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Mapping QTLs for grain yield and yield components under high and low phosphorus treatments in maize (*Zea mays* L.)

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ABSTRACT

A set of 210 $F_{2:3}$ families developed from 5003(107) and 178 were used to identify quantitative trait loci (QTL) under high and low phosphorus treatments at Taian and Yantai. Six agronomic traits, including GY, 100KW, EL, RN, KN and ED were evaluated. A genetic map comprising 207 SSR markers spanned 1755.1 cm in length with an average interval of 8.48 cm between adjacent markers. A total of 69 QTLs were identified for the six traits at two sites. Thirty-six distinct QTLs were identified from Taian, in which 7 out of 36 for GY, 7 for 100KW, 5 for EL, 5 for RN, 6 for KN and 6 for ED, while 33 distinct QTLs were identified at Yantai, in which 6 out of 33 for GY, 5 for 100KW, 5 for EL, 7 for RN, 5 for KN and 5 for ED. In addition, three stable common loci crossing the two phosphorus treatment sites are in the interval umc2215–bnlg1429, umc1464–umc1829 and umc1645–bnlg1839 were detected on chromosome 1, 5 and 10. Our results suggest the presence of these QTLs may contribute to fine-mapping, identification of candidate genes and MAS strategies for maize improvement purposes under phosphorus deficiency combining traditional breeding approaches.

1. Introduction

Phosphorus (P) is one of the essential macronutrients for plant growth and development. Plants usually take up P as phosphate (Pi) from the soil solution, however the concentration of Pi in the soil solution is low [1], which in turn cannot satisfy the demand of plants. Hence, P is one of the most unavailable and inaccessible macronutrients in the soil and frequently the most limiting element for plant growth and development [2–5]. Inorganic P fertilizers have been applied to the field to support the crop growth. Unfortunately, although these inorganic P fertilizers can provide P for the crops, they also increase the cost of plant production and exhaust the non-renewable phosphate resources. It has been estimated that the P resources will be depleted within the next 60–90 years [6]. Furthermore, many of the applied inorganic P fertilizers have caused serious pollution to environment. Thus, the development of cultivars with P efficiency, which comprises acquisition efficiency to acquire P from the environment, may represent an effective solution to this problem. Therefore, a better understanding of grain yield and yield components traits conferring phosphorus efficiency is needed.

Maize is a crop of global economic importance and due to its diversity in visual striking phenotype; maize also serves as an excellent vehicle to communicate the benefits of plant science and agricultural researches [7]. Low concentration of Pi in the soil can significantly affect maize growth. Soil P availability is critical for the early growth and development of maize [8]. Some researches have been carried out to screen and improve the P effective in maize, most of which focused on maize inbred lines [9–13]. Liu et al. [14] concluded that efficient use of P in the calcareous soil is related to large root system, greater ability to acidify the rhizosphere, and positive response of APase production and excretion to low P conditions. Plénet et al. [15,16] analyzed the growth of maize under phosphorus deficiency and found that the grain yield was significantly reduced under P deficiency. Thus developing P efficient cultivars becomes the most effective way to increase P usage, by which high yield under low P condition can be realized.

Molecular markers have been used to study complex, quantitative traits in different crop species [17]. Through marker-assisted selection (MAS), markers related to specific genes can be used to facilitate the selection of desired genotypes [18]. Quantitative trait

Abbreviations: QTL, quantitative trait loci; SSR, simple sequence repeat; GY, grain yield per plant; RN, row number per ear; KN, kernel number per row; 100KW, 100-kernel weight; EL, ear length; ED, ear diameter; MAS, marker-assisted selection; HP, high phosphorus; LP, low phosphorus.

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loci (QTL) provided an effective approach to understand the genetic basis of grain yield and yield components associated with P efficiency. Several QTLs involved in the expression of different yield components have already been detected in maize [19–27], but none of these studies were conducted under conditions of low phosphorus in the field. In recent years, the importance of maize growing under low phosphorus conditions has been well documented and many studies have constructed QTL map under low P conditions, most of which focused on root traits [28–32]. For example, Zhu et al. [29–31] detected 9 QTLs for seminal root traits, 14 QTLs for lateral toots traits and 11 QTLs for root hair length under low and high phosphorus conditions; Chen et al. [32] mapped a total of 75 QTLs for phosphorus efficiency and relative biologic characteristics. However, reports on QTLs mapping of grain yield and yield components for phosphorus efficiency are relatively few in maize. The objectives of this study were to use $F_{2:3}$ families derived from a cross between 5003(107) and 178 to (1) investigate the inheritance of grain yield and yield components, (2) identify simple sequence repeat (SSR) markers associated with QTLs for grain yield and yield components under high and low phosphorus treatments at Taian and Yantai, and (3) analyze the common regions of QTLs for multi-traits which may be useful for improving grain yield under low phosphorus condition by means of marker-assisted selection.

