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ORIGINAL PAPER

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Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply

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Abstract Low phosphorus availability is a primary constraint for plant growth in terrestrial ecosystems. Lateral root initiation and elongation may play an important role in the uptake of immobile nutrients such as phosphorus by increasing soil exploration and phosphorus acquisition. The objective of this study was to identify quantitative trait loci (QTLs) controlling lateral root length (LRL), number (LRN), and plasticity of the primary seedling root of maize under varying phosphorus availability. Using a cigar roll culture in a controlled environment, we evaluated primary root LRL and LRN at low and high phosphorus availability in 160 recombinant inbred lines (RILs) derived from a cross between maize genotypes B73 and Mo17, which have contrasting adaptation to low phosphorus availability in the field. Low phosphorus availability increased LRL by 19% in Mo17, the phosphorus-efficient parent, but significantly decreased LRL in B73, the phosphorus-inefficient genotype. Substantial genetic variation and transgressive segregation for LRL and LRN existed in the population. The plasticity of LRL ranged from −100% to 146.3%, with a mean of 30.4%, and the plasticity of LRN ranged from −82.2% to 164.1%, with a mean of 18.5%. On the basis of composite interval mapping with a LOD threshold of 3.27, one QTL was associated with LRN plasticity, five QTLs were associated with LRL and one QTL was associated with LRN under high fertility. Under low fertility, six QTLs were associated with LRL and one QTL with LRN. No QTLs were detected for plasticity of LRL. A number of RILs exceeded Mo17, the phosphorus-efficient parent, for LRL, LRN, and plasticity. The detection of QTLs for these traits, in combination with the observation of transgressive segregants in our population, indicates that favorable alleles can be combined to increase seedling lateral root growth in maize.

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Introduction

Low soil phosphorus availability is a primary constraint to plant growth over much of the earth's surface (Lynch and Deikman 1998), principally because phosphorus is tightly bound to soil constituents, such as Fe and Al oxides or recalcitrant organic matter, which make it unavailable to plants (Sample et al. 1980; Barber 1995). In agricultural systems, the application of phosphorus fertilizer is necessary to maintain and improve crop yields and to meet the needs of continued population growth. Intensive fertilization is not affordable by many farmers in developing countries and also is a primary source of runoff pollution that threatens surface water resources in the USA and other developed nations (Council NNR 1989; Francis 1990). In addition, intensive fertilization is restricted by the fact that high-grade phosphorus ore deposits are a limited, nonrenewable resource (Cathcart 1980; Netzer 1987). Therefore, sustainable agricultural production systems of the future will need to maximize crop output while minimizing phosphorus input (Lynch 1998). This will be facilitated by the development of more phosphorus-efficient crop cultivars that will yield more per unit of phosphorus input.

Root architecture, defined as the spatial configuration of the root system (Lynch 1995), may be especially important for phosphorus acquisition efficiency (PAE), since the relative immobility of phosphorus makes its acquisition dependent on soil exploration in time and space (Barber 1995). Our research with common bean (*Phaseolus vulgaris*) has demonstrated the value of using

root traits to select for enhanced PAE (Lynch and Beebe 1995). In bean, the identification and genetic tagging of specific traits contributing to PAE have resulted in the identification of genotypes with substantially greater PAE than existing cultivars. These genotypes are presently being used in bean breeding in Asia, Africa, and Latin America (CIAT 1999). In bean, the most useful traits to date with respect to selecting for PAE have been architectural traits governing root branching and root gravitropism (Lynch and Beebe 1995; Lynch and Brown 2001).

Lateral rooting might be a beneficial root trait conferring phosphorus efficiency by increasing soil exploration and phosphorus solubilization. Lateral roots arise from pre-existing roots and develop from the pericycle (Macleod and Thompson 1979). In red pine, fir, and cedar, lateral root development is under genetic control (He 1962a, b, 1968). White lupin shows a concerted regulation of lateral root development in response to low phosphorus availability (Johnson and Vance 1996). In this study the high phosphorus-treated plants initiated fewer clustered tertiary meristems, and the emergence of these meristems was delayed compared with low phosphorus-treated plants. In lupin, lateral roots exude large amounts of citrate, which increases phosphorus solubilization (Johnson et al. 1996).

