

Identification of QTLs for phosphorus utilization efficiency in maize (*Zea mays* L.) across P levels

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Abstract It is necessary to develop maize plants that are productive when grown in phosphorus (P) deficient soils because of the high cost of P supplementation in soils. The shoot phosphorus utilization efficiency, the whole phosphorus utilization efficiency of plant and root/shoot ratio as well as the quantitative trait loci associated with these traits were determined for a $F_{2:3}$ population derived from the cross of two contrasting maize (*Zea mays* L.) genotypes, 082 and Ye107. A total of 241 $F_{2:3}$ families were evaluated in replicated trials under deficient and normal phosphorus conditions in 2007 at Southwest University. The genetic map constructed by 275 SSR and 146 AFLP markers spanned 1,681.3 cM in length with an average interval of 3.84 cM between adjacent markers. Phosphorus was determined in harvested plants separated into two portions, roots and shoots with leaves. The sum of the two portions was used as an expression for P in the whole plant. By using composite interval mapping, a total of 5–8 distinct QTLs were identified

under deficient and normal phosphorus, respectively. SPUE and WPUE under deficient phosphorus were controlled by one QTL, which was in the interval bnlg1518–bnlg1526 (bins 10.04) on chromosome 10. The loci of QTLs were same for SPUE, WPUE and RSR under normal phosphorus, which were in the interval bnlg1518–bnlg1526 (bins 10.04) and P2M8/a-bnlg1839 (bins 10.07) on chromosome 10. Unlike regions conferring phosphorus utilization efficiency and root shoot ratio under normal phosphorus, the region under deficient phosphorus showed that genes controlling phosphorus utilization efficiency or root shoot ratio might be different. These results may be useful to breeding programs in marker assisted selections to identify phosphorus tolerant genotypes.

Keywords Maize · QTL analysis · Phosphorus utilization efficiency · Root shoot ratio · Deficient phosphorus · Normal phosphorus

Introduction

Crops cultivated in soils with low phosphorus (P) content have very low productivity. The cost to supplement soils with this nutrient is prohibitive for many farmers (Jones and Darrah 1995; Hinsinger and Gilkes 1996; Riley and Barber 1971; Hinsinger 2001). The efficiency of P uptake and utilization is defined as the internal P concentration required for a plant to produce 90% of the maximum yield (Pratapbhanu et al. 2002).

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The ability to uptake and use P efficiently for biomass production is an important to plant growth under phosphorus deficiency, and the biomass production would affect the final grain yield. This is often called internal P requirement and is the P concentration in the plant to produce for yield (Pratapbhanu et al. 2002). Genetic difference in response to deficient phosphorus has been reported in maize for P-use efficiency (Agrama and Moussa 1996; Guingo and Hébert 1997). A three- to five-fold variation in biomass accumulation has been detected among maize inbred lines after 6 weeks of growth in a low- P soil (Landi et al. 1998, 2001, 2002).

Molecular markers can be used to study the inheritance of phosphorus efficiency and root traits and identify specific loci associated with the expression of these traits (Agrama and Moussa 1996; Junyi et al. 2008; Guingo et al. 1998; Xiaolong Yan et al. 2004; Zhu et al. 2005). The QTLs of root hair length, lateral branch length in hydroponics were studied, and a QTL flanked by *npi409-nc007* for root hair length was mapped on chromosome 5 (Zhu and Lynch 2004). The QTLs of seminal root length and number were detected, and the results suggested that epistatic interactions were important in controlling genotypic variation associated with seedling seminal root traits (Zhu et al. 2006), while the detection of QTLs for Lateral root initiation and elongation, in combination with the observation of transgressive segregants, indicated that favorable alleles can be combined to increase seedling lateral root growth in maize (Zhu et al. 2005). The QTLs for shoot P utilization efficiency (SPUE) was also detected in wheat by Su et al. (2006).

The objective of this paper was to determine the quantitative trait loci (QTLs) for shoot phosphorus utilization efficiency (SPUE), whole phosphorus utilization efficiency (WPUE), and root shoot ratio (RSR) across P levels (deficient phosphorus and normal phosphorus), which might be of use in improving phosphorus efficiency by means of marker-assisted selection.

