.8
	RW-SUDP1	5.13	2.04	3.09**	3.36	1.66–5.54	0.6358	0.1415	81.8
	RL-SUDP1	18.24	13.21	5.03*	15.46	10.68–20.83	3.5008	1.0398	77.1
	FN-SUDP1	234	158	76*	183	122–258	568	201	73.8
<b>SUDP2</b>	PAE-SUDP2	4.48	2.25	2.23**	3.54	1.80–5.04	0.3839	0.0389	90.8
	RW-SUDP2	5.25	2.52	2.73**	5.9	3.00–8.4	1.0665	0.2716	79.7
	RL-SUDP2	32.15	25.55	6.6*	30.35	19.78–42.31	19.5634	6.1441	76.1
	FN-SUDP2	388	286	102**	334.57	220–469	2084.7124	665.5678	75.8

\* and \*\* denote significance at 5% and 1% levels, respectively.

**Table 2** *F* value of ANOVA for effects

Traits	Source of variation	SS	Degree of freedom	<i>F</i> value
PAE	Genotypes	507.22	240	34.01**
	Environments	286.77	3	1538.17**
	Error	44.74	720	—
	Total variation	838.73	963	—
RW	Genotypes	538.39	240	29.02**
	Environments	1112.08	3	4795.05**
	Error	55.66	720	—
	Total variation	1706.13	963	—
RL	Genotypes	5528.36	240	7.13**
	Environments	38532.94	3	3976.32**
	Error	2325.74	720	—
	Total variation	46387.04	963	—
FN	Genotypes	853073.10	240	16.97**
	Environments	3820885.00	3	6079.56**
	Error	150835.40	720	—
	Total variation	4824794.00	963	—

\*\* indicates significances with a probability level of 1%.

**Table 3** Analysis of correlation among PAE, RW, RL, and FN

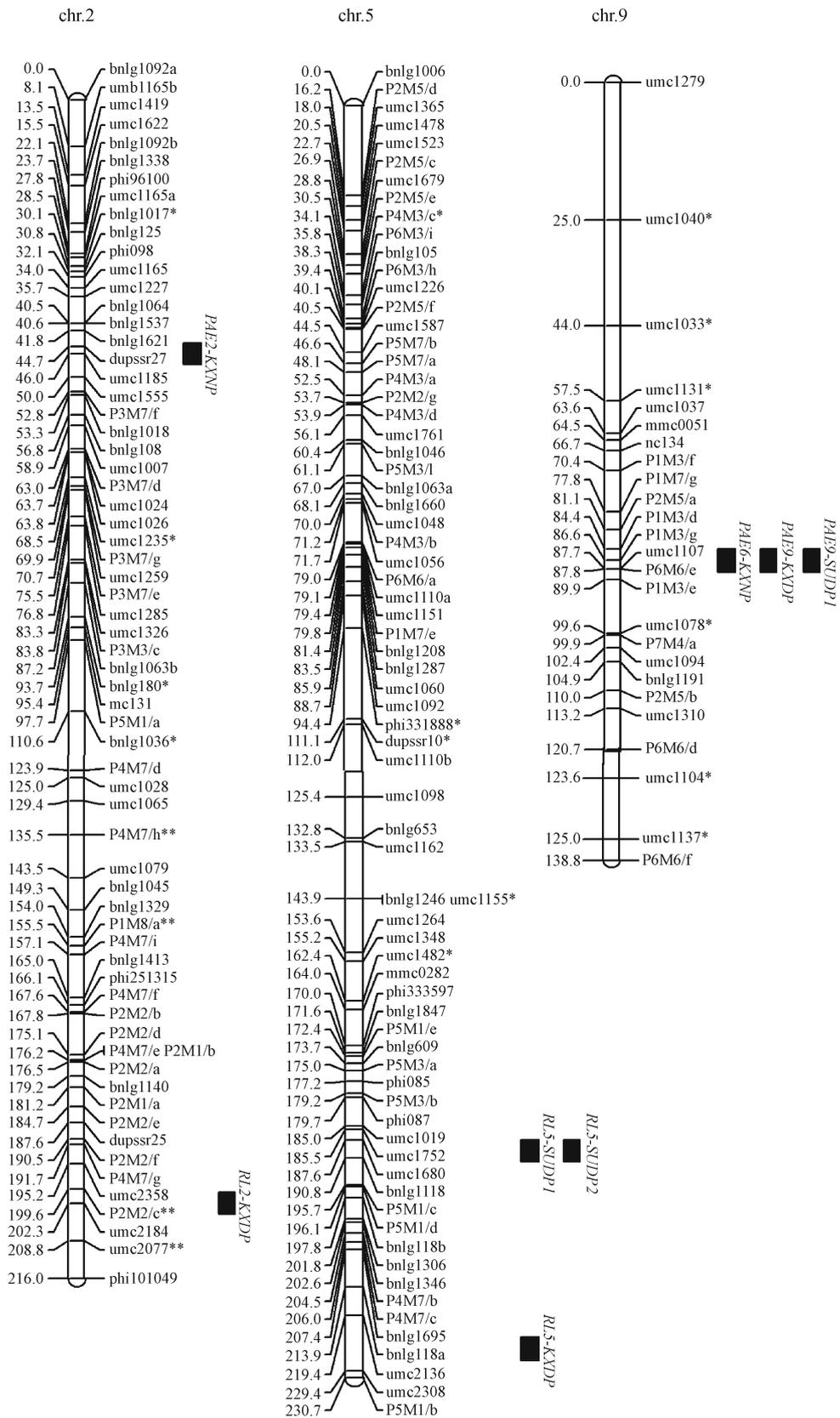
Traits	PAE	RW	RL
RW	0.9539**	—	—
RL	0.7936**	0.8089**	—
FN	0.8631**	0.9088**	0.9410**