Maize (*Zea mays* L.) is generally considered to have a high fertility requirement, but for more than a century variation for phosphorus efficiency has been known to exist among maize genotypes (Anonymous 1887; Naismith et al. 1974; Da Silva and Gabelman 1993; Kaeppler et al. 2000; Gaume et al. 2001; Zhu and Lynch 2004). Growth differences among maize genotypes in a low phosphorus environment have been characterized using a sand-alumina culture system (Da Silva et al. 1992; Da Silva and Gabelman 1993) as has growth at low phosphorus availability and response to mycorrhiza in soil (Kaeppler et al. 2000). Both studies found significant variation among maize genotypes with respect to biomass accumulation at low phosphorus availability. Biomass accumulation among 21 maize inbred lines ranged from 0.58 to 1.69 g for 4-week-old plants (Da Silva and Gabelman 1993). Among 28 inbred lines, it ranged from 0.56 g to 3.15 g after 6 weeks of growth in the low phosphorus soil experiment (Kaeppler et al. 2000). Five quantitative trait loci (QTLs) for root/shoot biomass at low phosphorus in the NY821 × H99 population were detected, which accounted for 46% of the total phenotypic variation for total plant dry weight (Reiter et al. 1991). Three QTLs were identified in the B73 × Mo17 population on chromosomes 1, 7, and 8 in solution culture (Kaeppler et al. 2000).

We have recently demonstrated that genotypic variation in lateral rooting may be an important component of the genetic variation for efficient phosphorus acquisition in maize (Zhu and Lynch 2004). Five maize recombinant inbred lines (RILs) derived from a cross between B73 and Mo17 with contrasting lateral rooting were grown in sand culture in a controlled environment. Genotypes with enhanced or sustained lateral rooting at low phosphorus availability had greater phosphorus acquisition and biomass accumulation and a higher relative growth rate than genotypes with reduced lateral rooting under the same condition. The genotypes varied in the phosphorus investment required for lateral root elongation due to genetic differences in the specific root length (which was correlated with root diameter) and phosphorus concentration in the lateral roots. Lateral root extension required less biomass and phosphorus investment than the extension of other root types. Two distinct cost-benefit analyses—one using phosphorus acquisition rate as a benefit and root respiration as a cost, the other using plant phosphorus accumulation as a benefit and phosphorus allocation to lateral roots as a cost—showed that lateral rooting was advantageous under conditions of low phosphorus availability. These results suggest that enhanced lateral rooting under phosphorus stress may be harnessed as a useful trait for the selection and breeding of more phosphorus-efficient maize genotypes.

The objective of this research was to identify QTLs for lateral root length (LRL), number (LRN), and their plasticity in response to phosphorus stress, towards the long-term goals of elucidating the relative importance of each root type in maize for PAE and of developing genetic tools that will facilitate the breeding of more phosphorus-efficient maize genotypes.

Materials and methods

Mapping population

RILs from the cross B73 × Mo17 were originally supplied by Charles Stuber and Lynn Senior at North Carolina State University and increased at the University of Wisconsin, Madison, USA. Genotype Mo17 is phosphorus-efficient, which is defined as superior growth at suboptimal phosphorus availability, while B73 is phosphorus-inefficient (Kaeppler et al. 2000). A total of 160 RILs were analyzed in this study. The RIL population was previously genotyped with 196 restriction fragments length polymorphism (RFLP), simple sequence repeat (SSR), and isozyme markers (Senior et al. 1996). This genetic linkage map has 27 markers on chromosome 1, 14 on chromosome 2, 15 on chromosome 3, 23 on chromosome 4, 32 on chromosome 5, 21 on chromosome 6, 13 on chromosome 7, 17 on chromosome 8, 18 on chromosome 9, and 16 on chromosome 10. The map covers 1,703 cM with an average interval of 8.73 cM.

Experimental design

The experimental design was a randomized complete block design with a split plot arrangement of treatments.

The main plots were low- and high phosphorus; subplots comprised 162 genotypes (two parents plus 160 lines). There were three replicates in time, with six measurements per plant, for a total of 18 phenotypic observations per genotype.

