



Genetic analysis of agronomic traits associated with plant architecture by QTL mapping in maize

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ABSTRACT. Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, and increasing the grain yield and biomass has been among the most important goals of maize production. The plant architecture can determine the grain yield and biomass to some extent; however, the genetic basis of the link between the plant architecture and grain yield/biomass is unclear. In this study, an immortal F₉ recombinant inbred line population, derived from the cross Mo17 x Huangzao4, was used to detect quantitative trait loci (QTLs) for 3 traits associated with plant architecture under two nitrogen regimes: plant height, ear height, and leaf number. As a result, 8 and 10 QTLs were identified under the high nitrogen regime and low nitrogen regime, respectively. These QTLs mapped to chromosomes 1 (six QTLs), 2 (one QTL), 3 (one QTL), 7 (two QTLs), and 9 (eight QTLs), and had different genetic distances to their closest markers, ranging from 0 to 22.0 cM, explaining 4.7 to 20.5% of the phenotypic variance. Because of an additive effect, 9 and 9 could make the phenotypic values of traits increase and decrease to some extent, respectively. These results

are beneficial for understanding the genetic basis of agronomic traits associated with plant architecture and for performing marker-assisted selection in maize breeding programs.

Key words: Maize; QTL; Plant architecture; Nitrogen regime

INTRODUCTION

Maize (*Zea mays* L.) is one of the most important cereal crops worldwide, and increasing the grain yield and biomass per acre has been among the most important goals of maize production (Ku et al., 2010). Several decades of breeding efforts, striving for consistent performance under elite-hybrid popularization and high-density plantings, have enhanced the genetic gain of yield. The remarkable importance of plant architecture in maize is well underlined by retrospective analyses of hybrids (Tollenaar and Wu, 1999; Lu et al., 2010). Among the agronomic traits that have changed markedly as a result of selection, plant architecture, e.g., plant height (PH) and ear height (EH), has played a predominant role in adaptation to the historical increase in yield (Zhang et al., 2010). With the arable land gradually decreasing, it is likely that increased planting density will continue to be a target for selection in the future (Kebrom and Brutnell, 2007). Hence, breeding of maize with optimized plant architecture is regarded as one of the most important goals in maize breeding projects.

Many traits such as PH, EH, leaf number (LN), leaf angle (LA), and leaf orientation (LO) can be used to evaluate the efficiency of plant architecture. More significantly, these traits associated with plant architecture can be largely used to determine grain yield and biomass (Ribaut et al., 2007; Liao et al., 2011). To obtain plant varieties possessing the desired architecture, conventional breeding methods are useful; however, these methods are time-consuming due to the selection of superior individuals among segregating progenies resulting from hybridization (Ibitoye and Akin-Idowu, 2010). Moreover, the available maize materials are limited. An alternative solution is to utilize marker-assisted selection (MAS). MAS is a combination of traditional genetics and molecular biology and allows for the selection of genes that control traits of interest. Combined with traditional selection techniques, MAS has emerged as a valuable tool for selecting organisms with interesting traits during crop breeding (Stendal et al., 2006; Chen et al., 2010; Kumar et al., 2010; Jantaboon et al., 2011).

To perform MAS, an understanding of the genetic basis of traits is necessary, and quantitative trait locus (QTL) mapping for traits can help us achieve this purpose. Currently, QTL mapping has been applied for crop improvement (Kumar and Kumar, 2009), and a large number of molecular markers linked with traits have been obtained; moreover, some QTLs controlling agronomic traits have been successfully cloned (Zhou et al., 2011). In maize, numerous QTLs have been identified that control agronomic traits, and these QTLs have been mapped to 10 chromosomes in maize (Tsonev et al., 2009; Qiu et al., 2011). For the traits related to plant architecture, PH and EH have been frequently studied (Kraja and Dudley, 2000; Sibov et al., 2003; Lima et al., 2006; Malosetti et al., 2008; Bai et al., 2010), and a large number of QTLs were found to be located in different chromosomal regions. There are also many reports on QTL identification of the LN trait (Jiang et al., 1999; Lima et al., 2006; Tang et al., 2007; Wang et al., 2008), and several studies have been performed on the LA and LO traits (Mickelson et al., 2002; Lu et al., 2007; Ku et al., 2010). Therefore, QTL mapping of traits associated with plant architecture is very significant in maize.