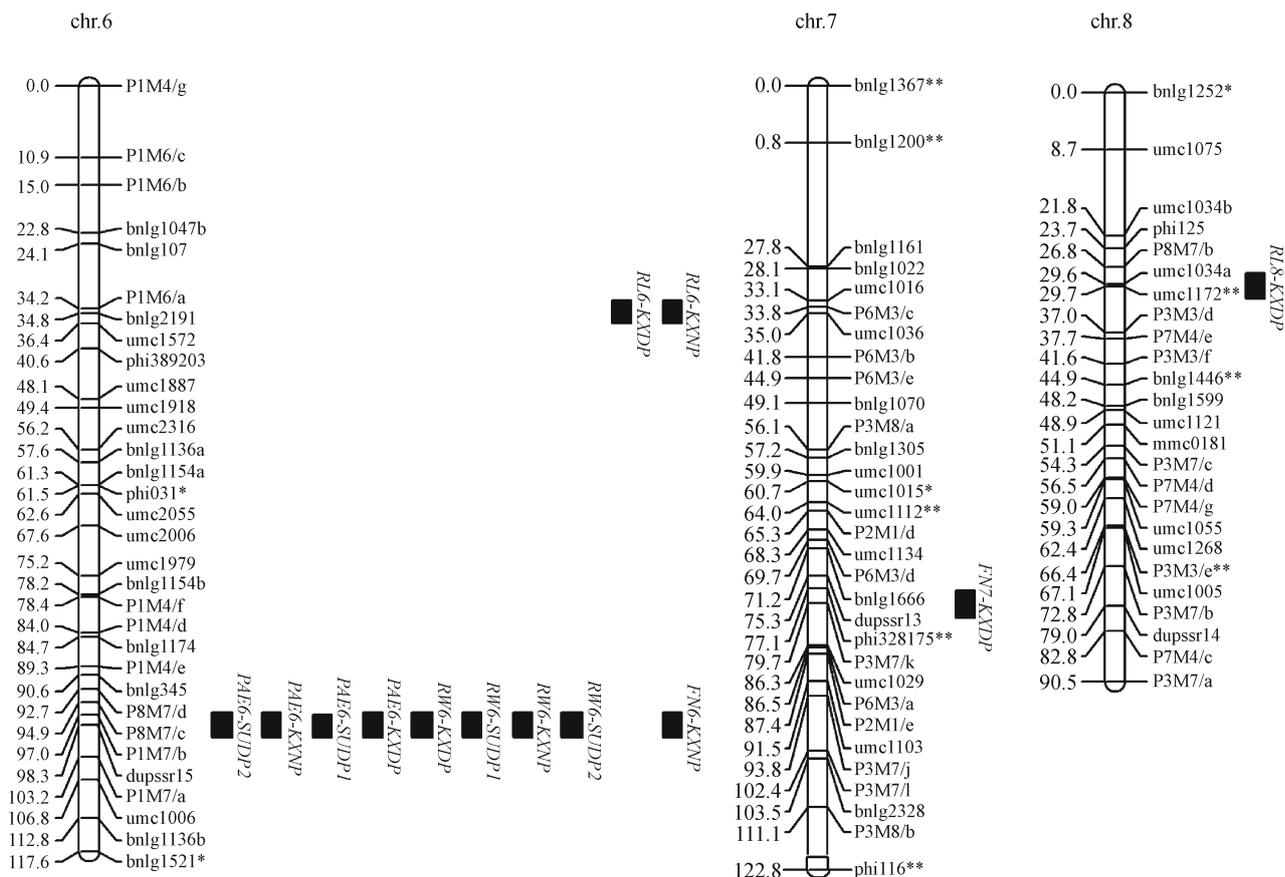
\*\* denotes significance at 1% level.