Plant growth and measurements

Maize seeds of the two parents and 160 F_{10}-derived RILs were surface sterilized for 1 min in a 0.5% solution of NaOCl and then washed in deionized H_2O before germination. In each replicate, one typical seed from the seed stock for a genotype was selected and wrapped in brown germination paper (Anchor Paper, St. Paul, Minn.) as a cigar roll. Two batches of 162 cigar rolls were soaked vertically in two plastic containers measuring 47.5×35×25 cm (length×width×height) filled with 5 l nutrient solution containing low or high levels of phosphorus. The low-phosphorus nutrient solution consisted of (in μ*M*): K (3,000), NO_3 (7,000), NH_4 (1,000), Ca (2,000), SO_4 (500), Mg (500), Cl (25), B (12.5), Mn (1), Zn (1), Cu (0.25), Mo (0.25), and EDTA-Fe (25), which had 0.2 μ*M* phosphorus. For the high-phosphorus nutrient solution, 0.5% (w/v) of alumina-buffered media was added to the low-phosphorus nutrient solution so that 62 μ*M* phosphorus was continuously maintained in the solution (Lynch et al. 1990). Seedlings were germinated in darkness in a growth chamber at 28 ± 1°C for 3 days, then grown at 28/24°C (light/dark) under a 14/10-h (light/dark) photoperiod with photosynthetically active radiation (PAR) of 200 μmol photons m^{-2} s^{-1}. The relative humidity was 65%. The nutrient solution pH was adjusted with 1 *M* KOH and 1 *M* HCl to 6.0 daily.

Plant seedlings were harvested 11 days after germination, and the roots were immediately preserved in 30% ethanol. At this time, the root system consisted of a primary root with emerged lateral roots and of one to seven emerging seminal roots that did not have visible lateral roots. After the seminal roots were removed from the root system, both the primary root and lateral roots were scanned using image analysis software (WinRhizo Pro, Régent Instruments, Québec, Canada). Total root length and the number of root tips, including primary root and lateral roots, were collected by the software. LRL was determined by subtracting the length of the primary root from the total root length. LRN was determined by subtracting one (for the primary root) from the total root number. LRL plasticity (i.e., change in the lateral rooting in response to phosphorus availability) was calculated as 100×(LRL under low phosphorus − LRL under high phosphorus)/LRL under high phosphorus. LRN plasticity was calculated as 100×(LRN under low phosphorus − LRN under high phosphorus)/LRN under high phosphorus. One seedling was sampled in each of the three replicates, for a total of three seedlings per RIL.

Data analysis

Of the 193 genotypes, 33 were not included in the analysis because of a high coefficient of variation (CV) among the three replicates, resulting in 160 lines for QTL analysis. The mean of the coefficient of variation was 18.6% for LRL at low phosphorus, 11.1% for LRN at low phosphorus, 11.2% for LRL at high phosphorus, and 12.2% for LRN at high phosphorus. The data from the inbred screening experiment were first subjected to ANOVA using a general linear model that included phosphorus and genotype as factorial treatments (Minitab, University Park, Pa.). Genotype and phosphorus levels were considered to be fixed effects and replicates to be random. In the cigar roll experiment, there was no significant difference among the replicates for LRN plasticity, while there was a significant difference among the replicates for LRL plasticity ($P < 0.01$). There was no significant difference for LRN among replicates at both low and high phosphorus, while there was significant difference for LRL at both low and high phosphorus ($P < 0.01$). Since the phosphorus level × genotype interaction was highly significant (data not shown; this interaction is indicative of a differential response of the genotypes to phosphorus level) for both LRL and LRN, there was no valid significance test for the main effects. To identify transgressive segregation, we performed a paired *t*-test for each inbred line relative to the most similar parent under different phosphorus treatments (Minitab). Normality of distributions across genotypes was evaluated by the *Z*-test (Minitab). Arithmetic mean values across three replicates were calculated for each variable for RILs and used for QTL mapping. Plasticity values were calculated using values across replications. Composite interval mapping (CIM) was conducted using PLABQTL (Utz and Melchinger 1999). For CIM, linkages between molecular markers and QTLs were determined by employing the covariate SELECT option of PLABQTL. This option applies step-wise multiple regression to select cofactors. All chromosome regions with an LOD of more than 3.27, giving an experiment-wise error rate of $P < 0.10$ and a comparison-wise error rate of 0.000538 based on the analysis of 186 intervals from the composite analysis, were considered to be significant. The additive effect of a marker was calculated as [(mean of the homozygous Mo17 class − mean of the homozygous B73 class)/2].

Results

Segregation for plasticity of LRL and LRN between the two parents

Low phosphorus availability had no significant effect on LRN in Mo17, the phosphorus-efficient parent, but significantly decreased LRL in B73, the phosphorus-inefficient parent ($P < 0.01$) (Fig. 1). Interestingly, LRL of Mo17 was stimulated 24% by low phosphorus availabil-