A segregating population must be used for QTL mapping. Previous studies of QTL mapping of maize agronomic traits focused on F_2 (Ribaut et al., 2007; Ku et al., 2010; Zhang et al., 2010). This kind of population has a deficiency, namely, temporality, similar to a backcross population (Bai et al., 2010). Thus, F_2 cannot be utilized again because there are no continual plants for DNA extraction and phenotypic analysis. In comparison, the recombinant inbred line (RIL) population is immortal and can be used in different regions and times because it consists of homogenous individuals. The RIL population has been widely used for QTL mapping in crops (Balint-Kurti et al., 2008; Du et al., 2009; Blair et al., 2010; Zhou et al., 2011), but it has rarely been used for QTL mapping for traits associated with plant architecture in maize (Tang et al., 2007; Liu et al., 2010). Additionally, the same type of segregating population derived from different parental lines likely provide different QTL identification results, including different location, number, and genetic effects. Thus, an RIL population that is derived from two parental lines and that is different from previous studies is necessary to be selected to map QTLs for PH, EH, and LN, associated with plant architecture in maize.

Moreover, QTL mapping can be affected by ecological conditions because the same genes under different environments might be expressed at different levels. For example, using the F_2 population from the cross X178 x B73, Xiao et al. (2005) identified 2 QTLs on chromosomes 1 and 9 in a well-watered environment. In contrast, in a water-stressed environment, 3 QTLs were mapped on chromosomes 1, 2, and 9. Until now, most ecological environments used for QTL mapping of maize traits have been focused on different water contents in the soil, involving different water regimes in the same field or different experimental regions with different rainfall rates (Messmer et al., 2009; Zhang et al., 2010; Hao et al., 2011). However, low nitrogen (N) conditions, for example, during agricultural drought, represent a major source of loss in maize yield. Currently, most maize in developing countries is produced under N-deficient conditions because of the low N availability in drought-prone environments, high price ratios between fertilizers and grains, limited availability of fertilizers, and low purchasing power of farmers (Ribaut et al., 2007). Thus, there is a growing interest in developing cultivars performing better under low N conditions. A better understanding of the genetic basis of the maize plant architecture under N-stressed conditions is necessary and can help facilitate the selection efficiency of crops for these environments.

Therefore, in this present study, an F_9 RIL population, derived from the cross between maize inbred lines Mo17 (Lancaster heterotic group in the USA) and Huangzao4 (Tangsiyingtuo heterotic group in China), were used to identify QTLs for 3 traits affecting plant architecture under 2 N regimes: PH, EH, and LN. The objectives were to i) better understand the genetic basis of plant architecture and ii) identify molecular markers for MAS in maize breeding projects.

MATERIAL AND METHODS

Maize materials

The experimental materials involved in this study included maize inbreds Mo17 (female) and Huangzao4 (male) as parents, and an F_1 hybrid and an F_9 segregation population consisting of 239 RILs. Mo17 and Huangzao4 are representative lines of the Lancaster and Tangsiyingtuo heterotic groups, respectively. The F_1 hybrid and the RIL population descended from the cross between these two parental lines.

Field experiments

At the Nanchong Academy of Agricultural Sciences, Nanchong city, China, these 242 lines were sown in a randomized complete block design with 6 replicates, 15 plants per plot in each replicate. Of the 6 replicates in each line, 3 were placed under a high N regime (HNR) by adding urea (300 kg/ha), and the other 3 were placed under a low N regime (LNR) with no added N-containing fertilizer. The average contents of total N and alkaline hydrolysis N at a depth of 30 cm in the original soil were 0.092 and 0.000056%, respectively.

