

QTL mapping of agronomic traits in maize (*Zea mays* L.) grown in a low-phosphorus environment

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Abstract

Growing maize in soils that lack available phosphorus, an essential nutrient for plant growth, can lead to dwarf plants with weak roots and small leaves. It is also difficult for plants to absorb phosphorus from the soil environment. Developing maize varieties that efficiently utilize phosphorus would help to overcome this problem. However, relevant QTL need to be identified to achieve this goal. In this study, a QTL analysis was conducted of a maize F_{2:3} population grown in a low-phosphorus soil environment at three different planting sites. The population consisted of 180 individual plants produced from a cross between a high-phosphorus efficiency genotype (082) and a low-phosphorus efficiency genotype (Ye107). The QTL analysis identified five stable QTLs associated with several important agronomic traits. The QTLs were identified in the same marker interval in the populations planted at the three different planting sites. Four QTLs identified the mapping population at one planting site were close to the five QTLs in the joint analysis of all planting sites, indicating that there may be common QTLs near these markers. Some one-cause-multiple-effect QTLs that may share genetic mechanisms were detected on chromosomes 1, 3, 4, 7, 9 and 10. These were QLA1-1 and QLW1-3, QLA3-1 and QLL3-3, QLA4-1 and QLL4-2, QPH7-1 and QTNB7-3, QPH9-2 and QTNB9-4, QLA9-1, QSD9-3 and QLW9-6, LA10-1 and QLW10-3, QLA10-1 and QLW10-3, and QLW10-3. QLW9-6, and LA10-1 and QLW10-3. This study provides a foundation for marker-assisted breeding of maize under low-phosphorus conditions.

1 Introduction

Crops require macronutrients such as nitrogen, phosphorus, and potassium, for optimal growth, development, and yield. Phosphorus is particularly important in cellular processes, including nucleic acid synthesis, photosynthesis, respiration, glycolysis, membrane synthesis and stabilization, redox reactions, signal transduction, and nitrogen fixation (García et al., 2024; Raghothama et al., 2005; Abel et al., 2002; Vance et al., 2003). Although total phosphorus content in most soils is high, the amount of phosphorus that can be readily absorbed and utilized by plants is low (Li et al., 2021; Prathap et al., 2022). Plant roots absorb phosphorus from the rhizosphere as phosphate (Pi), which is generally present in low concentrations in soil solutions. Therefore, the diffusion of Pi to roots for uptake is slow, making it difficult to obtain (Batjes et al., 1997; White et al., 2008).

Maize is one the most widely grown crops globally and is a staple food product for both animals and humans, and whose byproducts are utilized industrially for many purposes (Calderón-Vázquez et al., 2011). Growing maize in soils that lack available phosphorus can lead to dwarf plants with weak roots and small leaves. Symptoms of phosphorus deficiency in maize initially appear as chlorosis at the leaf tips and margins, which eventually turn purple-red in color. The purple-red discoloration gradually spreads to the base of the leaf before the leaf tip turns brown and dies. Phosphorus deficiency has a negative impact on root development, resulting in decreased root volume. A sparse panicle phenotype can also occur when female panicle pollination is disrupted due to a phosphorus deficiency, resulting in grain drying or an absence of fruit. Studies have found that if germinating maize seeds are deficient in phosphorus, symptoms of phosphorus deficiency can occur in growing plants even if sufficient phosphorus is provided at later stages of plant development (Chen, 2016). Therefore, low available soil phosphorus has represents an important limiting factor in determining maize yield (Zhang et al., 2020).

Natural soil phosphorus and phosphorus fertilizers are the main sources of phosphorus (P) required by maize (Song et al., 2009). Although the application of inorganic P fertilizers can alleviate symptoms of phosphorus deficiency, rock minerals, the primary source of inorganic P, are a limited resource that is only expected to last another 60 to 340 years (Laakso et al., 2018). The use of phosphorus fertilizers during the planting season is very low, representing only 10–20% of the supply needed by plants, with the remainder being supplied by the soil phosphorus pool. Although long-term applications of phosphorus fertilizer can increase soil phosphorus levels (Zeng et al., 2014), most of the phosphorus applied to the soil in agriculture is in an unavailable state, which can lead to wastage of phosphorus (M.A et al., 2004). Macdonald et al. (2011) demonstrated that only 51 per cent of the phosphorus fertilizer applied to a soil each year is taken up by crops. Phosphorus accumulation occurs from time to time. This indicates the use of large amounts of P fertilizers to increase crop yield is inefficient and not advisable.

Maize quality and yield can be improved through the selection of varieties with strong economic traits, including phosphorus utilization. The development of excellent varieties can be assisted by the identification of quantitative trait loci (QTLs) associated with phosphorus absorption and utilization that can be used to select favorable genotypes during the breeding process. QTLs associated with phosphorus-efficient genotypes can be combined with the selection of other important agronomic traits to obtain

superior genotypes. SSR (single sequence repeats) markers are uniformly distributed on chromosomes, are highly polymorphic, and allele-rich. They are codominant and can distinguish homozygote from heterozygote genetic traits. Due to their high resolution and easy detection, SSRs are widely used in the genetic analysis of crops, including genome mapping and characterization, phenotypic mapping, marker-assisted selection, and molecular ecology and diversity studies. (McCouch et al, 1997; Robinson et al, 2004). Notably, SSR markers can be used to identify QTLs associated with agronomic traits in mapping populations. The identification of QTLs associated with enhanced phosphorus utilization in low-phosphorus environments have been conducted in rice (Nirubana et al., 2020), wheat (Yang et al., 2021), soybean (Li et al., 2016), and barley (Gao et al., 2020). Several maize studies have also identified QTLs associated with tolerance to low-phosphorus environments (Joshi et al., 2021; Ma et al., 2021; Gu et al., 2016; Qiu et al., 2014; Sahito et al., 2020). For example, Zhu et al. (2005) utilized a population of 169 recombinant inbred lines (RILs) of maize grown at two phosphorus levels (low and high) and quantified root hair length and root hair length plasticity in the maize populations. QTL mapping in that study identified a single QTL associated with root hair length under low-phosphorus conditions. Ouma et al. (2021) measured phosphorus use efficiency and the heritability of related agronomic traits in 32 maize hybrids grown at two phosphorus levels (low and high) and found a significant relationship between shoot phosphorus content and phosphorus efficiency, suggesting that shoot phosphorus content may be a useful parameter for the selection of phosphorus efficiency in maize.