Materials and methods

Plant material

The mapping population included 241 $F_{2,3}$ families derived from a corresponding number of randomly

chosen F_2 plants of the cross between 082 (P deficiency tolerant genotype) and Ye107 (P deficiency susceptible genotype), which were known to differ for phosphorus efficiency and root traits. The F_2 families were reproduced in October 2006–February 2007 in Hainan, China. The $F_{2,3}$ families were reproduced in March 2007–July 2007 in Xiema, Beibei, China.

Field experiment

The experiment was designed as split plot design with three replications at Southwest University (SU) (29°48'N latitude, 106°33'E longitude; 150 m altitude), P was designed to main plot, the P levels are 0 and 50 kg per hectare, $F_{2,3}$ families along with F_1 and both parents lines were designed to sub plot. $F_{2,3}$ families along with F_1 and both parents lines were sowed during September to October in 2007. In Southwest University soil, the contents of total N, P, K and available N, P, K were 0.259, 0.602, 17.8, 14.1, 2.6, 121 mg kg⁻¹, respectively, the organic matter being 3.43 g kg⁻¹ and the pH being 7.9. Fertilizers were applied before sowing at rates of 120 kg N and 50 kg P per hectare under normal P application (NP), but only applied at rates of 120 kg N under deficient P application (DP). The area per split plot was 2.5 m². There were 10 plants in each plot. Cultivation was carried out according to standard practice.

Measurement of biologic traits

The plants were harvested on the 21st day after emergence of seedling. The above-ground biomass weight, and the root dry weight (RW) were determined after fresh plant materials were dried at 105°C for 30 min and 80°C for 72 h. The plant weight was the sum of the above-ground biomass weight and the root dry weight. The root/shoot ratio (RSR) was calculated by the root dry weight/the above-ground biomass weight.

Analysis of plant phosphorus content

Plants were dried at 60°C for 72 h, ground, and became ash at 500°C for 12 h, which was then 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 (Plenet et al. 2000). The plant phosphorus content was

calculated by plant weight \times plant phosphorus concentration. The shoot phosphorus utilization efficiency (SPUE) was calculated as the rate of above-ground biomass weight and total phosphorus content, while the whole phosphorus utilization efficiency of plant (WPUE) calculated as the rate of the whole plant weight and total phosphorus content (Wissuwa 2005; Su et al. 2006).

DNA isolation

Leaf tissues from the parental genotypes and 241 F₂ families were taken and stored at -20°C . Genomic DNA isolation was isolated according to CTAB (Rogers et al. 1989; Liu et al. 2000).

SSR analysis

SSR analysis was carried out with publicly available primer pairs (Maize GDB) (Sharopova1 and McMullen 2002). Amplifications was performed in a reaction volume of 25 ng DNA, 200 mM dNTP, 300 nM for each primer, 1.5 mM MgCl₂, 50 mM Tris pH 8.5, 20 mM KCl and 1 unit *Taq* polymerase. The PCR conditions were: 94°C for 1 min, 10 cycles of 94°C for 30 s, 68°C with 0.5°C lower after each cycle for 1 min, 72°C for 1 min followed by 30 cycles of 94°C for 30 s, 58°C for 1 min, 72°C for 1 min. The PCR products were detected with agarose and silver staining.

AFLP analysis

The AFLP analysis was made according to the method Vos Hogers et al. (1995). Total DNA (100 ng) was double-digested with restriction enzymes Pst I and MseI. The PCR was carried out by pre-amplification and selective amplification with one and three anchor bases at the 3' end, respectively. Eight pairs of selective primers in combination were used in the selective amplification. The primers included: PstI end primers P1(P^{+AGG}), P2(P^{+TAA}), P3(P^{+TAC}), P4(P^{+TAG}), P5(P^{+TAT}), P6(P^{+ACG}), P7(P^{+CGA}), P8(P^{+GTA}) as well as MseI end primers M1(M^{+CAA}), M2(M^{+CTA}), M3(M^{+CAG}), M4(M^{+CTC}), M5(M^{+CTG}), M6(M^{+CCA}), M7(M^{+CAT}) and M8(M^{+CGT}). After denaturalized, the PCR products were subsequently separated in denaturing polyacrylamide gel and silver-staining according to the method of Bassam et al. (1991).