Phenotype investigation and statistical analysis

During the flowering period, the middle 8 plants of each replicate of the 242 lines were individually recorded, and the means of the 3 traits, PH (centimeters; from plant base to tasseling tip), EH (centimeters; from plant base to ear base), and LN (total number of leaves), were calculated.

The SPSS 11.5 software (www.spss.com) was used to analyze the phenotypic data of the traits, as described by Liu et al. (2009). First, descriptive statistics was performed to calculate the mean and standard deviation (SD) for the parental lines and the F_1 hybrid, as well as the range, mean, SD, skewness, kurtosis, and frequency distribution for the RIL population. Second, ANOVA was performed to determine the significance of differences between individuals within the RIL population. According to Li et al. (2012), the broad-sense heritability of a population based on the 3 traits in the 2 N environments is calculated using the formula $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_e^2 / n)$, where σ_g^2 is the genotypic variance, σ_e^2 is the environmental variance, and n is the number of replicates. The variance between HNR and LNR were compared by ANOVA for the RIL population. Each of the 3 phenotypic traits was modeled independently using a mixed procedure, where the genotype, location, and interaction between the location and the genotype were defined as a fixed effect, whereas the replication within a location (block effect) was defined as a random effect. Finally, Pearson's correlation coefficients between the 3 traits in the 2 N regimes were calculated and analyzed.

QTL identification

To conduct the QTL mapping for PH, EH, and LN, the means of each line of the RIL population under the same N condition were computed for the 24 plants in 3 replicates. According to a previous linkage map that included 100 microsatellite markers and covered 1421.5 cM of the genome (Liu et al., 2009), QTL detection affecting the 3 traits was performed via composite interval mapping (CIM) (Wang et al., 2010), using the following control parameters: 10-cM window size, CIM standard model, 5 control markers, and forward regression method. The \log_{10} of the odds ratio (LOD) threshold value for the QTL significance was determined by the 1000-time permutation test ($\alpha = 0.05$) (Doerge and Churchill, 1996). The position, percentage of phenotypic variation, and genetic effects of the identified QTLs were estimated on the basis of the peak of the LOD curve region over the threshold values, and the identified QTLs were then mapped using the Mapchart 2.1 software (Voorrips, 2012).

RESULTS

Statistical analysis

Descriptive statistics of traits in the parental lines and the F₁ hybrid

The statistical results showed differences between Mo17, Huangzao4, and the F₁ hybrid (Table 1). The mean of the F₁ hybrid was significantly greater than that of the parental lines for all of the investigated traits under either N regime, a phenomenon best explained by heterosis. Of the two parents, Mo17 had a higher value for the PH trait, whereas Huangzao4 had a higher value for the LN trait. EH is a special trait, and Huangzao4 had a higher value under HNR. In contrast, under LNR, the value for the EH trait in Huangzao4 was lower than that in Mo17.

Table 1. Mean of F₁ hybrid and its parental lines across 2 nitrogen (N) regimes in 3 traits.

Traits	N regimes	Mo17 (mean ± SD)	HZ4 (mean ± SD)	F ₁ (mean ± SD)
PH (cm)	HNR	211.40 ± 10.40	181.90 ± 5.43	245.03 ± 6.01
	LNR	200.20 ± 6.40	173.23 ± 21.45	245.57 ± 4.59
EH (cm)	HNR	77.70 ± 5.77	82.90 ± 3.64	101.87 ± 4.80
	LNR	79.33 ± 15.33	78.77 ± 10.90	90.10 ± 12.01
LN	HNR	17.00 ± 0.10	18.50 ± 0.10	19.07 ± 0.12
	LNR	16.77 ± 0.45	18.53 ± 0.23	19.00 ± 0.00

HZ4 = Huangzao4; PH = plant height; EH = ear height; LN = leaf number; HNR = high N regime; LNR = low N regime

Descriptive statistics of traits in the RIL population

The results of the descriptive statistics for the 3 traits across the 2 N regimes in the RIL population are listed in Table 2. In general, there were no significant differences between the 2 N regimes for the same trait using the 3 parameters, including the range, mean, and SD. However, the skewness and kurtosis showed differences, and computation of the statistical significance of the differences between the 2 N regimes was deemed unnecessary. The frequency distribution graphs of the data derived from different RILs within the population are indicated in Figure 1. From these results, we concluded that the statistics of the 6-group data agreed well with a normal distribution, suggesting that the PH, EH, and LN of maize are quantitative traits that are controlled by multiple genes.