Zhang et al. (2014) conducted a meta-analysis of studies of the genetic analysis of traits related to low P tolerance in maize. The meta-analysis identified 191 QTLs of which 23 were consensus QTLs (cQTLs) and identified 200 candidate genes with those QTLs. Cheng et al. (2018) conducted a genome-wide association analysis in maize and identified multiple single nucleotide polymorphisms (SNPs) associated with multiple agronomic traits. QTLs provide a useful genetic marker for low P tolerance breeding in maize and can be used to identify and locate target trait genes. However, studies have focused on maize root or ear traits associated with maize yield (Gudu et al., 2021; Zhou et al., 2020; Yang et al., 2020). Fewer QTL mapping studies have focused on aboveground agronomic traits such as Leaf Area, Plant Height, Stem Diameter, Tassel Branch Number, Leaf Width, Leaf Length (LA, PH, TBN, LW, and LL, respectively). In the present study, a QTL mapping study of LF, PH, SD, TBN, LW, and LL was conducted in mapping population of maize genotypes growing in a low phosphorus environment at three locations. The study was conducted to provide a foundation for the marker-assisted breeding of maize cultivars with high-efficiency utilization of phosphorus.

2 Materials and methods

2.1 Plant material and field sites

The mapping population consisted of 180 $F_{2:3}$ families derived from randomly selected F_2 plants from a cross between inbred 082 (phosphorus-efficient genotype) and Ye107 (phosphorus-inefficient genotype). $F_{2:3}$ refers to the progeny population produced by self-crossing of F_2 generation plants, which is designated as a common localization population in the literature and mainly used for preliminary localization of quantitative traits controlled by multiple genes. The use of such populations can reduce test error and improve test accuracy (Zhu, C. et al 2007). Phosphorus efficiency and several phenotypic traits were measured in the field populations. Genetic diversity associated with phosphorus efficiency was identified by amplified fragment length polymorphism (AFLP) marker analysis in 33 lines. Clustering of the AFLP marker and phenotypic traits data revealed that the greatest difference in phosphorus use efficiency was between the 082 and Ye107 maize lines (Chen et al., 2008). Field studies were conducted in 2011 at Beibei (E1) and Hechuan (E2), and in 2012 at Beibei (E3), China. The average temperature in 2011 in Beibei was 18.62°C and 18.04°C in Hechuan. The average temperature in Beibei in 2012 was 17.70°C. F_2 genotypes and $F_{2:3}$ phenotypes were obtained. The soil at the Beibei field site was a sandy loam soil (pH of 6.6) with an organic matter content of 14600 mg kg⁻¹. Total N, total P, and total K were 890 mg kg⁻¹, 761 mg kg⁻¹, and 14200 mg kg⁻¹, respectively, at the Beibei site. Available N, P, and K levels were 8.9 mg kg⁻¹, 3.3 mg kg⁻¹, and 117 mg kg⁻¹, respectively, at the Beibei site. The soil at the Hechuan field site was also a sandy loam soil (pH of 7.3) with an organic matter content of 10.6 g kg⁻¹. Total N, P, and K levels were 734 mg kg⁻¹, 987 mg kg⁻¹, and 14100 mg kg⁻¹, respectively, at the Hechuan site. The available N, P, and K levels were 5.1 mg kg⁻¹, 3.5 mg kg⁻¹, and 105 mg kg⁻¹, respectively, at the Hechuan site.

The second national survey of soil nutrient grading standards (China) states that low phosphorus soils are defined as those with an effective phosphorus content < 5 mg kg⁻¹. Thus, soils at both the Beibei and Hechuan test sites would be classified as low phosphorus soils. Urea-based nitrogen fertilizer at a rate of 120 kg hm⁻² was applied at both locations. No phosphorus fertilizers were applied. Planting of the mapping population utilized a completely randomized block design with 180 individual plants, two 18 plants replicated plots for each genotype, with a final planting density of 45,000 hm². Intra-environmental errors were reduced through the use of replicated plots with same fertility level in each replicated plot. Bags were placed on mature plants to enable the phenotyping of self-pollinated plants.

2.2 Phenotypic data collection and analysis

LA (cm²), was measured with a leaf area meter, four agronomic traits were measured with a vernier caliper or a tape measure, PH (m), SD (cm), LW (cm), and LL (cm) (Ear leaves), and TBN (number) was measured by counting the number of tassel branches. The upper and lower leaves and corn ear position leaves were selected for measurement. Ear three leaves has the largest leaf area, the strongest photosynthetic rate, the longest functional period, and is the closest leaf to the maize cob, which means that it can transport nutrients to the cob in support of seed formation (Cui et al., 2023). Excel 2003 was used to record the data for each of the agronomic traits. IBM SPSS Statistics 26 software was used to determine statistical significance of the measured parameters between parents and groups, the correlation between traits, and the normal distribution of each trait. The absolute values of the peak and skewness of each trait in the three environments were less than 1, indicating that the measured data was normally distributed (Table 1). Generalized heritability was calculated using Equation 1; a broad sense heritability formula described by Knapp et al. (1985). The variables in the equation are genotype variance (σG^2), interaction variance between genotype and environment (σGE^2), variance of environmental error (σe^2), number of environments (n), and number of repetitions (r). Among the terms, σG^2 and σGE^2 are random, while the number of environment, and number of repetitions are fixed.