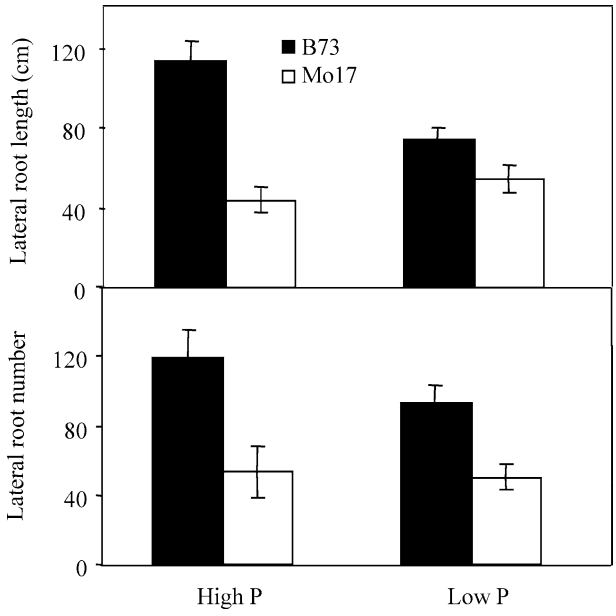

Fig. 1 Means of lateral root length and lateral root number for two parents, B73 and Mo17, under low and high phosphorus availability. *Bar* standard error of the mean, $n = 3$

ity, which was significant at $P < 0.06$ by a paired *t*-test (Fig. 1). Mo17 had significantly greater LRL plasticity (i.e., change in lateral rooting in response to phosphorus availability) and LRN plasticity than the phosphorus-inefficient parent, B73 ($P < 0.01$) (Fig. 2).

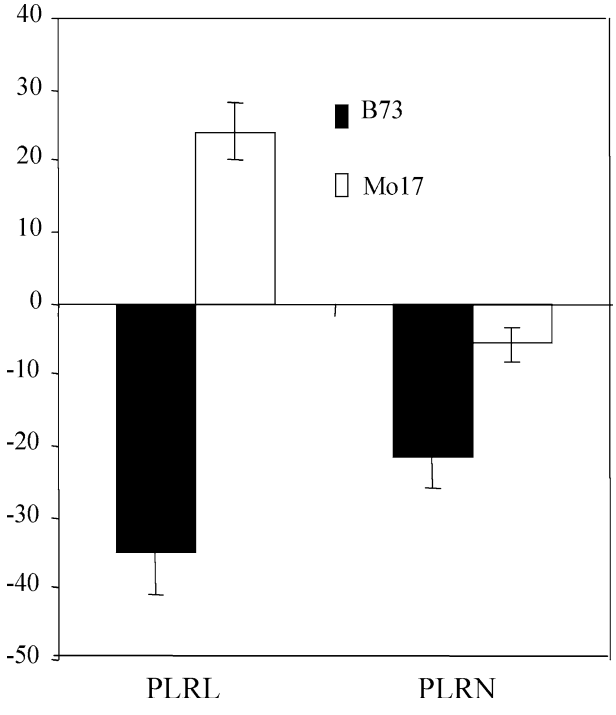

Fig. 2 Means of lateral root length plasticity (*PLRL*) and lateral root number plasticity(*PLRN*) for two parents, B73 and Mo17, under high and low phosphorus availability. PLRL was calculated as 100×(LRL under low P − LRL under high P)/LRL under high phosphorus availability; PLRN was calculated as 100×(LRN under low P − LRN under high P)/LRN under high phosphorus availability. *Bar* standard error of the mean, $n = 3$

Variation of lateral root traits among RILs

LRL of the population under low phosphorus ranged from 0 cm (no lateral roots) to 125.9 cm, with a mean of 52.1 cm; under high phosphorus culture, it ranged between 2.4 cm and 110.3 cm, with a mean of 40.9 cm (Fig. 3). The plasticity of LRL ranged from −100% to 146.3%, with a mean of 30.4% (Fig. 4). Transgressive segregation was observed for LRL plasticity, with four RILs showing significantly less transgressive segregation than B73 and 38 RILs showing significantly greater transgressive segregation than Mo17 ($P < 0.01$).