Linkage map construction

The Software Package Join Map Version 3.0 (Stam and Van Ooijen 2002) was used for the linkage analysis. With Kosambi's mapping function, the recombination frequency between linked loci was transformed into centimorgan (cM) distance. The χ^2 test was applied to identify markers with a distorted ($P < 0.01$) segregation from the expected ratios. All markers were used to construct map.

Statistical analysis of the data

Arithmetic means of three replicates were calculated for each trait of each F_{2:3} family, the parameters are fixed. 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). Heritability of traits for the F_{2:3} Families was estimated by 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 $\hat{\sigma}_E^2$ were the estimates of genetic and environment variance, respectively (Xiaolong Yan et al. 2004).

QTL analysis

The procedure of composite interval mapping (CIM) was used to identify QTLs and to estimate their effects. QTL mapping was performed with the software program Windows QTL Cartographer Version 2.5 (Wang et al. 2005). Two-locus analysis was conducted using QTL Network Version 2.0 <http://ibi.zju.edu.cn/software/qtl-network/>, where $P = 0.05$ was used as the threshold for detecting epistatic QTLs. Parameters for forward regression analysis were a window size of 10 cM, a walk speed of 2 cM, five background controls markers and probability thresholds of 0.05 each for the partial F test for both marker inclusion and exclusion. Significance threshold for QTL detection was calculated by 1, 000 random permutations of the phenotypic data at 5% level, LOD thresholds 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, being classified to additive (0–0.20), partial dominant (0.21–0.80), dominant (0.81–1.20) and over dominant (>1.20) according to Stuber and Sisco (1992) and Tuberosa et al. (1998).

Results

Genetic map

The genetic map constructed by 275 SSR and 146 AFLP markers spanned 1,681.3 cM in length with an average interval of 3.84 cM between adjacent markers. The linkage groups in present study ranged from 241.31 cM in chromosome 3 to 90.54 cM in chromosome 8, and the distances between markers from 3.02 cM in chromosome 5–7.54 cM on chromosome 10. Some alterations in marker positions were observed for chromosome 6 and 7 compared with the positions presented in maize conesus map (www.MDB.com). The umc1006 and bnlg1161 markers were located in bin 6.02 and 7.04 in MDB, while they were located in bin 6.06 and 7.02, respectively in our study.

Variation of phenotypic traits among F_{2:3} families

In two P levels, three traits (SPUE, WPUE and RSR) (Table 1) presented continuously segregating and approximately normally distributing, and absolute values of skewness and kurtness were less than 1.0, which indicated that all phenotypic traits were quantitative traits and 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 67.8 to 77.2% (Table 1).

The analysis of variance for SPUE, WPUE and RSR tested on the F_{2:3} families in two P levels, and was summarized in Table 2. The significant variances of genotypes and P levels indicated that three traits might be affected by both genotypes and P levels, and the genotypes × P levels interactions were also significant.

Correlation among traits at the two sites

The correlation coefficient among traits was shown in Table 3. WPUE is highly positively correlated ($r = 0.9977$) with SPUE, while RSR is highly negatively correlated ($r > 0.70$) with WPUE and SPUE.

Table 2 F value of ANOVA for effects

Traits	Source of variation	SS	Degree freedom	F value
SPUE	Genotypes	811.65	240	12.21*
	P levels	35.42	1	127.93*
	Error	66.45	240	
	Total variation	913.52	481	
WPUE	Genotypes	1053.76	240	10.29*
	P levels	88.44	1	207.20*
	Error	102.44	240	
	Total variation	1244.65	481	
RSR	Genotypes	4.56	240	12.05*
	P levels	0.20	1	127.44*
	Error	0.38	240	
	Total variation	5.14	481	

* Significances with a probability level of 0.0001

Table 1 Estimates of genetic variance ($\hat{\sigma}_G^2$), environment variance ($\hat{\sigma}_E^2$) among 241 F_{2:3} families from the cross of 082 × Ye107

Traits	Parents		F _{2:3} families				
	082	Ye107	Mean	Range	$\hat{\sigma}_G^2$	$\hat{\sigma}_E^2$	$h_b^2(\%)$
<i>DP</i>							
SPUE	4.26	4.44	3.77	1.49–9.60	2.4503	0.7527	76.5
WPUE	5.24	6.01	5.32	2.69–12.06	3.3022	0.9753	77.2
RSR	0.53	0.41	0.45	0.21–0.80	0.0122	0.0058	67.8
<i>NP</i>							
SPUE	4.02	4.21	3.23	1.43–8.05	1.2084	0.3964	75.3
WPUE	5.11	5.87	4.46	2.46–9.94	1.5154	0.6372	70.4
RSR	0.48	0.33	0.41	0.20–0.72	0.0084	0.0039	68.3