$$h^2 = \sigma G^2 / (\sigma G^2 + \frac{\sigma GE^2}{n} + \frac{\sigma e^2}{nr}) \quad (1)$$

2.3 Genetic map construction and QTL mapping

SSR markers covering 1800 whole maize genomes were selected from the maize genome database (<http://www.Maizegdb.org>) and screened for polymorphism using polyacrylamide gel electrophoresis to select markers with different banding patterns in the parents and F₁. A total of 249 polymorphic SSR primers were obtained, which were used to genotype the F₂ population. The SSR primers provided good discriminant capacity in F₂ population (Qiu et al., 2013). SSR markers required to map the populations were evaluated to create a database in Microsoft Excel containing the F₂ single plant number, the SSR primer names, and corresponding polyacrylamide gel electropherograms. The Haldane function of JoinMap 3.0 was used to convert the recombination rate into graph distance units in centimorgans (cM).

QTL Ici Mapping 3.0 software, which employs the inclusive composite interval mapping (ICIM) method, was used to perform single-environment QTL detection and all-environment combined QTL detection on the mapping populations. A step size of 1 cM was selected when performing the QTL detection, the LOD threshold was manually set to 2.0, and the significance level was set to 0.05. The mode of action of a gene was classified as either additive (A 0 to 0.21), partially dominant (PD 0.21 to 0.80), dominant (D 0.81 to 1.20), or over dominant (OD > 1.20). Taking QLA1-1 as an example of QTL nomenclature, Q represents the QTL (JQ indicates a joint-location QTL), LA represents leaf area (PH, SD, TBN, LW, and LL represent plant height, stem diameter, number of tassel branches, leaf width, and leaf length, respectively), the number 1 represents the name of the chromosome (i.e., chromosome 2, chromosome 3, chromosome 4, etc.), -1 represents the sequence number of the QTL on the designated chromosome.

3 Result

3.1 Analysis of agronomic traits

Six agronomic traits were measured in the two parents and the 180 $F_{2:3}$ family members planted at three locations over two growing seasons; Beibei 2011 (E1), Hechuan 2011 (E2), and Beibei 2012 (E3). The statistical analysis of the measured parameters in the 082 and Ye107 parents is shown in Table 2. Results indicated that the six traits significantly differed between the two parents. Data in Table 2 demonstrates that the traits exhibited substantial variability in the $F_{2:3}$ population, with a small degree of skewness and kurtosis across environments and a normal distribution. The range of variation range in the six agronomic traits in the three environments was 8.19%–24.24%. These data indicate that the six agronomic traits could be evaluated as quantitative traits for QTL mapping in the $F_{2:3}$ families.

Analysis of variance was performed on the six agronomic traits in the $F_{2:3}$ families (Table 3). Results indicate that LA, PH, TBN, LL, and LW were all significantly affected by genotype and environment; stem diameter was significantly affected by genotype but not by environment. Notably, genotype-environment interactions in the six traits were not significant, indicating that they were not significantly affected by genotype-environment interactions. In this regard, a significant gene-environment interaction indicates that the trait is affected by the main effect of genotype and environment, as well as their interaction, which would complicate any deterministic evaluation. The heritability of the six traits ranged from 0.69 to 0.79 indicating that the differences in the trait parameters measured in members of the $F_{2:3}$ families, were largely determined by genotype.

Correlation analysis of the mean values of the six traits in the three environments indicated strong positive correlations between the traits in the $F_{2:3}$ families (Table 4).

3.2 Genetic map construction

A total of 295 differential primers pairs were used from among the 1800 pairs of SSR primers covering the entire maize genome to screen for polymorphisms identified between parents and F_1 . Markers with unstable amplification or exhibiting minor differences in banding that were difficult to distinguish were discarded. In the end, a total of 266 SSR markers that could be consistently amplified and provide clear bands were used to genotype the populations and construct a join map. Linkage analysis was performed on all genotypes using JoinMap 3.0 utilizing the 266 pairs of differential SSR primers pairs. A genetic linkage map containing 10 linkage groups was constructed and found to contain 249 SSR loci (Figure 1). Notably as evidenced on the genetic map, the SSR markers were evenly distributed on all ten linkage groups in the maize genome. The total genetic distance was 1224.521 cM, and the average distance between markers was 4.92 cM. Each chromosome contained 18 to 43 SSR markers with an average of 24.9 SSR markers per chromosome.

3.3 QTL detection in the different individual environments

A total of 49 significant QTLs for the six traits were identified in the $F_{2:3}$ population across chromosomes 1, 2, 3, 4, 5, 7, 8, 9, and 10 (Table 5) in the three individual environments. The LOD values of the QTLs ranged from 2.51 to 21.17, and the phenotypic contribution rates ranged from 4.23% to 40.31%. The largest number of QTLs (11) was detected for the TBN trait, and were unevenly distributed on seven chromosomes. The lowest number of QTLs (1) was detected for the SD trait. Details of the identified QTLs are provided in the following sections.

3.3.1 Leaf area

Nine QTLs associated with leaf area were identified in the three different individual environments (Table 5). The phenotypic contribution of these QTLs ranged from 6.06% to 13.35%, and were unevenly distributed on chromosomes 1, 3, 4, 9, and 10. The five QTLs on chromosomes 1, 3, and 4 were synergistic with the alleles from the female parent (082), and the four QTLs on chromosomes 9 and 10 were synergistic with the alleles from the male parent (Ye107). Four QTLs were detected in two or three different environments: QLA1-1, QLA4-1, QLA9-1, and QLA10-1. Among them, the phenotypic contribution of QLA1-1 and QLA4-1 exceeded 10%.