LRN of the population under low phosphorus ranged from 8.0 cm to 188.0 cm, with a mean of 88.8 cm; under high phosphorus culture, it ranged between 29.7 cm and 169.7 cm, with a mean of 89.7 cm (Fig. 5). The plasticity of LRN ranged from −82.2% to 164.1%, with a mean of 18.5% (Fig. 6). Transgressive segregation was also observed for plasticity of LRN, with three RILs showing significantly less transgressive segregation than B73 and

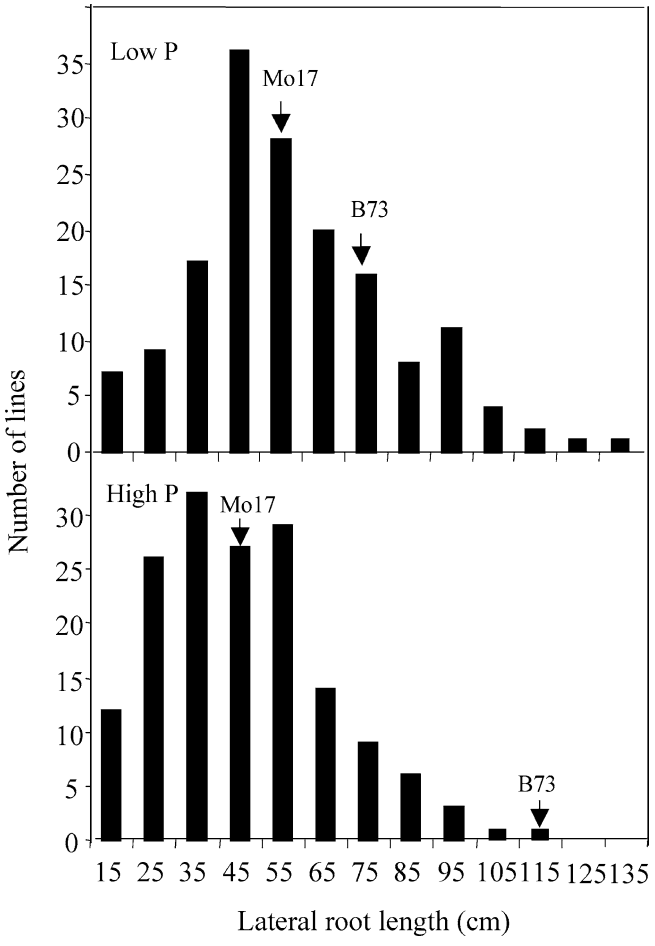

Fig. 3 Frequency distribution of lateral root length under conditions of low phosphorus and high phosphorus availability in 160 RILs derived from B73 × Mo17. $n = 3$

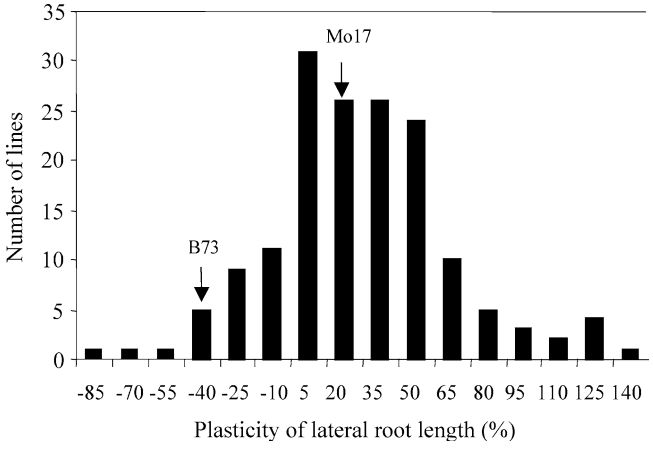

Fig. 4 Frequency distribution of the plasticity of lateral root length (LRL) in a population of B73 × Mo17 RILs, calculated as 100×(LRL under low P – LRL under high P)/LRL under high phosphorus availability