2. Materials and methods

2.1. Experimental population

The population used in this study consisted of 210 $F_{2:3}$ families derived from a cross between 5003(107) and 178, which were known to differ in grain yield and yield components under condition of low phosphorus. 5003(107) is a phosphorus inefficient genotype, while 178 is a phosphorus efficient genotype. 178 showed significantly higher grain yield than 5003(107) at maturity. The F_2 families were produced from October 2006 to February 2007 in the Hainan province, China. The $F_{2:3}$ families were produced from April 2007 to August 2007 in Taian city, Shandong province, China.

2.2. Field experiment

The $F_{2:3}$ families along with two parent lines were evaluated during May–August in 2008 at two locations, Taian (TA), Shandong province, China (36°16′ N latitude, 117°15′ E longitude), where the average daytime temperature is 14 °C and the average rainfall per year is 697 mm, and Yantai (YT) Shandong province, China (37°57′ N latitude, 121°16′ E longitude), where the daily temperature and average yearly rainfall are 12 °C and 652 mm, respectively. The soil P concentration was determined by the Olsen et al. method as described by Okalebo et al. [49]. Although the experiment was grown in different locations of the same province, the soil type was the same and neither P fertilizer nor manure was applied to the field before planting in 2007. The soil content of available P before fertilization was 5.3 mg kg^{-1} in Taian and 5.6 mg kg^{-1} in Yantai. In each location two phosphorus treatments were used. The high phosphorus (HP) treatment was applied 50 kg ha^{-1} of P, 63 kg ha^{-1} of K in the form of potassium dihydrogen phosphate before sowing, 180 kg ha^{-1} of N in the form of urea with 120 before sowing and 60 at stem elongation stage. For the low phosphorus (LP) treatment, nil P, 63 kg ha^{-1} of K as potassium chloride before sowing were applied, and 180 kg h^{-1} of N as urea were applied 120 kg before sowing and 60 kg at stem elongation stage. The experiment was arranged in a complete block design with three replicates. Maize was planted in rows spaced 0.4 m apart, 3 m in length. To ensure the growth of 15 plants per plot, 45 seeds were prepared per row, with three seeds sown together, but only one plant was prepared during the seedling stage. The field management followed common practice for maize production and crops were irrigated twice during the growing season.

2.3. Trait evaluation

At the time of harvest, 10 plants from the middle of each plot were harvested by hand for trait measurements. Six agronomic traits were measured, including grain yield per plant (GY, g), 100-kernel weight (100KW, g), ear length (EL, cm), row number per ear (RN), kernel number per row (KN) and ear diameter (ED, cm). The average values of three replications of the six traits were used for data analysis.

2.4. Phenotypic data analysis

The basic data from each plant was averaged, and the mean value of each trait was computed, followed by a calculation of the measured trait for each $F_{2:3}$ families of three replicates from different P treatments at two locations. Data analysis was performed using SAS 8.0 statistical software package [50]. Broad-sense heritability (h^2) of measured traits was computed as previously described by Knapp et al. [40], $h^2 = \delta_g^2/(\delta_g^2 + (\delta_{gl}^2/n) + \delta_e^2/rn)$, where δ_g^2 is the genetic variance, δ_{gl}^2 is the interaction of genotype with locations, δ_e^2 is error variance, γ is the number of replications, and n is the number of locations. The estimates of δ_g^2, δ_{gl}^2 and δ_e^2 were obtained by analysis of variance (ANOVA).

2.5. SSR analysis

In total, 860 pairs of SSR markers were selected from the maize genome database (http://www.maizegdb.org) to screen polymorphism between two parents, 5003(107) and 178. Genomic DNA was isolated from fresh young leaf tissues of both the parents (5003(107) and 178) and the 210 F_2 families using CTAB procedure [33]. PCR reactions were performed in a PTC200 Peltier Thermal Cycler (Bio-Rad Inc., USA) in a total volume of 15 μL, containing 1× buffer, 1.8 mmol L^{-1} $MgCl_2$, 0.25 mmol L^{-1} dNTPs, 0.24 μmol L^{-1} of each primer, 1 U *Taq*-polymerase and 40 ng genomic DNA as the template. PCR was performed at 94 °C for 5 min, followed by 30 cycles of 95 °C for 30 s, 56 °C for 35 s, 72 °C for 40 s, followed by a final extension step for 5 min at 72 °C before cooling to 4 °C. PCR amplification products and 8 μL loading buffer were denatured at 95 °C for 5 min, and chilled on ice before loading 6 μL on a 6% polyacrylamide gel with 8 mol urea/L and 1× TBE. Samples were run at constant power (60 W) for approximately 1 h, and visualized by silver staining [34].

2.6. Linkage map and QTL analysis

Molecular linkage maps were constructed by MAPMAKER 3.0 [35]. The recombination frequency between linked loci was transformed into centimorgan (cM) distances using Kosambi's mapping function [36]. Analyses of QTL location, origin of positive alleles, and effects of QTLs were performed using the software Windows QTL Cartographer version 2.5 [37] based on composite interval mapping [38]. Forward regression was analyzed using a window size of 10 cM, a walk speed of 2 cM and five control markers. We performed 1000 permutations on all traits in each environment to establish the empirical LOD thresholds at 5% probability level [39]. The LOD score peaks of >2.5 (default criteria) indicated the existence of QTLs. QTL positions were assigned at the point of maximum LOD score in the regions under consideration.