Table 3 Analysis of correlation among WPUE, SPUE and RSR

	WPUE	SPUE
SPUE	0.9977*	
RSR	-0.8486*	-0.8672*

* Significance at 1% level

QTL analysis

Analysis of QTLs associated with traits under deficient phosphorus

A total of five QTLs were identified: two for SPUE, two for WPUE, and one for RSR (Table 4).

Two regions were found to influence SPUE, which were located in the interval bnl345-P8M7/d (bins 6.05) on chromosome 6 and bnl1518-bnl1526 (bins10.04) on chromosome 10. But there is a gap (30 cm) in chromosome 10, near to bnl1526, this QTL had no effect. The alleles from the QTL mapped on chromosome 6, which contribute to increase SPUE, were from the lower phosphorus utilization efficiency parental genotype 082 (P1). Estimates of the genetic effects presented partial dominance.

Two regions were found to influence WPUE, which were located in the interval bnl1518-bnl1526 (bins 10.04) and P2M8/a-bnl1839 (bins10.07) on chromosome 10. The alleles from 2 QTLs mapped, which contribute to increase WPUE,

were from the lower phosphorus utilization efficiency parental genotype 082 (P1). Estimates of the genetic effects presented over dominance and additive.

One region was found to influence RSR, which was located in the interval P1M3/d-P1M3/g (bins 9.04) on chromosome 9. The alleles from the QTL mapped, which contribute to increase RSR, were from the higher root/shoot ratio parental genotype 082 (P1). Estimates of the genetic effects presented partial dominance.

Analysis of QTLs associated with traits under normal phosphorus

A total of eight QTLs were identified under normal phosphorus condition: three for SPUE, three for WPUE, and two for RSR (Table 4).

Two regions were found to influence three traits, i.e., SPUE, WPUE, and RSR, which were located in the interval umc1013-bnl2228 (bins 1.08) on chromosome 1 and bnl1070-P3M8/a (bins7.03) on chromosome 7. Two regions explained 14% of total phenotypic variance of SPUE, 13% of WPUE, and 18% of RSR. The alleles from 2 of 3 QTLs mapped (67%), which contribute to increase the phosphorus utilization efficiency (SPUE and WPUE), were from the higher phosphorus utilization efficiency parental genotype Ye107 (P2); and the favorable alleles from the 1 remaining QTL mapped (33%) were from the lower phosphorus utilization efficiency parental

Table 4 Quantitative trait loci (QTLs) detected for SPUE, WPUE and RSR with the F_{2,3} families from the cross of 082 × Ye107

Name	C ^a	QP ^b	Interval markers	Closest Marker	Bins	LOD	R ² % ^c	A ^d	D ^e	GA ^f
SPUE6-DP	6	90.6	bnlg345-P8M7/d	bnlg345	6.05	2.65	1	-0.1473	0.6253	PD
SPUE10-DP	10	69.2	bnlg1518-bnl1526	bnlg1526	10.04	2.61	5	-0.4864	0.0717	OD
SPUE1a-NP	1	141.0	umc1013-bnl2228	umc1013	1.08	4.79	13	0.6113	-0.3889	OD
SPUE1b-NP	1	146.7	bnlg100-bnl1268b	bnlg100	1.09	3.73	9	0.4808	-0.2073	OD
SPUE7-NP	7	51.1	bnlg1070-P3M8/a	bnlg1070	7.03	2.98	1	-0.0432	-0.4276	A
WPUE10a-DP	10	69.2	bnlg1518-bnl1526	bnlg1526	10.04	2.61	5	-0.5582	0.0631	OD
WPUE10b-DP	10	152.2	P2M8/a-bnl1839	bnlg1839	10.07	2.52	1	-0.1751	3.2825	A
WPUE1a-NP	1	141.0	umc1013-bnl2228	umc1013	1.08	4.62	12	0.6714	-0.4295	OD
WPUE1b-NP	1	146.7	bnlg100-bnl1268b	bnlg100	1.09	3.83	10	0.5424	-0.2242	OD
WPUE7-NP	7	51.1	bnlg1070-P3M8/a	bnlg1070	7.03	3.31	1	-0.0579	-0.4887	A
RSR9-DP	9	86.6	P1M3/d-P1M3/g	P1M3/g	9.04	2.76	1	0.014	0.0455	PD
RSR1-NP	1	141.0	umc1013-bnl2228	umc1013	1.08	4.22	11	-0.0474	0.0345	OD
RSR7-NP	7	57.2	P3M8/a-bnl1305	bnlg1305	7.03	2.89	7	-0.0369	0.0325	OD