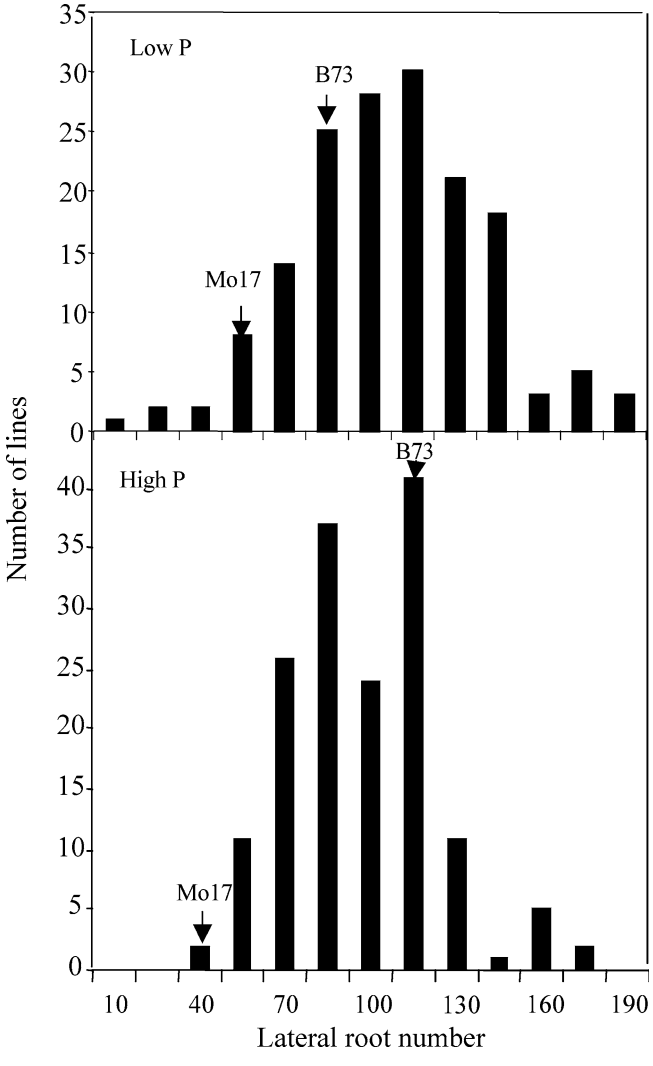

Fig. 5 Frequency distribution of lateral root number under low phosphorus and high phosphorus availability in 160 RILs derived from B73 × Mo17. $n = 3$

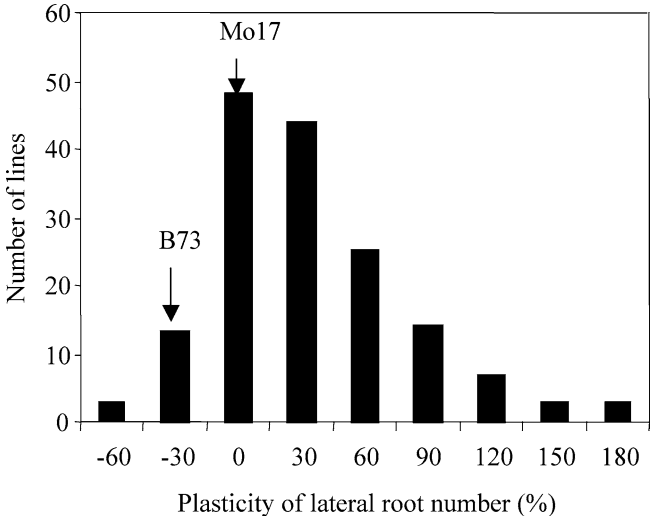

Fig. 6 Frequency distribution of lateral root length under low phosphorus and high phosphorus availability in 160 RILs derived from B73 × Mo17. $n = 3$

67 RILs showing significantly greater transgressive segregation than Mo17.

Composite interval mapping

QTLs were detected for five traits, including LRL and LRN at low phosphorus, LRL and LRN at high phosphorus, and LRN plasticity (Table 1, Fig. 7). Five QTLs flanked by *phi001*/*csu3*, *csu164a*/*phi055*, *nc004*/*umc36b*, *bn16.16*/*umc17*, *phi070*/*umc62*, and *bn17.08*/*phi121* on chromosomes 1, 2, 3, 6, and 8, respectively, were identified for LRL at low phosphorus (Table 1), which combined contributed 30% of the phenotypic variation in the population. A QTL flanked by umc131/nc003 was detected for LRN at low phosphorus, which had an additive effect of −11.6% and an LOD value of 3.86. Five QTLs flanked by *nc003*/*umc36b*, *bn15.37*/*umc60*, *umc52*/*npi449b*, *umc169*/*phi006*, and *tip5*/*umc07* were detected for LRL on chromosomes 2, 3, 4, and 8 under high phosphorus culture, which combined explained 45.6% of the phenotypic variation in the population. A coincident QTL flanked by *nc003*/*umc36b* was also found for LRN at high phosphorus (Table 1).

One locus was detected for LRN plasticity. This QTL was located on chromosome 4 flanked by nc005/umc66a (Table 1), which had an LOD value of 4.19 and explained 10.2% of phenotypic variation in the population. The most likely position of each QTL detected for these five traits is plotted in Fig. 7. No significant QTLs were detected for the plasticity of LRL.