3.3.2 Plant height

Three QTLs associated with plant height were identified on chromosomes 7 and 9 in the three individual environments (Table 5). Their LOD values were between 2.86 and 3.38, and their phenotypic contribution of the QTLs was between 7.85% and 8.36%.

QPH7-1 on chromosome 7 was detected in two different environments. These QTLs were all partially dominant, and their synergistic genes were all from the female parent (082).

3.3.3 Stem diameter

Two QTLs associated with stem diameter were identified in the three individual environments (Table 5). They were all located between markers bnlg128 and bnlg1129 on chromosome 9 and named QSD9-3. Their phenotypic contribution of the QTLs was 8.02 and 7.35%. The QTLs were partially dominant, and the paternal parent (Ye107) gene had a synergistic effect.

3.3.4 Number of tassel branches

Eighteen QTLs associated with tassel branch number were identified on chromosomes 1, 2, 3, 5, 7, 8, and 9 in the three individual environments (Table 5). Eleven were partially dominant, and the synergistic genes came from the female parent (082). Five of these QTLs were detected in two or three individual environments: QTBN1-2, QTBN3-2, QTBN5, QTBN7-2, and QTBN7-3. The phenotypic contribution of these QTLs ranged from 4.20% to 16.38%. Three QTLs had a phenotypic contribution rate of > 10%: QTBN3-2, QTBN5, and QTBN7-2.

3.3.5 Leaf width

Eleven QTLs associated with leaf width were identified in the three different individual environments and were distributed on chromosomes 1, 9, and 10 (Table 5). Their phenotypic contribution ranged between 6.80% to 40.31%. There were six synergistic QTLs from the female parent 082 and five synergistic QTLs from the male parent Ye107. Four of the QTLs were detected in two or three environments: QLW1-3, QLW9-6, QLW10-2, and QLW10-3. QLW1-3, QLW9-6, and QLW10-3 had a phenotypic contribution rate of > 10%.

3.3.6 Leaf length

Six QTLs associated with leaf length were identified in the three different individual environments (Table 5). Three were found in the same marker interval on chromosome 3 and one on chromosome 4: QLL3-3 and QLL4-2. The phenotypic contribution of QLL4-2 was > 10% in all three environments. The synergistic QTL on chromosome 3 came from the male parent Ye107, and the synergistic QTL on chromosome 4 came from the female parent 082.

3.4 QTL identification in joint analysis across all three environments

The combined analysis of all environments identified 49 QTLs associated with the measured agronomic traits (Table 6). Five QTLs (QLA9-1, QSD9-3, QTBN7-2, QTBN9-5, and QLW9-6) were detected in the same marker interval in the individual and combined environment QTL analysis, indicating that these QTLs were not affected by the environment, which can stabilize heredity. QPH7-1, QLW10-3, QLL3-3, QLL4-2 were detected in the single-environment analysis while JQPH7-1, JQPH7-2, JQLW1, JQLL3, JQLL4 were detected in the joint analysis of all environments. Notably, all of them were located in the vicinity of the same markers (phi034, umc1016, umc1991, umc2033, and umc1313), suggesting that there may be common QTLs at the positions of these markers. Some QTLs detected in the joint analysis were not detected in the single-environment analysis, suggesting that they likely have a small effect that cannot be detected unless more environments are included. In this regard, different planting densities, water and fertilizer levels, and climatic conditions all have the potential to differentially impact agronomic traits and contribute to variability in QTL detection.

3.5 Prediction analysis of candidate genes

One SSR was located between the markers umc1991-umc2029. This marker controls leaf area and leaf width traits. Based on the Zea mays-B73-REFERENCE- GRAMENE-4.0 in the maize genome database (<http://www.Maizegdb.org>), candidate genes present in the chr1-233,951,533-245,372,021 regions were identified and analyzed. A total of three predicted genes were obtained by functional annotation of candidate genes in the genetic database Zeamap and the NCBI website. Zm00001d032678 is Haloacid dehalogenase-like hydrolase (HAD) superfamily protein, Zm00001d032768 is CCT motif family protein, and Zm00001D032850 is a Pi transporter protein2 (Table 7).

4 Discussion

Plants exposed to low-phosphorus stress undergo a series of physiological responses that can negatively affect plant growth and other agronomic traits. Studies have shown that the genetic mechanisms underlying phosphorus efficiency are quite complex (Wissuwa et al., 2001; Leiser et al., 2014; Zhou et al., 2016). Multiple genes with relatively minor effects contribute to a quantitative effect that can exhibit substantial variation (Swanson-Wagner et al., 2010). If a QTL can be detected in two or more environments and its contribution in one environment is greater than 10%, the QTL is considered to be environmentally insensitive (Peng et al., 2011). In our study, QTLs with phenotypic contribution of > 10% were as follows: QLA1-1, QLA4-1 correlated with leaf area; QTNB3-2, QTNB7-2, QTNB5 correlated with spike branching number, QLW1-3, QLW9-6, QLW10-3 correlated with blade width; and QLL4-2 correlated with leaf length. A total of 9 main effect QTLs were identified.

Brown et al. (2011) and Tuberosa et al. (2002) demonstrated that QTLs affecting related traits tend to reside in the same or adjacent chromosomal segments owing to shared genetic mechanisms in the traits. Moncada et al. (2001) stated that intervals that can be co-located and associated with multiple traits may have linkage or epistatic effects and may also contain one or more closely linked QTLs. In this regard, we identified several QTLs located in close proximity to one another that may share genetic mechanisms (QLA1-1 and QLW1-3, QLA3-1 and QLL3-3, QLA4-1 and QLL4-2, QPH7-1 and QTNB7-3, QPH9-2 and QTNB9-4, QLA9-1 and QSD9-3 and QLW9-6, LA10-1 and QLW10-3).

