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ORIGINAL PAPER

Quantitative trait loci mapping of leaf angle and leaf orientation value in maize (*Zea mays* L.)

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Abstract A major limiting factor for high productivity of maize (*Zea mays* L.) in dense planting is light penetration through the canopy. Plant architecture with a narrower leaf angle (LA) and an optimum leaf orientation value (LOV) is desirable to increase light capture for photosynthesis and production per unit area. However, the genetic control of the plant architecture traits remains poorly understood in maize. In this study, QTL for LA, LOV, and related traits were mapped using a set of 229 $F_{2:3}$ families derived from the cross between compact and expanded inbred lines, evaluated in three environments. Twenty-five QTL were detected in total. Three of the QTL explained 37.4% and five of the QTL explained 53.9% of the phenotypic variance for LA and LOV, respectively. Two key genome regions controlling leaf angle and leaf orientation were identified. qLA1 and qLOV1 at nearest marker umc2226 on chromosome 1.02 accounted for 20.4 and 23.2% of the phenotypic variance, respectively; qLA5 and qLOV5 at nearest bnlg1287 on chromosome 5 accounted for 9.7 and 9.8% of the phenotypic variance, respectively. These QTL could provide useful information for marker-assisted selection in improving performance of plant architecture with regard to leaf angle and orientation.

Introduction

Maize is one of the most important cereal crops worldwide, and increasing grain yield per acre has been one among the most important goals of maize production. Several decades of breeding effort striving for consistent performance under high-density plantings have enhanced the genetic gain of yield. The remarkable importance of plant architecture in maize is well underlined by the retrospective analysis of the hybrids (Russell 1984, 1985, 1991; Duvick 1977, 1992, 2005; Tollenaar and Wu 1999; Troyer 2001; Duvick and Cassman 1999; Sakamoto et al. 2006). Among the agronomic traits that have changed markedly as a result of selection, plant architecture, e.g. leaf angle, has played a predominant role in adaptation to the historical increase (ca. fourfold) that has occurred in plant density from 1950 to the present (Duvick 2005). With arable land gradually decreasing, it is likely that planting density will continue to be a target for selection in the years ahead (Kebrom and Brutnell 2007). Therefore, breeding of maize with optimized plant architecture is regarded as one of the most important goals to improve maize yield.

Two parameters, leaf angle and leaf orientation value, can be used to evaluate the efficiency of plant architecture. While leaf angle (LA) is the main plant architecture trait influencing the penetration of light into the canopy in maize, varieties with similar LA, but different rigid length from the leaf collar to the flagging point (where leaf blade and soil surface become parallel) have different capacities to capture light. Leaf orientation value (LOV) was proposed by Pepper et al. (1977) to further explain the above phenotypic difference (see detailed illustration in Fig. 1 and formula 1). LOV was affected by LA and the ratio between the length from leaf collar to flagging point and the entire length of the leaf. In densely planted stands, maize plants with a relatively

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Fig. 1 Schematic explaination of θ, L_f, and LL. θ leaf angle, L_f the length from the beginning of the ligula to flagging point of the leaf, *LL* the length from the beginning of the ligula to tip of the leaf (LL = $L_f + B$); LOV is calculated from formula as shown in "Materials and methods"

wide leaf angle and lower leaf orientation value will increase leaf shade and decrease photosynthetic efficiency, whereas plants with relatively narrow leaf angle and high leaf orientation value will display a plant architecture that is more efficient in capturing light for photosynthesis, improving grain filling, and increasing grain yield. Thus, maize hybrids with an optimum light-allowing leaf angle are more productive. The liguleless2 hybrid has upright leaf angles, thus allowing more light penetration into the canopy, and a positive correlation has been suggested between the narrow leaf angle and higher crop yield (Pendleton et al. 1968; Lambert and Johnson 1978). When liguleless2 and normal hybrids were compared, an astounding 41.2% of grain yield increase was seen in erect leaf genotypes (Pendleton et al. 1968). The effects of leaf orientation and plant density on maize yield were evaluated using hybrids B14 × Oh43 and Oh43 × R177 with normal, liguleless1, and liguleless2 genotypes at three planting densities (Lambert and Johnson 1978). The results showed the liguleless2 hybrids had significantly higher yields relative to the normal leaf hybrids at the two highest planting densities (75,000 and 90,000 plants/ha). A record high yield of 27,750 kg/ha was achieved with Pioneer® brand hybrid 34N44, which has a narrow leaf angle, at planting densities of 108,360 plants/ha in 2002 (Sun 2003).