**Table 4** Quantitative trait loci (QTLs) detected for PAE, RW, RL, and FN with the  $F_{2:3}$  families from the cross of 082 × Ye107

Name	C	QP	Interval markers	Closest marker	Bins	LOD	$R^2$ (%)	$TR^2$ (%)	A	D	GA	Dir
PAE6-SUDP2	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.16	3	4	0.1542	0.0981	PD	082
PAE2-KXNP	2	46.0	umc1185- umc1555	umc1185	2.03	2.56	2	12	-0.1356	0.3246	OD	Ye107
PAE6-KXNP	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.32	4	9	0.2113	0.0982	PD	082
PAE9-KXNP	9	86.6	P1M3/d- P1M3/g	P1M3/g	9.04	2.56	2	11	0.1603	0.2409	OD	082
PAE6-KXDP	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	2.53	3	9	0.1930	0.0850	PD	082
PAE9-KXDP	9	86.6	P1M3/d- P1M3/g	P1M3/g	9.04	2.51	2	8	0.1360	0.2790	OD	082
RW6-SUDP2	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.16	3	4	0.2570	0.1635	PD	082
RW6-KXNP	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.31	3	4	0.1762	0.1042	PD	082
RW6-KXDP	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.16	3	4	0.1428	0.0908	PD	082
RW6-SUDP1	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	2.55	3	8	0.2070	0.0632	PD	082
RL2-KXDP	2	202.3	umc2184-umc2077	umc2184	2.09	2.50	7	12	0.8525	-0.4424	PD	082
RL5-KXDP	5	225.4	umc2136-umc2308	umc2308	5.08	2.51	7	14	-0.8562	0.1103	A	Ye107
RL6-KXDP	6	34.8	bnlg2191-umc1572	bnlg2191	6.02	2.52	3	10	0.4887	-0.9058	OD	082
RL8-KXDP	8	29.7	umc1034a-umc1172	umc1172	8.04	2.60	1	5	0.3077	0.4169	OD	082
RL6-KXNP	6	34.8	bnlg2191-umc1572	bnlg2191	6.02	2.68	1	11	0.3870	-0.9502	OD	082
RL5-SUDP2	5	189.6	umc1680-bnlg1118	bnlg1118	5.07	2.64	3	10	-1.1913	2.6496	OD	Ye107
FN7-KXDP	7	79.8	P3M7/k-umc1029	P3M7/k	7.04	2.75	3	10	5.9138	0.1840	A	082
FN5-SUDP1	5	189.6	umc1680-bnlg1118	bnlg1118	5.07	2.75	3	11	-6.6313	14.3741	OD	Ye107
FN6-KXNP	6	98.3	dupssr15- P1M7/a	dupssr15	6.06	3.15	3	7	7.4892	4.2827	PD	082

C is chromosome, QP is QTL position,  $R^2$  is proportion of variance explained by QTL at test site, and  $TR^2$  is the total proportion of variance explained by QTL at test site. A, D, GA, and Dir represent additive, dominance, gene action, and direction, respectively.