The QTL QPH7-1 on chromosome 7 that is associated with plant height is similar to two previously published QTLs associated with maize height in low-phosphorus and adequate-phosphorus environments (Cai et al., 2012; Xi et al., 2018). Xi et al. (2018) also identified several linked QTLs for agronomic traits in low-phosphorus environments. Xu Cheng et al. (2018) in a genome-wide association study identified 259 candidate genes under low phosphorus conditions, of which 98 showed differential expression in transcriptome data. Similar to our results, the candidate genes that they identified were annotated in the three main gene ontology (GO) categories “biological regulation,” “metabolic process,” “cellular process”.

We identified three candidate genes, Zm00001d032678 is related to phosphorus; Zm00001d032768 is involved in biological processes such as plant stress tolerance; and Zm00001d032850 is a Pi transporter protein. Among these candidate genes, Zm00001d032678 belongs to the same family as OsHAD1, a gene investigated by Pandey, B. K. et al. (2017). It was found that OsHAD1 can increase Pi accumulation. Perhaps, Zm00001d032678 has the same function as OsHAD1. Zm00001d032768 is a CCT motif family protein. The CCT gene family in rapeseed (*Brassica napus*) is involved in plant stress resistance (Yu, et al., 2024). Low phosphorus definitely represents a condition that is detrimental to plant health. Therefore, perhaps this gene is activated in a low phosphorus environment. Pi is transported by Pi transporters. Zm00001d032850 is a Pi transporter protein and identified as a potential candidate gene. Other investigators studies identified mirR399 under low P conditions (Hu et al., 2011, Du et al., 2018, Dai et al., 2016). The homolog of mirR399 in rice (LTN1) is associated with changes in root morphology changes under low P conditions. MirR399 transcripts are strongly induced in maize by P deficiency. Therefore, the expression of the identified candidate genes should be compared with MirR399 and LTN1 to gain insight into their potential role in phosphorus use efficiency and related traits.

5 Conclusions

In the present study, QTL mapping of six agronomic traits was conducted utilizing 180 F_{2:3} plants grown in three low-phosphorus environments. Nine major QTLs were identified across chromosomes 1, 3, 4, 5, 7, 9, and 10. The LOD values of these QTLs and their contributions to phenotypic variation were high. The QTLs were located in different segments of different chromosomes. This may be because the agronomic traits linked to these QTLs are quantitative traits controlled by multiple genes. Five QTLs that control leaf area, leaf diameter, tassel branch number, and leaf width were identified in our study in the QTL analyses of individual environments and all three environments combined, indicating that these QTLs are only affected by the environment to a small degree and may be stably inherited. We also identified three candidate genes. Our data indicate that the stable QTLs and identified candidate genes have high potential value in the genetic improvement of maize traits under low phosphorus conditions. Our results provide an important foundation for the genetic improvement of maize with low-phosphorus tolerance using marker assisted selection.

ABBREVIATIONS

QTL Quantitative trait loci

LA Leaf area

PH Plant height

SD Stem diameter

TBN Tassel branch number

LW Leaf width

LL Leaf length

Declarations

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ADDITIONAL INFORMATION AND DECLARATIONS

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Conflict of interest

The authors declare no competing interests.

Author contribution

Conceptualization, HLW, XLH and HBQ; methodology, XLH; software, ZZ; validation, XMZ and MW; investigation, HLW and XLH; resources, HBQ and XMZ; data curation, HLW and XLH; writing—original draft preparation, XLH; writing—review and editing, HLW and XLH; project administration, HBQ; All authors have read and agreed to the published version of the manuscript.

Data availability

The following information was supplied regarding data availability:

The raw measurements are available in the Supplemental Data S1.

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Tables

Table 1. Variation in the quantitative assessment of six agronomic traits in the F2:3 families of maize.

Trait	Env	minimum	maximum	Mean	SD ^b	Skewness	Kurtosis	CV (%) ^c
LA	E1	259.81	648.95	470.16	76.53	-0.14	-0.23	16.28%
	E2	255.04	648.95	447.69	85.82	-0.14	-0.41	19.17%
	E3	259.81	652.77	492.63	73	-0.21	0.15	14.82%
PH	E1	1.27	2.46	1.9	0.21	-0.22	0.66	11.05%
	E2	1.27	2.25	1.85	0.21	-0.43	-0.19	11.35%
	E3	1.27	2.26	1.92	0.18	-0.85	1.17	9.38%
SD	E1	4.88	8.40	6.15	0.58	0.24	0.62	9.43%
	E2	4.46	8.40	6.1	0.65	0.05	0.45	10.66%
	E3	4.96	8.40	6.22	0.58	0.5	0.96	9.32%
TBN	E1	5.67	20.75	12.57	2.8	0.19	-0.04	22.28%
	E2	5.67	23.84	12.21	2.96	0.36	0.79	24.24%
	E3	5.67	21.50	12.93	2.89	0.11	-0.23	22.35%
LW	E1	6.49	10.39	8.62	0.75	-0.18	-0.07	8.70%
	E2	6.49	10.23	8.45	0.82	-0.22	-0.29	9.70%
	E3	6.49	10.80	8.79	0.72	-0.18	0.36	8.19%
LL	E1	50.85	91.83	72.09	7.92	-0.33	0.05	10.99%
	E2	47.25	91.42	69.87	9.01	-0.25	-0.18	12.90%
	E3	49.34	92.25	74.32	7.4	-0.55	0.66	9.96%

Notes:

leaf area (LA), plant height (PH), stem diameter (SD), tassel branch number (TBN), leaf width (LW), and leaf length (LL). Measurements were taken from plants growing in two different locations and growing seasons (Env): Beibei in 2011 (E1), Hechuan in 2011 (E2), and Beibei in 2012 (E3).

^bSD, standard deviation of phenotypic data. ^cCV, coefficient of variation.