A large body of QTL data for plant architecture, e.g. plant height, ear height, leaf length and width, tassel branch number and angle, and yield components, are currently available in maize (Berke and Rocheford 1995; Frova et al. 1999; Austin et al. 2001; Mickelson et al. 2002; Yan et al. 2003; Lima et al. 2006; Ribaut et al. 1996; Tang et al. 2007; Wang et al. 2008a, b). In rice, QTL for leaf and tiller angle have been researched extensively, and recent advances in the cloning and characterization of *LA1, TAC1, PROG1* and *OsLIC* have shed light on the molecular mechanisms that control tiller angle in rice (Li et al. 1999; Li et al. 1998; Qian et al. 2001; Yu et al. 2005; Shen et al. 2005; Xu et al. 1998; Yu et al. 2007a, b; Wang et al. 2008a, b; Chen et al. 2008; Li et al. 2007; Tan et al. 2008; Jin et al. 2008). However, only three QTL mapping studies for leaf angle and leaf orientation in maize have been published (Mickelson et al. 2002; Yu et al. 2006; Lu et al. 2007). Mickelson et al. (2002) identified nine QTL for leaf angle, and speculated that the QTL on chromosome 7 has an additive effect in the IBMRIL population. Lu et al. (2007) detected six QTL for leaf angle and eight QTL for leaf orientation in a $F_{2:3}$ population. The QTL on chromosome 3 and two QTL on chromosome 8 had an additive effect for leaf orientation, whereas all six QTL for leaf angle showed partial dominance or over dominance. Nine QTL for leaf angle were detected in two different $F_{2:3}$ populations and two QTL on chromosomes 1 and 2, respectively, indicated additive effects in one of the populations (Yu et al. 2006). Inconsistent results in terms of QTL locations have been found in the above studies, indicating that further investigations of the QTL underlying the phenotypic variance of these traits are needed.

Studies have supported that leaf angle, leaf orientation, and other morphological traits contribute to adaptation to dense planting and affect yield, so it is important to study the molecular mechanisms of these traits. However, the molecular basis of leaf angle and leaf orientation value remains unknown to date. The objectives of this experiment were to (1) identify further genomic regions of QTL for leaf angle and leaf orientation, (2) estimate the magnitude and type of their genetic effects, and (3) provide information for fine mapping and marker-assisted selection.

Materials and methods

Population development

Yu82 was crossed with Shen137 during the spring of 2005 at the Scientific Research and Education Center of Henan Agricultural University near Zhenzhou, Henan, China.

During the winter of 2005, F_1 plants were self pollinated at Sanya, Hainan, China. In the spring of 2006, F_2 plants from a single F_1 ear were self pollinated to develop 229 $F_{2:3}$ families. The 229 F_2 individuals served as the mapping population and 229 $F_{2:3}$ families were used to identify quantitative trait loci (QTL) for leaf angle, leaf orientation value, leaf length, leaf width, plant height, and ear height.

The parents of this population were chosen based on distinct plant architecture and maize germplasm groups. Yu82 is an inbred line with compact plant architecture derived from a Chinese Stiff Stalk germplasm, a heterotic group used broadly in China, while Shen137 is an inbred line with expanded plant architecture derived from a Chinese non-Stiff Stalk germplasm, also a heterotic group used broadly in China.

Field trials and trait evaluation

The 229 $F_{2:3}$ families, two parents and F_1 were evaluated in three environments: Sanya, Hainan province, in the winter of 2006 and Zhengzhou, Henan province, during 2007 and again in 2008. Each field experiment followed a randomized complete block design with three replications. Each plot included one row that was 4 m long and 0.67 m wide, with a total of 15 plants at a density of 52,500 plants/ha.

Ten days after pollen shed, five consecutive plants from the middle of each plot were chosen for evaluation of the six morphological traits: leaf angle (LA), leaf orientation value (LOV), leaf length (LL), leaf width (LW), plant height (PH), and ear height (EH). LA was determined for three consecutive leaves (the first leaf above uppermost ear, the leaf of the ear and the first leaf below the ear) as the angle of each leaf from a plane defined by the stalk below the node subtending the leaf. LL was determined for the three leaves as the length from the beginning of the ligula to tip of the leaf. LW was determined as the typical width across the widest portion of the leaf. LOV was calculated as follows:

$$\mathrm{LOV} = 1/n \sum (90 - \theta) \times (L_\mathrm{f}/\mathrm{LL}) \qquad (1)$$

where θ is the measured leaf angle, L_f is the length from beginning of ligula to flagging point of the measured leaves, LL is the leaf length, and n is the number of leaves measured (Pepper in 1977). A schematic explanation is shown in Fig. 1. PH was measured from the ground to the top of the tassel and EH was measured from the ground to the node of the ear. Trait values for each family were reported as the average from five plants in each replication. The overall performance was the average over the three experimental environments.