**Figure 1** Linkage map of QTLs for PAE, RW, RL, and FN.

In KXNP, KXDP, and SUDP2, there existed one QTL detected to influence PAE and located in the interval P1M3/d–P1M3/g (bins 9.04) on Chromosome 9 (Table 4 and Fig. 1). The QTL on Chromosome 9 explained 8%–11% of total phenotypic variance of PAE. The alleles from the QTL on chromosome 9, which contribute to increase the PAE, were from the higher phosphorus efficiency parental genotype 082 (P1) and the estimates of the genetic effects presented over dominance.

In KXNP and KXDP, one QTL was detected to influence RL and located in the interval bnlgl2191-umc1572 (bins 6.02) on Chromosome 6 (Table 4 and Fig. 1). The QTL explained 10%–11% of total phenotypic variance RL. The alleles from the QTL, contributing to increasing the RL, were from the higher phosphorus efficiency parental genotype 082(P1) with the estimates of the genetic effects over dominance.

One distinct QTL of PAE was identified in bin 2.03 in KXNP, and three distinct QTLs of RL were identified in bin 2.09, 5.08, and 8.04 in KXDP. One distinct QTL of RL was detected in bin 5.07 in SUDP2, and three distinct QTLs of FN were detected in bins 7.04, 5.07, and 6.06 in KXDP, SUDP1, and KXNP, respectively.

QTL affecting phosphorus absorption efficiency and root weight was detected simultaneously in bin 6.06 in all four

environments, while QTL affecting taproot length and fiber number was only detected in one or two environments (Table 4). The results suggested that taproot length and fiber number were more easily affected by the environment than phosphorus absorption efficiency and root weight.

## Discussion

In maize (*Zea mays* L.), the QTLs affecting root traits were detected on chromosomes bins 1.03, 1.06, 1.08, 2.03, and 2.04 (Tuberosa et al., 2003). The concentrations of QTLs on Chromosome 1 were found in a previous study (Tuberosa et al., 2003). This region harbors QTLs for root traits in hydroponics in both Lo964 × Lo1016 (Tuberosa et al., 2002) and Ac7729 × Ac7643/TZSRW (Tuberosa et al., 2003), QTLs for root traits in both Lo964 × Lo1016 and Polj17 × F-2, and QTL for root volume in B73 × Mo17 (Kaeppeler et al., 2000). In a previous study, the region for QTL on bin 6.06 was for the QTL of root pulling force in hydroponics in Lo964 × Lo1016 (Tuberosa et al., 2002).

In our study, among QTLs mapped for phosphorus absorption efficiency and root-related traits, one QTL was detected in two environments, one QTL was detected in three

environments, and one (bin 6.06) was detected in all four environments. The genomic regions in dupssr15 locus (bin 6.06) for QTL of RW were free from the environment it affects, while others were more affected by environments. The QTLs conferring PAE and RW of Chromosome 6 were relatively stable across environments. The QTL detected at the same marker intervals in four environments indicated that QTLs are not easily affected by environmental factors and that the QTL detected to influence RW was in the interval dupssr15- P1M7/a (bins 6.06) on Chromosome 6 across P levels and two different sites. QTLs affecting phosphorus absorption efficiency and root weight were detected in KXDP, KXNP, SUDP1, and SUDP2, which is the first time for QTLs to be detected in the meantime across P levels and different sites, and the QTLs affecting RW was located in the same region in four environments at the same time, which means the QTLs had high stability in deficient and normal P application. It is so important to improve P absorption in maize that QTL might be considered as the candidate QTLs for phosphorus absorption efficiency and root weight. It is interesting to find the same QTL for trait RW, which suggests that phosphorus utilization efficiency is affected both by phosphorus absorption efficiency and root weight traits, and root weight and phosphorus absorption efficiency might be controlled by the same gene.