^a Chromosome; ^b QTL position; ^c Proportion of variance explained by QTL at test site; ^d Additive; ^e Dominance; ^f GA-Gene action

genotype 082 (P1). The alleles from 2 QTLs mapped, which contribute to increase the root/shoot ratio, were from the lower RSR parental genotype Ye107 (P2); Estimates of the genetic effects presented over dominance or additive.

One region was found to influence two traits, i.e., SPUE and WPUE, which was located in the interval bnlgl100–bnlgl1268b (bins 1.09) on chromosome 1. The region explained 9% of total phenotypic variance of SPUE and 10% of WPUE. Estimates of the genetic effects presented over dominance.

Epistatic interactions

In present study, some QTLs were involved in epistatic QQ (QTL \times QTL) interactions (Table 5), which responsible for phosphorus utilization efficiency. Epistatic interactions included one QTL \times QTL interactions involving two QTLs in deficient phosphorus and five QTL \times QTL interactions involving eight QTLs in normal phosphorus. A strong interaction between two QTLs (SPUE6-DP and SPUE10-DP) was identified. (10 of 13 QTLs detected following single-locus analysis (CIM) were also detected following two-locus analysis either in the same or adjacent intervals for three traits).

Discussion

Three QTLs of phosphorus utilization efficiency were detected in rice, which were located on chromosome 2, 4 and 12 (Wissuwa et al. 1998); three QTLs of SPUE were detected which were located on linkage map 2D, 3B and 6D, while two QTLs of WPUE were detected in wheat, whose locations on linkage map

were 2D and 7A (Cao et al. 2001). The QTL for relative P use efficiency was detected in rice, with a location on chromosome 10 (Ming et al. 2000). Compared with previous study (Wissuwa et al. 1998; Cao et al. 2001), the present study designing different P levels first detected and compared QTLs for phosphorus utilization efficiency across P levels, and found that these QTLs were located on different chromosome/linkage map.

SPUE had positive correlation with WPUE, while negative correlation with RSR. Under normal phosphorus conditions, two traits (SPUE and RSR) are closely linked to WPUE in the interval bnlgl1518–bnlgl1526 (bins 10.04) and P2M8/a–bnlgl1839 (bins10.07) on chromosome 10, while SPUE closely linked to WPUE in the interval bnlgl1518–bnlgl1526 (bins 10.04) on chromosome 10 under deficient phosphorus. Collocation, pleiotropy or co-segregated might explain that.

The alleles for phosphorus utilization efficiency traits were contributed only by a poorly performing genotype 082 under deficient phosphorus conditions, while both 082 and Ye107 contributed favorable alleles for phosphorus utilization efficiency traits under normal phosphorus conditions. It is interesting to note that the favorable alleles might be separate source across P levels. In addition, there exist the genotypes \times P levels interactions. From a breeding perspective, it would increase the degree of difficulty for breeding high phosphorus utilization efficiency lines which have the ability to adapt to different P levels.

Compared with QTLs of root traits detected by Tuberosa et al. (2002), one region for SPUE and WPUE of deficient phosphorus occurred on the same region with QTL of root weight in Lo964 \times Lo1016.