Table 2. Descriptive statistics of the recombinant inbred line population across 2 nitrogen (N) regimes in 3 traits.

Traits	N regimes	Range	Mean ± SD	Skewness	Kurtosis
PH (cm)	HNR	124.10-265.00	198.54 ± 22.81	-0.037	0.190
	LNR	135.40-266.90	199.33 ± 22.77	0.047	-0.255
EH (cm)	HNR	39.30-116.10	78.13 ± 13.18	0.008	0.097
	LNR	47.10-117.00	77.11 ± 13.00	0.165	-0.132
LN	HNR	15.40-22.00	18.54 ± 1.20	0.361	0.158
	LNR	14.90-21.80	18.32 ± 1.20	0.371	0.220

SD = standard deviation; PH = plant height; EH = ear height; LN = leaf number; HNR = high N regime; LNR = low N regime.

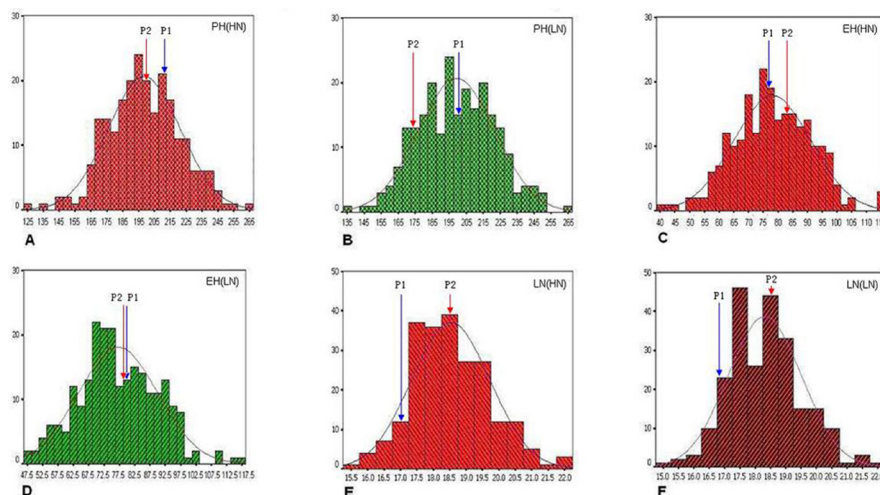


Figure 1. Frequency distribution of 3 traits associated with plant architecture in the population including 239 recombinant inbred lines. Horizontal axis for trait values and longitudinal axis for number of individuals. **A.** Plant height (PH) under high N (HN) regime; **B.** PH under low N (LN) regime; **C.** ear height (EH) under HN regime; **D.** EH under LN regime; **E.** leaf number (LN) under HN regime; **F.** LN under low N regime.

ANOVA of traits in the RIL population

The results of ANOVA for the 3 traits in the RIL population under the 2 N regimes are shown in Table 3. According to the F values, the 239 RILs of the population presented significant differences at $P < 0.01$ in the 3 traits under both N regimes. Thus, our maize population could be used for QTL mapping for the 3 agronomic traits across different N environments.

Table 3. ANOVA of the recombinant inbred line population across 2 nitrogen (N) regimes in 3 traits.