Broad-sense heritability (h^2) for each trait was computed according to Knapp et al. (1985). The heritability was calculated as follows:

$$h^2 = \sigma_\mathrm{g}^2 / \left(\sigma_\mathrm{g}^2 + \sigma_\mathrm{ge}^2/n + \sigma_\mathrm{e}^2/nr \right)$$

where σ_g^2 is the genetic variance, σ_ge^2 is genotype-by-environment interaction, σ_e^2 is the error variance, r is the replication number, and n is the number of environments. The estimates of σ_g^2, σ_ge^2, and σ_e^2 were obtained by analysis of variance (ANOVA) using the general linear model procedure of the statistical software SPSS 12.0. Simple Pearson correlation coefficients (r) were calculated between the traits, using the adjusted means of the $F_{2:3}$ families.

Molecular linkage construction and QTL analysis

A total of 896 pairs of simple sequence repeat (SSR) markers were chosen from the maize genome database (maizeGDB; http://www.maizegdb.org) to detect polymorphisms between the two parents. Ultimately, 222 markers that clearly had distinct co-dominant segregation were used to genotype the 229 F_2 individuals. Linkage analysis was done with the software package Mapmaker/Exp version 3.0 at the LOD threshold of 3.0 (Lander et al. 1987). Chi-square values were generated for each marker to test for expected segregation ratios.

QTL mapping was done using the composite-interval mapping method of Windows QTL cartographer version 2.5 software (Wang et al. 2007). For CIM, Model 6 of the Zmapqtl module was used for detecting QTL and their effects. The genome was scanned at every 2 cM, with a window size of 10 cM to exclude control markers (covariates) around the tested interval (Tang et al. 2007; Trachsel et al. 2009). Five control markers were identified by forward and backward regression. Empirical threshold levels for declaring QTL significant at the 5% genome wide type I error level were obtained by performing 1,000 random permutations. Additive and dominance effects of the detected QTL were also estimated by the Zmapqtl procedure.

Gene action was determined by the ratio of the absolute value of the estimated dominance effect divided by the absolute value of the estimated additive effect following Stuber et al. (1987) (additive 0–0.20, partial dominance 0.21–0.80, dominance 0.81–1.20, over dominance >1.20).

Results

Performance of leaf angle, leaf orientation value, and other morphological traits

Some differences were seen among traits between the two parents (Table 1). The leaf angle for parent Yu82 (P_1) was 20.1° less than the angle for parent Shen137 (P_2).

Table 1 Leaf angle, leaf orientation value, and other agricultural traits in the $F_{2:3}$ population and its parents

Population	LA (degree)	LOV	LL (cm)	LW (cm)	PH (cm)	EH (cm)
yu82 (P_1) (mean)	16.83 ± 0.23	73.10 ± 0.40	78.87 ± 0.42	7.60 ± 0.10	176.87 ± 0.71	51.63 ± 0.69
shen137 (P_2) (mean)	36.93 ± 0.21	38.80 ± 0.36	84.53 ± 0.31	8.80 ± 0.13	195.03 ± 0.75	77.13 ± 0.72
F_1 (mean)	26.67 ± 0.18	53.70 ± 0.39	96.23 ± 0.36	10.30 ± 0.12	227.97 ± 0.67	85.30 ± 0.62
$F_{2:3}$ population						
Mean	27.50 ± 2.26	55.85 ± 4.13	85.90 ± 2.94	8.89 ± 0.40	201.04 ± 8.65	69.12 ± 6.01
Range	19.45–35.04	44.82–69.12	77.42–94.13	7.51–9.94	174.14–221.07	53.07–88.07
Skewness	0.06	0.105	−0.23	−0.12	−0.25	−0.07
Kurtosis	0.21	−0.04	0.24	0.16	−0.16	0.14
σ^2_g	613.73	142.8	70.48	1.27	52.73	279.54
σ^2_{ge}	402.64	48.82	44.39	0.88	17.28	192.98
σ^2_e	74.88	11.98	13.25	0.42	6.645	39.32
H^2_B	81.15	89.03	81.25	78.92	89.03	72.95
Confidence interval	78.66–86.88	84.36–93.25	73.68–88.42	69.82–85.63	84.36–93.25	63.56–80.76