Discussion

Our phenotypic data indicate that lateral root elongation and LRN were modulated by low phosphorus

Table 1 List of detected QTLs with a LOD threshold 3.27 for traits at low and high phosphorus using composite interval mapping

Parameter	Position	Chromosome	LOD	VAR%	Additive effect[a]
Under low phosphorus					
Lateral root length	*phi001/csu3*	1	3.94	7.15	−5.7
	csu164a/phi055	1	3.36	4.04	−4.3
	nc003/umc36b	2	4.73	9.98	−7.5
	bn16.16/umc17	3	5.27	3.97	4.5
	phi070/umc62	6	3.30	4.85	−4.8
	bn17.08a/phi121	8	4.25	5.38	5.0
Lateral root number	*umc131/nc003*	2	3.86	10.4	−11.6
Under high phosphorus					
Lateral root length	*nc003/umc36b*	2	7.10	14.4	−7.9
	bn15.37/umc60	3	5.33	10.7	7.7
	umc52/npi449b	4	3.92	6.82	−5.1
	umc169/phi006	4	3.95	7.14	5.2
	tpi5/umc07	8	3.31	6.50	−5.2
Lateral root number	*nc003/umc36b*	2	5.89	13.6	−11.1
Plasticity					
Lateral root number	*nc005/umc66a*	4	4.19	10.2	6.8

[a]Positive values indicate that Mo17 carries the allele for an increase in the trait, while negative values indicate that B73 contributes the allele for an increase in the trait

availability in most of the RILs investigated. This result is consistent with our observation that mostly distinct QTLs controlled lateral root traits under different phosphorus levels, and demonstrates that phosphorus availability significantly affects lateral root branching and length. Genotypes that respond to low phosphorus availability with increased lateral rooting may be able to acquire more phosphorus in low phosphorus environments.

Table 1 indicates that (1) B73 contributed more favorable alleles for LRL and LRN than Mo 17 at both low and high phosphorus levels, and (2) Mo17 contributed more favorable alleles for plasticity of LRN than B73. These results are consistent with the parental phenotypes. We also detected significant transgressive segregation for these traits in our population, confirming that both parents contributed alleles for these traits. It is likely that there are multiple QTLs controlling the traits, with favorable alleles coming from both parents. However, we did not detect any QTLs for plasticity of LRL. This is unexpected. Re-evaluation of the data for plasticity of LRL at a more liberal LOD threshold of 2.0 did result in additional QTLs for this trait.

The QTL on chromosome 2 flanked by *nc003/umc36b* was significant for LRL under both low and high phosphorus availability. Interestingly, this locus also contributed alleles for LRN at high phosphorus availability. This QTL appears to control a genetic determinant of LRN that is not sensitive to phosphorus. It is possible that this QTL would respond differently to other nutrients, since other essential elements such as nitrogen and potassium were kept constant in this experiment.

Reiter et al. (1991) reported that three marker loci, *umc42b*, *umc138*, and *umc117* on chromosome 3, 6, and 8, respectively, were significantly associated with root dry weight under low-phosphorus stress in a maize NY821 × H99 $F_{2:3}$ population. Interestingly, the molecular marker *umc60* on chromosome 3 explained more than 5% of the total genetic variation for dry weight in their study (Reiter et al. 1991). We detected a QTL in our study which controlled LRL at high phosphorus; this QTL is in an interval that overlaps with the QTL reported by Reiter et al. (1991). Future work will resolve whether this chromosome region contains a QTL that is having similar effects across populations.

A QTL flanked by *phi001/csu3* on chromosome 1 for LRL at low phosphorus was coincident with a QTL previously reported for seed phosphorus reserve (Zhu et al. 2005). One possible explanation for this is that seed phosphorus reserves may permit enhanced lateral rooting under low-phosphorous conditions. A genomic region near *umc66a* on chromosome 4 has been found to contain QTLs controlling grain yield across maize populations and water deficit across populations (Tuberosa et al. 2002). A significant QTL was detected in this chromosome region in our study for LRN plasticity, indicating that epistatic or linked genes in this region of chromosome 4 control multiple root and performance traits across populations.

Zobel (1986) has proposed that there are five distinct types of angiosperm roots—tap, lateral, adventitious, basal, and "collateral"—based on genetic, physiological, and anatomical evidence. Distinct classes of roots may have distinct architectures, genetic control, and responses to environmental variables (Rundel and Nobel 1991; Lynch and van Beem 1993; Zobel 1996). Very little is known about the correlation of genetic control among root types in maize. In a field study (Zhu 2003), we found that the total LRL of the primary root (x) was significantly associated with the total LRL of seminal roots (y) for 7-week-old seedlings from eight maize genotypes grown under conditions of low and high phosphorus. The linear regression formula was $y = 1.292x + 121.1 (R^2 = 0.260,\ df = 14,\ P < 0.05)$. A simi-