Traits	N regimes	Source of variation	Sum of squares	d.f.	Mean square	F	Significance
PH (cm)	HNR	Between groups	367490.10	236	1557.16	16.56**	<0.01
		Within groups	44476.85	473	94.03		
	LNR	Between groups	365621.49	236	1549.24	13.35**	
		Within groups	54793.58	472	116.09		
EH (cm)	HNR	Between groups	122413.64	236	518.70	12.81**	<0.01
		Within groups	19146.47	473	40.48		
	LNR	Between groups	119330.16	236	505.64	11.75**	
		Within groups	20313.07	472	43.04		
LN	HNR	Between groups	993.29	236	4.21	20.20**	<0.01
		Within groups	95.63	459	0.21		
	LNR	Between groups	1008.34	236	4.27	23.18**	
		Within groups	86.28	468	0.18		

d.f. = degrees of freedom, excluding three missing values. **Significant probability at 0.01 level. PH = plant height; EH = ear height; LN = leaf number; HNR = high N regime; LNR = low N regime.

Comparisons between HNR and LNR for the 3 traits of the RIL population

The heritability was high for all experimental traits, ranging from 97.24 to 98.61% (Table 4). LN had the highest heritability (98.36% under HNR and 98.61% under LNR). EH

had the lowest heritability (97.24% under LNR). Statistical analysis using a mixed model for the differences between the HNR and LNR demonstrated that the differences due to the genotypes were significant at $P < 0.01$ for the 3 traits. The differences due to the N regime were also significant at $P < 0.01$ for LN and EH; however, no interaction from the genotype x N regime was different in the 2 N regimes.

Table 4. Comparison between low and high nitrogen (N) regimes of the recombinant inbred line population in heritability, genotype, N regime, and genotype x N regime.

Traits	N regimes	Heritability (%)	Genotype		N regime		Genotype x N regime	
			F	Pr > F	F	Pr > F	F	Pr > F
PH (cm)	HNR	98.03	29.83	<0.01**	2.18	>0.05	0.83	>0.05
	LNR	97.56						
EH (cm)	HNR	97.46	23.88	<0.01**	8.96	<0.01**	0.98	>0.05
	LNR	97.24						
LN	HNR	98.36	43.17	<0.01**	97.05	<0.01**	1.18	>0.05
	LNR	98.61						

**Significant probability at 0.01 level. PH = plant height; EH = ear height; LN = leaf number; HNR = high N regime; LNR = low N regime.

Correlation analysis between different traits in the RIL population

The 3 traits across the 2 N regimes were further correlated on the basis of the statistical average of the 239 RILs (Table 5). All of the 15 correlation coefficient values derived from the 3 traits crossed by the 2 N regimes displayed positive correlations at the $P < 0.01$ level.

Table 5. Correlation analysis among the 3 traits for the recombinant inbred line population across 2 nitrogen (N) regimes.

	PH (ln)	EH (hn)	EH (ln)	LN (hn)	LN (ln)
PH (hn)	0.95**	0.78**	0.72**	0.32**	0.30**
PH (ln)		0.73**	0.75**	0.28**	0.29**
EH (hn)			0.92**	0.53**	0.51**
EH (ln)				0.49**	0.53**
LN (hn)					0.95**

**Correlation is significant at 0.01 level (Pearson's correlation, two-tailed). PH (hn) = plant height under high N regime; PH (ln) = plant height under low N regimes; EH (hn) = ear height under high N regime; EH (ln) = ear height under low N regime; LN (hn) = leaf number under high N regime; LN (ln) = leaf number under low N regime.

QTL identification

The results of the QTL detection for the PH, EH, and LN traits are shown in Table 6. Eighteen QTLs were detected under the 2 N regimes: 8 under HNR and 10 under LNR. These QTLs were mapped to chromosomes 1 (six QTLs), 2 (one QTL), 3 (one QTL), 7 (two QTLs), and 9 (eight QTLs). The mapping intervals to the closest markers ranged from 0 to 22.0 cM (Figure 2). From the R^2 values in Table 6, the 18 QTLs accounted for 4.7 to 20.5% of the phenotypic variance. Under HNR, these QTLs for PH, EH, and LN could explain 17.3, 31.8, and 55.8% of the phenotypic variance, respectively. In contrast, under LNR, the QTLs accounted for 15.6, 51.0, and 57.6% of the phenotypic variance, respectively. Due to additive effects, 9 and 9 could make phenotypic values of traits increase and decrease to some extent,

respectively. Notably, a dominant genetic effect of the QTLs could not be computed in this experiment because the individuals in the RIL population were homologous.