LA leaf angle, *LOV* leaf orientation value, *LL* leaf length, *LW* leaf width, *PH* plant height, *EH* ear height, σ^2_g genotypic variance of measured traits, σ^2_{gy} genotype and environment interaction variance of measured traits, σ^2_e residual error variance of measured traits, H^2_B the broad-sense heritability of measured traits, *confidence interval* the confidence intervals of broad-sense heritability between 5 and 95% significance levels

Similarly, the leaf orientation value for P_1 was 34.4 higher than the value for P_2. However, LL, LW, PH, and EH of the Yu82 parent were 5.7, 1.2, 18.1, and 25.5 cm shorter than the same traits in the P_2, respectively. The values for LA and LOV for the F_1 plant were between the values measure for P_1 and P_2. Values of the other four traits were higher in the F_1 than in the highest value parent (P_2). The values of the measured traits among $F_{2:3}$ families showed a pattern of continuous distribution around the mean (Table 1). Broad-sense heritability for LA, LOV, LL, LW, PH, and EH reached 81.2, 89.0, 81.3, 79.0, 89.0 and 73.0%, respectively (Table 1).

The six measured traits were phenotypically correlated (Table 2). LA showed the most significant negative correlation to LOV ($r = -0.72$) and LOV had the most significant negative correlation to EH ($r = -0.33$). LL had the most significant positive correlation to PH ($r = 0.52$) and also a significant positive correlation to EH ($r = 0.23$). PH showed the most significant positive correlation to EH ($r = 0.55$).

SSR data analysis and genetic linkage map construction

The percent of missing data in the genotyping of the mapping population across 222 SSR loci was low (2.96%). Statistical tests showed that most of the 222 SSR markers followed the expected 1:2:1 ratio. The linkage map consisted of all ten maize chromosomes allocated to ten linkage groups, spanning a total length of 1864.7 cM with an average marker interval of 8.40 cM (Fig. 1). 220 of the 222 SSR loci in this linkage map were consistent with the chromosome bin locations in the maizeGDB maps. Two loci, ZCT421 and umc1987, on chromosome 1 and 7, respectively, in maizeGDB map were located on chromosome 4 and 2, respectively.

Table 2 Correlation coefficients between leaf angle, leaf orientation and other morphological traits in the $F_{2:3}$ population

Trait	LA	LOV	LL	LW	PH
LOV	−0.72**				
LL	−0.15	0.05			
LW	0.15	0.08	0.14		
PH	−0.01	−0.13	0.52**	0.11	
EH	0.12	−0.33**	0.23*	0.14	0.55**

LA leaf angle, *LOV* leaf orientation value, *LL* leaf length, *LW* leaf width, *PH* plant height, *EH* ear height

* Significant at $P < 0.05$; ** Significant at $P < 0.01$

QTL analysis

QTL for LA, LOV, and other morphological traits were mapped to all maize chromosomes except for chromosome 6 and chromosome 8 (Table 3; Figs. 1, 2). Among 25 QTL detected for the traits, three were associated with LA, five were associated with LOV, and 17 were associated with other morphological traits.

The three QTL associated with LA were located on chromosomes 1, 2, and 5, and together contributed 37.4% of the phenotypic variance (individual variance ranged from 7.3 to 20.4%). The QTL, qLA1, located on chromosome 1, showed additive effect, accounting for 20.4% of the phenotypic variance. The other two QTL were detected on chromosome 2 and chromosome 5 and showed partial

Table 3 QTL for LA, LOV, LL, LW, PH and EH based on combined data across environments for 229 $F_{2:3}$ families