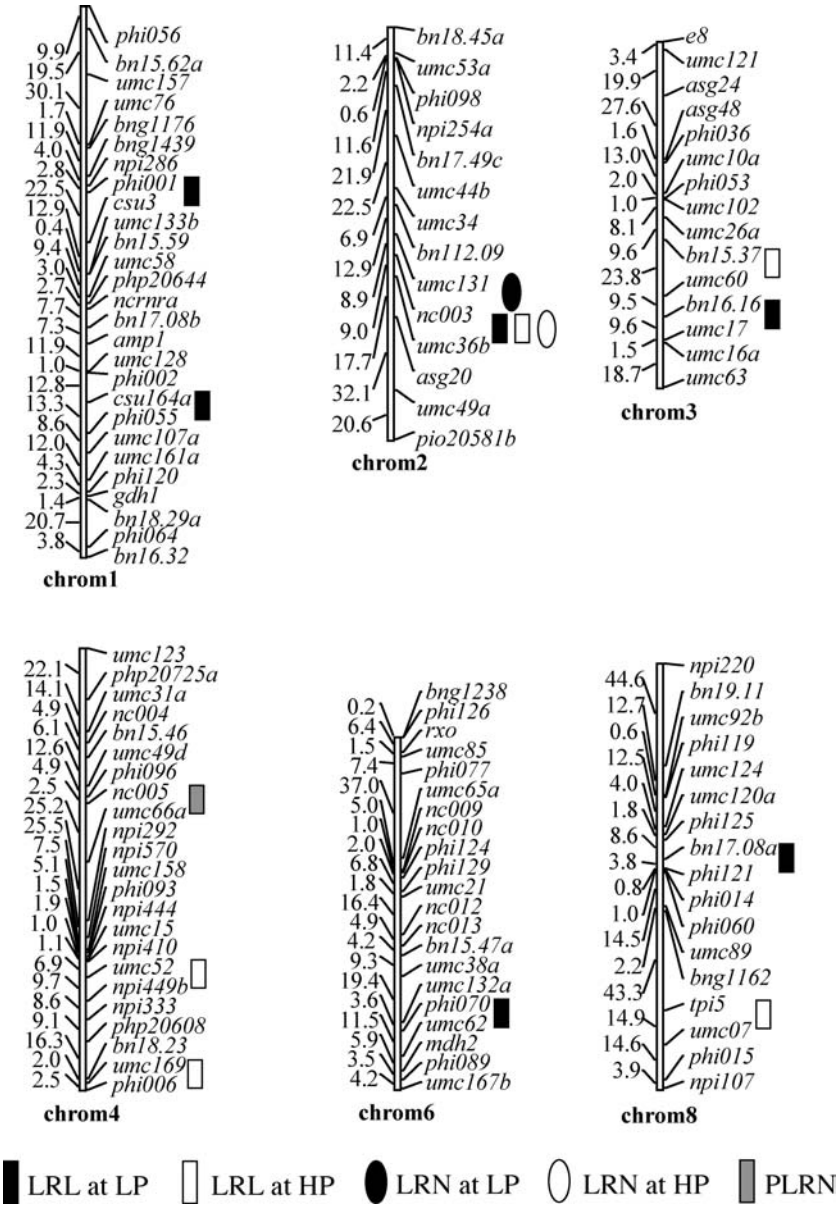

Fig. 7 Most likely locations of gene loci on chromosomes 1, 2, 3, 4, 6, and 8 for lateral root length (*LRL*) and lateral root number (*LRN*) under conditions of low phosphorus (*LP*) and high phosphorus (*HP*), and plasticity of lateral root number (*PLRN*). The *designation on the right* is the marker name, on the *left* is the map distance based on the Kosambi function

lar correlation was found for total LRN between primary root and seminal roots ($R^2 = 0.367$, $df = 14$, $P < 0.01$). These data suggest that the QTLs we detected for lateral root branching on the primary root may also be important in explaining lateral root branching of other root types in this population. We have not yet tested this experimentally on the genotypes described in this paper.

In conclusion, our results demonstrate that substantial genetic variation exists for the length, number, and plasticity of lateral roots originating from the primary root in this population. The QTLs we have identified begin to provide a genetic basis for lateral rooting in maize in response to phosphorus availability. Further genetic analyses could be conducted through the evaluation of these traits in other populations. Comparisons could be made to evaluate the consistency of QTL detection for the same trait in various backgrounds and to identify QTLs with larger effects not observed in our experiments. Our data suggest that favorable alleles can be combined to promote lateral root growth, which will facilitate in improving phosphorus efficiency in maize production.

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