Table 2. Analysis of significant differences in the quantitative assessment of six traits in maize parents, inbred lines 082 and Ye107.

	Ye107	082	Ye107	082
Trait	Mean		SD ^b	
LA	535.63	614.46*	42.78	20.81
PH	1.89**	1.51	0.08	0.07
SD	7.30*	5.77	0.36	0.60
TBN	4.67	16.33**	1.15	1.53
LW	9.40*	8.23	0.46	0.25
LL	75.90	96.03**	2.33	1.50

Notes:

leaf area (LA), plant height (PH), stem diameter (SD), tassel branch number (TBN), leaf width (LW), and leaf length (LL). ^bSD, standard deviation of phenotypic data.

*p<0.05, **p<0.01.

Table 3. Joint analysis of the variance in the quantitative assessment of six agronomic traits of F_{2:3} families of maize.

Trait	G	E	G*E	H ²
LA	20.42**	14.42**	0.11	0.69
PH	28.98**	6.72**	0.21	0.79
SD	29.48**	3.59	0.19	0.77
TBN	30.03**	5.078*	0.17	0.79
LW	30.05**	12.49**	0.12	0.78
LL	21.44**	13.89**	0.12	0.70

Notes:

leaf area (LA), plant height (PH), stem diameter (SD), tassel branch number (TBN), leaf width (LW), and leaf length (LL). The effects of genotype (G), environment (E), and their interaction (G*E) were assessed, and the broad-sense heritability (H²) was calculated.

*p<0 .05, **p<0 .01.

Table 4. Correlation analysis of six agronomic traits in F_{2:3} families of maize grown in different environments.

Evn	Trait	LA	PH	SD	TBN	LW
E1	PH	0.554**				
	SD	0.614**	0.371**			
	TBN	0.502**	0.354**	0.423**		
	LW	0.810**	0.305**	0.571**	0.338**	
	LL	0.890**	0.606**	0.502**	0.510**	0.464**
E2	PH	0.656**				
	SD	0.652**	0.460**			
	TBN	0.536**	0.441**	0.445**		
	LW	0.837**	0.411**	0.616**	0.382**	
	LL	0.915**	0.700**	0.566**	0.549**	0.558**
E3	PH	0.580**				
	SD	0.570**	0.358**			
	TBN	0.469**	0.431**	0.406**		
	LW	0.786**	0.308**	0.521**	0.298**	
	LL	0.866**	0.623**	0.434**	0.473**	0.383**

Notes:

leaf area (LA), plant height (PH), stem diameter (SD), tassel branch number (TBN), leaf width (LW), and leaf length (LL). Measurements were taken from plants growing in two different locations and two growing seasons (Env): Beibei in 2011 (E1), Hechuan in 2011 (E2), and Beibei in 2012 (E3).

**p<0 .01.

Table 5. QTLs associated with the genetic inheritance of six agronomic traits in single-environment analyses of the F_{2:3} population of maize.

Trait	QTL name	Env	Left Marker	Right Marker	Position	LOD	PVE (%)	Add	Dom	Gene action
LA	QLA1-1	E1	umc1991	umc2029	56	5.13	13.35	36.06	-24.29	PD
		E3	umc1991	umc2029	55	4.90	11.85	32.59	-22.36	PD
	QLA3-1	E2	umc2033	bnlg2136	94	2.51	6.42	30.14	7.57	PD
	QLA4-1	E1	umc1313	umc1101	62	3.19	8.62	30.02	15.12	PD
		E3	umc1313	umc1101	63	3.90	10.75	29.09	22.15	PD
	QLA9-1	E1	bnlg128	bnlg1129	88	3.22	7.72	-27.41	18.04	PD
		E3	bnlg128	bnlg1129	88	3.18	7.60	-27.58	12.73	PD
	QLA10-1	E1	bnlg594	umc1993	64	2.73	6.06	-10.64	-36.68	OD
E2		bnlg594	umc1993	64	2.95	7.70	-14.85	-45.75	OD	
PH	QPH7-1	E1	phi034	umc1016	89	3.29	8.21	0.08	0.03	PD
		E2	phi034	umc1016	89	3.38	8.36	0.09	0.02	PD
	QPH9-2	E3	umc2121	umc1519	53	2.86	7.85	-0.01	0.13	OD
SD	QSD9-3	E1	bnlg128	bnlg1129	88	2.88	8.02	-0.26	0.06	PD
		E2	bnlg128	bnlg1129	88	2.62	7.35	-0.25	0.08	PD
TBN	QTBN1-2	E1	umc2047	umc1991	48	2.53	4.20	0.56	-0.93	OD
		E3	umc2047	umc1991	45	2.66	4.48	0.80	-0.79	D
	QTBN2-1	E1	umc1079	umc2079	39	5.04	8.86	0.62	1.45	OD
	QTBN2-2	E3	umc2403	umc1227	84	3.95	7.72	1.17	0.15	A
	QTBN3-2	E1	umc1965	bnlg1325	121	9.13	16.38	1.63	0.07	A
		E2	umc1965	bnlg1325	119	5.48	15.05	1.74	-0.73	PD
		E3	umc1965	bnlg1325	119	6.01	14.18	1.55	0.23	A
	QTBN5	E1	umc1225	bnlg118	10	7.22	11.49	1.39	0.59	PD
		E2	umc1225	bnlg118	8	4.45	9.20	1.28	0.75	PD
		E3	umc1225	bnlg118	11	6.25	12.23	1.43	0.88	PD
	QTBN7-2	E1	umc1671	umc1412	14	6.87	10.46	1.25	-0.43	PD
		E3	umc1671	umc1412	15	7.40	14.75	1.53	-0.55	PD
	QTBN7-3	E1	phi034	umc1016	89	4.35	6.45	1.02	0.21	PD
		E2	phi034	umc1016	89	4.54	9.45	1.32	0.18	A
	QTBN7-4	E2	umc2197	umc1671	13	2.89	5.70	0.84	-0.78	D
	QTBN8	E1	bnlg1065	bnlg240	38	3.79	5.98	1.05	0.24	PD
	QTBN9-4	E1	umc2121	umc1519	53	3.10	4.48	0.31	1.12	OD
	QTBN9-5	E3	umc1519	umc1657	54	3.86	7.33	0.51	1.42	OD
LW	QLW1-3	E1	umc1991	umc2029	59	7.56	15.48	0.40	-0.14	PD
		E2	umc1991	umc2029	60	7.65	11.73	0.38	-0.12	PD
		E3	umc1991	umc2029	59	7.28	17.63	0.40	-0.18	PD