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## References

- Chen J, Cai Y L, Xu L, Wang J G, Zhang W L, Wang G Q, Xu D L, Chen T Q, Lu X G, Sun H Y, Huang A Y, Liang Y, Dai G L, Qin H N, Huang Z C, Zhu Z J, Yang Z G, Xu J, Kuang S F (2011). Identification of QTLs for biomass production in maize (*Zea mays* L.) under different phosphorus levels at two sites. *Front Agric China*, 5 (2): 152–161
- Chen J, Xu L (2011). Comparative mapping of QTLs for H<sup>+</sup> secretion of root in maize (*Zea mays* L.) and cross phosphorus levels on two growth stages. *Front Agric China*, 5(3): 284–289
- Chen J, Xu L, Cai Y, Xu J (2008). QTL mapping of phosphorus efficiency and relative biologic characteristics in maize (*Zea mays* L.) at two sites. *Plant Soil*, 313(1–2): 251–266
- Chen J, Xu L, Cai Y, Xu J (2009). Identification of QTLs for phosphorus utilization efficiency in maize (*Zea mays* L.) across P levels. *Euphytica*, 167(2): 245–252
- Guingo E, RHébert Y, Charcosset A (1998). Genetic analysis of root traits in maize. *Agronomie*, 18L: 225–235
- Helentjaris T, Wright S, Weber D (1986). Construction of a genetic linkage map in maize using restriction fragment polymorphisms. *Maize Genet Coop News Lett*, 60: 118–120
- Hinsinger P (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil*, 237(2): 173–195
- Hinsinger P, Gilkes R J (1996). Mobilization of phosphate from phosphate rock and alumina-sorbed phosphate by the roots of ryegrass and clover as related to rhizosphere pH. *Eur J Soil Sci*, 47 (4): 533–544
- Kaeppler S M, Parke J L, Mueller S M, Senior L, Stuber C, Tracy W F (2000). Variation among maize inbred lines and detection of quantitative trait loci for growth at low phosphorus and responsiveness to arbuscular mycorrhizal fungi. *Crop Sci*, 40(2): 358–363
- Kosambi D (1944). The estimation of map distances from recombination values. *Ann Eugen*, 12: 172–175
- Stuber C W, Sisco P (1992). Marker-facilitated transfer of QTL alleles between elite inbred lines and responses in hybrids. Proc. 46th Annual Corn and Sorghum Research. Conference, Am. Seed Trade Assoc., Washington, DC, USA. 104–113
- Tuberosa R, Parentoni S, Kim T S, Sanguineti M C, Phillips R L (1998a). Mapping QTLs for ABA concentration in leaves of a maize cross segregating for anthesis date. *Maize Genet Coop News Lett*, 72: 72–73
- Tuberosa R, Salvi S, Sanguineti M C, Maccaferri M, Giuliani S, Landi (2003). Searching for quantitative trait loci controlling root traits in maize: a critical appraisal. *Plant and Soil*, 255: 35–54
- Tuberosa R, Sanguineti M C, Landi P, Giuliani M M, Salvi S, Conti S (2002). Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Plant Mol Biol*, 47(5–6): 697–712
- Tuberosa R, Sanguineti M C, Landi P, Salvi S, Casarini E, Conti S (1998b). RFLP mapping of quantitative trait loci controlling abscisic acid concentration in leaves of drought-stressed maize (*Zea mays* L.). *Theor Appl Genet*, 97(5–6): 744–755
- Wu J X, Jenkins J N, McCarty J C, Zhong M, Swindle M (2007). AFLP marker associations with agronomic and fiber traits in cotton. *Euphytica*, 153(1–2): 153–163
- Yan X, Liao H, Beebe S E, Blair M W, Lynch J P (2004). QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant Soil*, 265(1–2): 17–29
- Zhu J, Kaeppler S M, Lynch J P (2005). Mapping of QTL controlling root hair length in maize (*Zea mays* L.) under deficient phosphorus. *Plant Soil*, 270: 299–310
- Zhu J, Lynch J P (2004). The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays* L.) seedlings. *Funct Plant Biol*, 31(10): 949–958
- Zuber M S (1996). Evaluation of corn root systems under various environments. Proc Annu Corn Sorghum Ind Res Conf, 23: 67–75