Table 6. QTLs identified based on a recombinant inbred line population from the cross Mo17 x Huangzao4 across 2 nitrogen (N) regimes.

Traits	N regimes	QTL name	Chromosome	Closest marker (bin)	Position (cM)	Interval (cM) ^a	LOD	R ²	Additive effect
PH (cm)	HNR	<i>qPH-hn1</i>	1	Umc1035 (1.06)	93.5	5.9	7.1	17.3	-9.6
	LNR	<i>qPH-ln1</i>	1	Umc1035 (1.06)	92.5	6.9	6.3	15.6	-9.2
EH (cm)	HNR	<i>qEH-hn1</i>	1	Umc1358 (1.07)	110.4	2.1	6.1	10.0	-4.3
		<i>qEH-hn9a</i>	9	Nc134 (9.03)	63.6	6.0	5.3	11.5	-4.5
	LNR	<i>qEH-hn9b</i>	9	Bnlg1375 (9.07)	121.0	0.0	6.9	10.3	4.3
		<i>qEH-ln1a</i>	1	Bnlg1178 (1.02)	22.0	22.0	3.0	17.2	5.4
		<i>qEH-ln1b</i>	1	Bnlg1866 (1.03)	51.0	0.0	3.1	4.7	2.9
		<i>qEH-ln1c</i>	1	Umc1358 (1.07)	109.4	3.1	5.7	9.8	-4.2
		<i>qEH-ln9a</i>	9	Phi065 (9.03)	54.4	0.0	7.2	10.6	-4.2
LN	HNR	<i>qLN-hn9b</i>	9	Bnlg1375 (9.07)	121.0	0.0	6.0	8.7	3.9
		<i>qLN-hn2</i>	2	Bnlg125 (2.03)	94.7	3.0	4.2	8.3	-0.4
		<i>qLN-hn7</i>	7	Umc1295 (7.04)	33.3	18.9	3.8	14.1	0.5
	LNR	<i>qLN-hn9a</i>	9	Nc134 (9.03)	63.6	6.0	6.0	14.5	-0.5
		<i>qLN-hn9b</i>	9	Bnlg1129 (9.08)	135.0	8.6	6.2	18.9	0.5
		<i>qLN-ln3</i>	3	Bnlg1035 (3.05)	73.6	2.0	3.6	8.3	0.4
		<i>qLN-ln7</i>	7	Bnlg1792 (7.02)	27.3	16.0	4.5	15.3	0.5
		<i>qLN-ln9a</i>	9	Phi022 (9.03)	43.7	3.1	7.4	13.5	-0.5
		<i>qLN-ln9b</i>	9	Bnlg1375 (9.07)	129.0	8.0	7.8	20.5	0.5

^aInterval between QTL and its closest marker; R² = percentage of phenotypic variation explained by QTL. LOD = log 10 of odds ratio; PH = plant height; EH = ear height; LN = leaf number; HNR = high N regime; LNR = low N regime.