	QLW9-6	E1	bnlg128	bnlg1129	88	6.52	13.00	-0.40	0.04	A
		E2	bnlg128	bnlg1129	88	7.73	12.25	-0.43	-0.04	A
		E3	bnlg128	bnlg1129	90	4.93	11.97	-0.36	0.09	PD
	QLW10-2	E1	mmc0501	umc1582	17	3.54	6.80	0.30	0.03	A
		E2	mmc0501	umc1582	17	4.92	7.33	0.34	0.04	A
	QLW10-3	E1	bnlg594	umc1993	64	16.80	38.94	-0.01	-0.95	OD
		E2	bnlg594	umc1993	64	21.17	40.31	-0.02	-1.05	OD
	QLW10-4	E3	umc1432	mmc0501	16	2.67	5.92	0.26	-0.02	A
LL	QLL3-3	E1	umc2033	bnlg2136	93	3.44	8.01	3.37	-0.31	A
		E2	umc2033	bnlg2136	93	2.68	6.49	3.42	-0.15	A
		E3	umc2033	bnlg2136	93	3.86	8.81	3.32	-0.49	A
	QLL4-2	E1	umc1313	umc1101	64	5.85	16.85	4.48	1.76	PD

Notes:

Measurements were taken from plants growing in two locations and growing seasons (Env): Beibei in 2011 (E1), Hechuan in 2011 (E2), and Beibei in 2012 (E3).

PVE (%), Percentage of phenotypic variance explained. Add, Additive effect of the QTL; positive values indicate that the alleles for higher trait values are contributed by 082, and negative values indicate that the alleles for higher trait values are contributed by Ye107. Dom, Dominance effect of the QTL.

Table 6. Joint analysis of QTLs for six agronomic traits in F_{2:3} populations of maize in all environments.

Trait	QTL name	Left Marker	Right Marker	Position	LOD (A)	LOD (A by E)	PVE (%)	Add
LA	JQLA1	umc1128	bnlg1025	428	7.99	0.06	8.67	23.07
	JQLA2	umc1579	umc2403	343	2.47	0.05	1.93	10.89
	JQLA3	bnlg1452	umc2033	1149	6.42	0.09	6.89	20.75
	JQLA4	umc1667	umc2405	233	6.74	0.04	6.49	19.93
	JQLA5	umc1850	bnlg1660	1066	2.68	0.01	2.82	13.14
	JQLA6	umc2165	bnlg1759	688	3.54	0.00	2.51	12.29
	JQLA8-1	umc1665	umc2199	446	4.03	0.01	4.71	16.90
	JQLA8-2	umc1765	umc1460	819	3.06	0.03	2.14	11.34
	JQLA9	bnlg128	bnlg1129	1084	3.05	0.12	2.47	-12.36
PH	JQPH1-1	umc1538a	bnlg1347a	47	3.06	0.01	2.32	-0.03
	JQPH1-2	dupssr26	umc1243	1082	3.04	0.04	2.35	-0.03
	JQPH2	umc2248	umc1579	331	2.49	0.01	2.86	0.04
	JQPH4	dupssr34	umc1667	202	2.48	0.13	3.00	0.04
	JQPH6	umc1014	umc2006	167	3.52	0.28	2.83	-0.04
	JQPH7-1	umc1409	phi034	650	4.73	0.03	3.84	0.04
	JQPH7-2	umc1016	umc2327	842	3.33	0.07	2.80	0.04
	JQPH8	umc1765	umc1460	819	2.91	0.01	2.20	0.03
	JQPH10	umc2021	zmrr2pcr	900	2.63	0.03	2.06	-0.03
SD	JQSD3	umc2002	phi053	708	4.39	0.11	4.80	0.13
	JQSD4	bnlg490	bnlg1937	24	3.11	0.21	2.62	-0.09
	JQSD5	umc1274	umc1784	900	5.49	0.08	4.17	-0.12
	JQSD6	umc1621	umc2059	1213	4.32	0.01	3.52	0.11
	JQSD8	bnlg1782	umc1665	418	4.02	0.05	5.17	0.14
	JQSD9	bnlg128	bnlg1129	1081	2.62	0.01	2.04	-0.09
	JQSD10	bnlg1677	umc2351	716	2.63	0.01	3.81	-0.12
TBN	JQTBN1	umc1306	umc2047	221	2.80	0.02	2.51	0.45
	JQTBN2	umc1579	umc2403	423	3.89	0.22	2.54	0.45
	JQTBN3	bnlg1452	umc2033	1225	6.62	0.01	5.53	0.68
	JQTBN5	bnlg118	bnlg1118	24	6.93	0.05	5.18	0.66
	JQTBN7	umc1671	umc1412	40	2.80	0.05	2.34	0.44
	JQTBN9-1	umc1492	umc2121	373	4.92	0.01	4.97	0.64
	JQTBN9-2	umc1519	umc1657	502	2.80	0.12	2.31	0.43
	JQTBN10	bnlg1074	umc2003	371	2.63	0.17	1.80	0.38
LW	JQLW1	umc2047	umc1991	235	3.21	0.16	2.30	0.12
	JQLW2	umc2079	umc1541	240	4.22	0.02	2.99	-0.13