Table 5 QTLs interactions (epistasis) involving (QTL \times QTL) for SPUE, WPUE and RSR in maize detected in F_{2,3} families following two-locus analysis

Name	Interval markers	Bins	Name	Interval markers	Bins	QQ interactions ^a
SPUE6-DP	bnlg345–P8M7/d	6.05	SPUE10-DP	bnlg1079–bnlg1518	10.03	1.21
SPUE1b-NP	dupssr12–phi002b	1.08	SPUE7-NP	bnlg1666–dupssr13	7.04	0.78
SPUE7-NP	bnlg1666–dupssr13	7.04	SPUE1a-NP	bnlg1564–phi002a	1.07	–0.43
WPUE1a-NP	bnlg1564–phi002a	1.07	WPUE1b-NP	dupssr12–phi002b	1.08	–0.04
WPUE7-NP	bBnlgl1666–dupssr13	7.04	WPUE1a-NP	bnlg1564–phi002a	1.07	–0.25
RSR1-NP	bnlg1564–phi002a	1.07	RSR7-NP	umc1015–umc1112	7.03	–0.21

^a QTL \times QTL interactions (additive \times additive effect)

On bin 10.04, the region of QTL for SPUE and WPUE had been found for QTLs of root traits [primary root weight (R1 W) and adventitious root weight (R2 W)]. Two regions for SPUE, WPUE, and RSR of normal phosphorus occurred on the same region with QTLs of root weight and length in Lo964 × Lo1016. On bin 1.07, the region of QTLs for SPUE, WPUE, and RSR had been found for QTLs of root traits (primary root diameter, secondary root weight, root pulling force, and brace root number). On bin 7.03, the region of QTLs for SPUE, WPUE, and RSR had been found for QTLs of root traits [adventitious root weight (R2 W) and primary root length (R1L)]. The roots themselves are significant sources of phosphorus utilization efficiency and root shoot ratio.

Unlike regions conferring phosphorus utilization efficiency and root shoot ratio under normal phosphorus, the region under deficient phosphorus showed that genes controlling phosphorus utilization efficiency or root shoot ratio might be different. It might be emergency reaction when some genes were activated at the time of maize plant growth under deficient P stress.

In some cases, due to epistatic interactions, different QTLs might mask the effects of each other. In our study, epistatic interactions also exists. Epistatic interactions, which make a substantial contribution to phosphorus utilization efficiency, had to be considered when breeding maize varieties with high P efficiency.

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References

Agrama RHAS, Moussa ME (1996) Mapping QTLs in breeding for drought tolerance in maize (*Zea mays* L.). *Euphytica* 91:89–97. doi:10.1007/BF00035278

Bassam BJ, Caetano AG, Gresshof PM (1991) Fast and sensitive silver staining of DNA in polyacrylamide gels. *Ann Biochem* 196(1):80–83. doi:10.1016/0003-2697(91)90120-1

Cao WD, Jia JZ, Jin JY (2001) Identification and interaction analysis of QTL for phosphorus use efficiency in wheat. *Zhijiu Yingyang Yu Feiliao Xuebao*. *Plant Nutr Fertil Sci* 7(3):285–290

Chen J, Xu L, Cai Y (2008) QTL mapping of phosphorus efficiency and relative biologic characteristics in maize (*Zea mays* L.) at two sites. *Plant Soil* 313:251–266. doi:10.1007/s11104-008-9698-x

Guingo E, Hébert Y (1997) Relationships between mechanical resistance of the maize root system and root morphology, and their genotypic and environmental variation. *Maydica* 42:265–274

Guingo E, Hébert Y, Charcosset A (1998) Genetic analysis of root traits in maize. *Agronomy* 18:225–235. doi:10.1051/agro:19980305

Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant Soil* 237:173–195. doi:10.1023/A:1013351617532

Hinsinger P, Gilkes RJ (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* 47:533–544. doi:10.1111/j.1365-2389.1996.tb01853.x

Jones DL, Darrah PR (1995) Influx and efflux of organic acids across the soil-root interface of *Zea mays* L. and its implications in rhizosphere C flow. *Plant Soil* 173:103–109. doi:10.1007/BF00155523

Landi P, Albrecht B, Giuliani MM, Sanguineti MC (1998) Seedling characteristics in hydroponic culture and field performance of maize genotypes with different resistance to root lodging. *Maydica* 43:111–116

Landi P, Giuliani MM, Darrah LL, Tuberosa R, Conti S, Sanguineti MC (2001) Variability for root and shoot traits in a maize population grown in hydroponics and in the field and their relationships with vertical root pulling resistance. *Maydica* 46:177–182