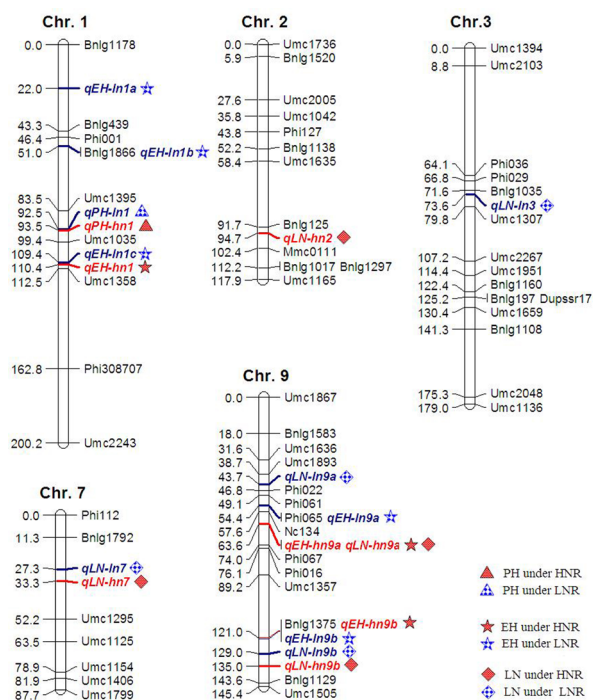


Figure 2. Chromosomal positions of the QTLs for plant height (PH), ear height (EH), and leaf number (LN). The 18 QTLs were indicated with different shapes and colors, red for high N regime (HNR) and blue for low N regime (LNR).

The 18 QTLs were analyzed and mapped (Table 6 and Figure 2). However, the actual number of QTLs should be less than 18 because some QTLs were identified under both N regimes and can be combined on the basis of their chromosomal positions and respective additive effects. For example, the distance between *qPH-hn1* and *qPH-ln1* in the map was only 1.0 cM, and the additive effect of each locus was nearly identical; thus, it was concluded that these loci represented the same QTL.

DISCUSSION

Plant architecture is one of the most important agronomic traits in maize and is related to grain yield and biomass. Plant architecture has long attracted the attention of breeders for achieving the ideal architecture in production of crop plants (Ku et al., 2010). To understand the genetic basis more clearly and develop MAS for plant breeding, 3 key quantitative traits associated with plant architecture, PH, EH, and LN, were selected for QTL mapping by using an immortal RIL population across 2 N regimes.

For traits PH and EH, many studies on QTL mapping have been reported, and a large number of QTLs have been identified on 10 chromosomes in maize (Kraja and Dudley, 2000; Sibov et al., 2003; Lima et al., 2006; Malosetti et al., 2008; Bai et al., 2010). No new QTLs were identified for PH and EH, and our experiments were similar to previous studies in many aspects such as the identity of the parents, population type, genetic map, and ecological conditions. However, previous studies were focused on F₂ populations (Malosetti et al., 2008; Zhang et al., 2010). The F₂ population can only be used once because the plants cannot propagate. In contrast, the RIL population used in our study is immortal; hence, it could be applied again in different regions and times because of the homogenous population (Bai et al., 2010). In addition, previous environments designed for QTL mapping of PH and EH were mainly based on differences in the water content of the soil (Malosetti et al., 2008; Zhang et al., 2010). Different N regimes, which are described herein, have rarely been used for QTL detection (Agrama et al., 1999).

Only a few studies have reported QTLs for LN (Jiang et al., 1999; Tang et al., 2007; Wang et al., 2008). Previous results indicated that all 10 chromosomes in maize contain QTLs controlling LN, except for chromosome 5. Compared with previous studies, some QTLs identified in the present study were new loci; for example, one QTL mapped to bin 9.07-9.08 of chromosome 9. Previously analyzed ecological environments included mainly different locations during the same year or different years at the same location. To the best of our knowledge, this is the first study to map QTLs for LN under different N regimes.

Among the QTLs identified in our experiment, 3 EH loci had 0 cM of mapping distance to linked markers: 1 QTL was identified under both N regimes (*qEH-hn9b* or *qEH-ln9b*), and 2 QTLs were identified only under LNR (*qEH-ln1b* and *qEH-ln9a*). This finding suggested that the linked markers co-segregated with the genes controlling the traits, and they could hence be used for MAS. The other QTLs, with over 0 cM of mapping interval to their closest markers, may be mapped in more detail by using other molecular markers that target specific chromosomal regions. This research is in progress with the established immortal RIL population and genetic map.

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