	JQLW3	umc1458	umc2377	1810	2.55	0.01	2.59	-0.12
	JQLW5	umc1019	umc1722	169	4.34	0.05	3.20	0.13
	JQLW6	umc1621	umc2059	1214	4.85	0.04	3.46	0.14
	JQLW8	umc1665	umc2199	433	3.11	0.04	2.57	0.12
	JQLW9-1	bnlg1191	bnlg1525	695	3.93	0.01	3.81	-0.15
	JQLW9-2	bnlg128	bnlg1129	1178	3.95	0.03	4.31	-0.16
	JQLW10	umc1506	bnlg594	472	4.33	0.02	5.97	0.19
LL	JQLL1	phi227562	umc1538a	6	3.31	0.04	2.33	1.23
	JQLL2	umc1579	umc2403	343	2.58	0.02	2.02	1.14
	JQLL3	bnlg1452	umc2033	1140	6.33	0.42	4.52	1.75
	JQLL4	umc1999	umc1313	468	3.99	0.41	5.26	1.87
	JQLL5	umc2111	dupssr10	463	3.47	0.03	2.40	1.26
	JQLL8	umc1765	umc1460	819	5.14	0.01	3.58	1.52
	JQLL10	bnlg210	umc1345	214	4.26	0.73	4.23	-1.66

Notes:

PVE (%), Percentage of phenotypic variance explained. Add, Additive effect of the QTL; positive values indicate that the alleles for higher trait values are contributed by 082, and negative values indicate that the alleles for higher trait values are contributed by Ye107.

Table 7. Predicted maize genes within the QTL interval.

Number	Gene ID	Gene description	Chr1 Location
1	Zm00001d032678	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein	233,951,533-234,840,412
2	Zm00001d032768	CCT motif family protein	236,863,389-238,487,010
3	Zm00001D032850	phosphate transporter protein2	240,081,753-241,566,874

Notes:

The physical location reference Zea mays -B73-REFERENCE- GRAMENE-4.0.

Figures

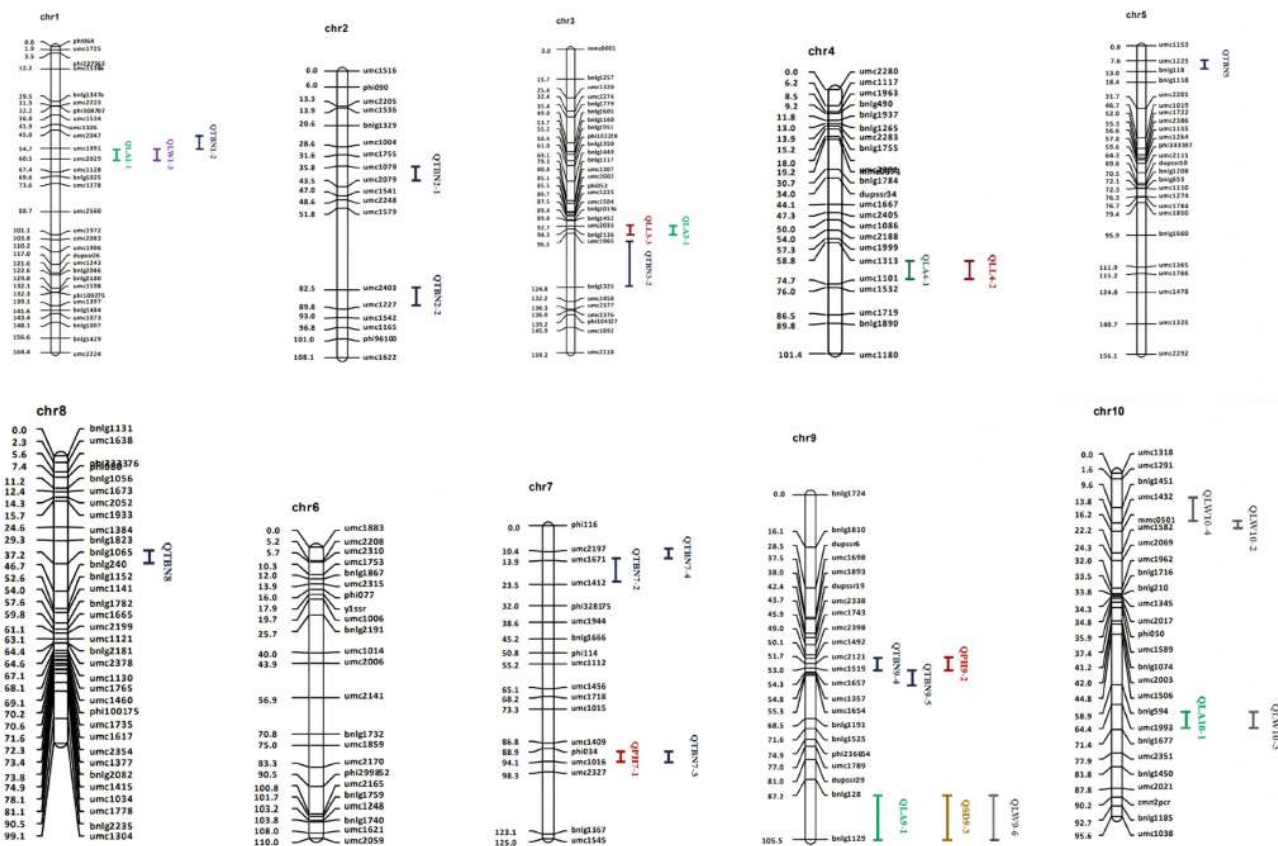


Figure 1

Linkage map showing the distribution of QTLs for agronomic traits in an F2:3 population.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementalDataS1.xlsx](#)