Landi P, Salvi S, Sanguineti MC, Stefanelli S, Tuberosa R (2002) Development and preliminary evaluation of near-isogenic maize lines differing for a QTL which affects leaf ABA concentration

Liu D, Coloe S, Baird R, Pedersen J (2000) Rapid mini-preparation of fungal DNA for PCR. *J Clin Microbiol* 38(1):471

Ming F, Mi GH, Zhang FS (2000) Identification of quantitative trait loci affecting tolerance to low phosphorus in rice (*Oryza Sativa* L.). *Kexue Tongbao*. *Chin Sci Bull* 45:520–524

Plenet D, Etchebest, Mollier A, Pellerin S (2000) Growth analysis of maize field crops under phosphorus deficiency I. Leaf Growth. *Plant Soil* 223:117–130. doi:10.1023/A:1004877111238

Pratapbhanu S, Bhadoria et al (2002) Phosphorus efficiency of wheat and sugar beet seedlings grown in soils with mainly calcium, or iron and aluminium phosphate. *Plant Soil* 246:41–52. doi:10.1023/A:1021567331637

Riley D, Barber SA (1971) Effect of ammonium and nitrate fertilisation on phosphorus uptake as related to root-induced pH changes at the root-soil interface. *Soil Sci Soc Am Proc* 35:301–306

Rogers SO, Rehner S, Bledsoe C et al (1989) Exaction of DNA from Basidiomycetes for ribosomal DNA hybridization. *Can J Bot* 67:1235–1243

Stam P, Van Ooijen JW (2002) Join Map™ version 3.0: software for the calculation of genetic linkage map. CPRO-DLO, Wageningen, the Netherlands, 1–5

- Stuber CW, Sisco PH (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, pp 104–113
- Su JY, Xiao YM, Li M et al (2006) Mapping QTLs for phosphorus-deficiency tolerance at wheat seedling stage. *Plant Soil* 281:25–36. doi:[10.1007/s11104-005-3771-5](https://doi.org/10.1007/s11104-005-3771-5)
- Tuberosa R, Sanguineti MC, Landi P et al (1998) RFLP mapping of quantitative trait loci controlling abscisic acid concentration in leaves of drought-stressed maize (*Zea mays* L.). *Theor Appl Genet* 97:744–755. doi:[10.1007/s001220050951](https://doi.org/10.1007/s001220050951)
- Tuberosa R, Sanguineti MC, Landi P et al (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* 48:697–712. doi:[10.1023/A:1014897607670](https://doi.org/10.1023/A:1014897607670)
- Vos Hogers R, Bleeker M, Reijans M et al (1995) AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Res* 23(21):4404–4414
- Wang S, Basten CJ, Zeng ZB (2005) Windows QTL Cartographer 2.5. Department of Statistics, NCSU, Raleigh. (<http://statgen.ncsu.edu/qtlcart/WQTLCart.htm>)
- Wissuwa M (2005) Combining a modelling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. *Plant Soil* 269:57–68. doi:[10.1007/s11104-004-2026-1](https://doi.org/10.1007/s11104-004-2026-1)
- Wissuwa M, Yano M, Ae N (1998) Mapping of QTL for phosphorus-deficiency tolerance in rice (*Oryza sativa* L.). *Theor Appl Genet* 97:777–783. doi:[10.1007/s001220050955](https://doi.org/10.1007/s001220050955)
- Xiaolong Yan R, Hong L, Steve E et al (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant Soil* 265:17–29. doi:[10.1007/s11104-005-0693-1](https://doi.org/10.1007/s11104-005-0693-1)
- Zhu J, Lynch JP (2004) The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays* L.) seedlings. *Funct Plant Biol* 31:949–958. doi:[10.1071/FP04046](https://doi.org/10.1071/FP04046)
- Zhu JM, Mickelson SM, Kaepler SM et al (2005) Detection of quantitative trait loci for seminal root traits in maize (*Zea mays* L.) seedlings grown under differential phosphorus levels. *Theor Appl Genet* 113(1):1–13. doi:[10.1007/s00122-006-0260-z](https://doi.org/10.1007/s00122-006-0260-z)
- Zhu JM, Kaepler SM, Lynch JP (2006) Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theor Appl Genet* 111(4):688–695. doi:[10.1007/s00122-005-2051-3](https://doi.org/10.1007/s00122-005-2051-3)