Trait	Chr.	QTL	Closest marker	Position (cM)	Support interval (cM)	LOD	Gene effect		R2	Gene action[c]	$LOD^{d}_{0.05}$
							Additive[a]	Dominant[b]			
LA	1	qLA1	umc2226	51.5	48.7–53.5	10.8	2	−0.4	20.4	A	3.2
	2	qLA2	Phi328189	125.7	123.7–127.7	3.8	1.2	−0.5	7.3	PD	
	5	qLA5	bnlg1287	58.9	56.9–68.0	4.7	1.4	−0.9	9.7	PD	
LOV	1	qLOV1	umc2226	51.1	48.7–53.5	11	−2.5	−0.7	23.2	A	3.2
	4	qLOV4	umc1999	212.6	210.6–216.8	3.3	−1.7	0.4	5.6	PD	
	5	qLOV5	bnlg1287	58.9	56.9–68.0	4.9	−2.2	0.3	9.8	PD	
	9	qLOV9a	umc2130	75.2	71.2–80.7	4	−0.9	−0.8	7.7	OD	
	9	qLOV9b	dupssr29	168.7	164.1–172.4	3.6	−1.7	0.2	7.6	A	
LL	7	qLL7a	umc1015	68.2	62.2–72.3	5.5	2.2	−0.4	14.3	A	3.1
	7	qLL7b	umc2190	123.6	119.4–125.6	3.7	−1.9	0.4	8	PD	
	10	qLL10	Phi059	36.1	30.1–38.3	4.1	−1.1	0.8	9.9	PD	
LW	1	qLW1	umc1085	291.4	287.4–300.3	3.9	−0.2	0.2	8.7	PD	3.3
	3	qLW3	umc2258	90.4	85.1–94.4	9.2	0.3	0.1	20.4	PD	
	7	qLW7	bnlg339	73.2	70.2–81.2	5.8	0.3	−0.2	9.6	PD	
	9	qLw9	umc1657	135.1	129.1–139.2	7.2	0.3	0	12.6	A	
PH	2	qPH2	umc1622	10.9	5.0–14.9	3.7	−4.2	5.7	7.8	OD	3.0
	3	qPH3	unc2127	124.6	120.0–126.6	3.2	−5.2	2.7	6.5	PD	
	7	qPH7	umc2325	36.3	32.3–40.3	5.7	7.3	−3.5	16	PD	
EH	1	qEH1a	umc2226	51.1	48.7–53.5	3.7	3.3	−1.7	6.5	PD	3.0
	1	qEH1b	umc2029	269.1	265.1–271.9	4.1	−3.3	0.9	6.8	PD	
	4	qEH4a	mmc0371	95.9	91.9–97.9	3.1	2.5	0.2	6.7	A	
	4	qEH4b	umc2046	212.6	210.6–216.8	7	2.2	2.2	12.1	D	
	7	qEH7a	umc2325	36.3	32.3–40.3	3.1	3.7	−2.2	6.4	PD	
	7	qEH7b	umc1015	68.2	62.2–72.3	5.6	4.6	−2.9	11.9	PD	
	10	qEH10	bnlg1655	46.6	44.3–50.6	4	2.7	−1.5	5.1	PD	

LA leaf angle, *LOV* leaf orientation value, *LL* leaf length, *LW* leaf width, *PH* plant height, *EH* ear height, *$LOD_{0.05}$* logarithm of odds at $P < 0.05$ significance level, R^2 contribution rate

[a] Additive effect: positive values indicated that Shen137 carries the allele for an increase in the traits, while negative values indicated that Yu82 contributed the allele for an increase in the trait value

[b] Dominance effects were doubled because $F_{2:3}$ families were used rather than F_2 individuals

[c] Gene action was estimated by (d)/(a): *A* (additive effect) 0–0.2, *PD* (partial dominance) 0.21–0.80, *D* (dominance) 0.81–1.20 and *OD* (over dominance) >1.20

[d] $LOD_{0.05}$ logarithm of odds threshold at $P < 0.05$ genomewide risk level

dominance and accounted for 9.7 and 7.3% of the variance, respectively. All the alleles decreasing LA were contributed by Yu82 (P_1).

The five QTL affecting LOV were located on chromosomes 1, 4, 5, and 9, and accounted for 53.9% of phenotypic variance, with individual effects ranging from 5.6 to 23.2%. The QTL qLOV9a on chromosome 9 showed overdominance and accounted for 7.7% of phenotypic variance. Three QTL detected on chromosomes 1 and 9, respectively, showed an additive effect, while two QTL on chromosome 4 and 5 showed partial dominance. All the alleles associated with increased LOV were contributed by Yu82 (P_1).

The three QTL for LL were detected on chromosomes 7 and 10, and accounted for 32.2% of the phenotypic variance, with individual effects ranging from 8.0 to 14.3%. The QTL qLL7a located on chromosome 7 showed an additive effect. The other two QTL BC3F3 population with the markers developed from the target region (Chen Y., personal communication) detected on chromosome 7 and 10 showed partial dominance. All the alleles for shortened LL were contributed by Shen137 (P_2)$_,$ except for qLL7a.

The four QTL were associated with LW on chromosomes 1, 3, 7, and 9. These four QTL accounted for 51.3% of the phenotypic variance, with individual effects ranging

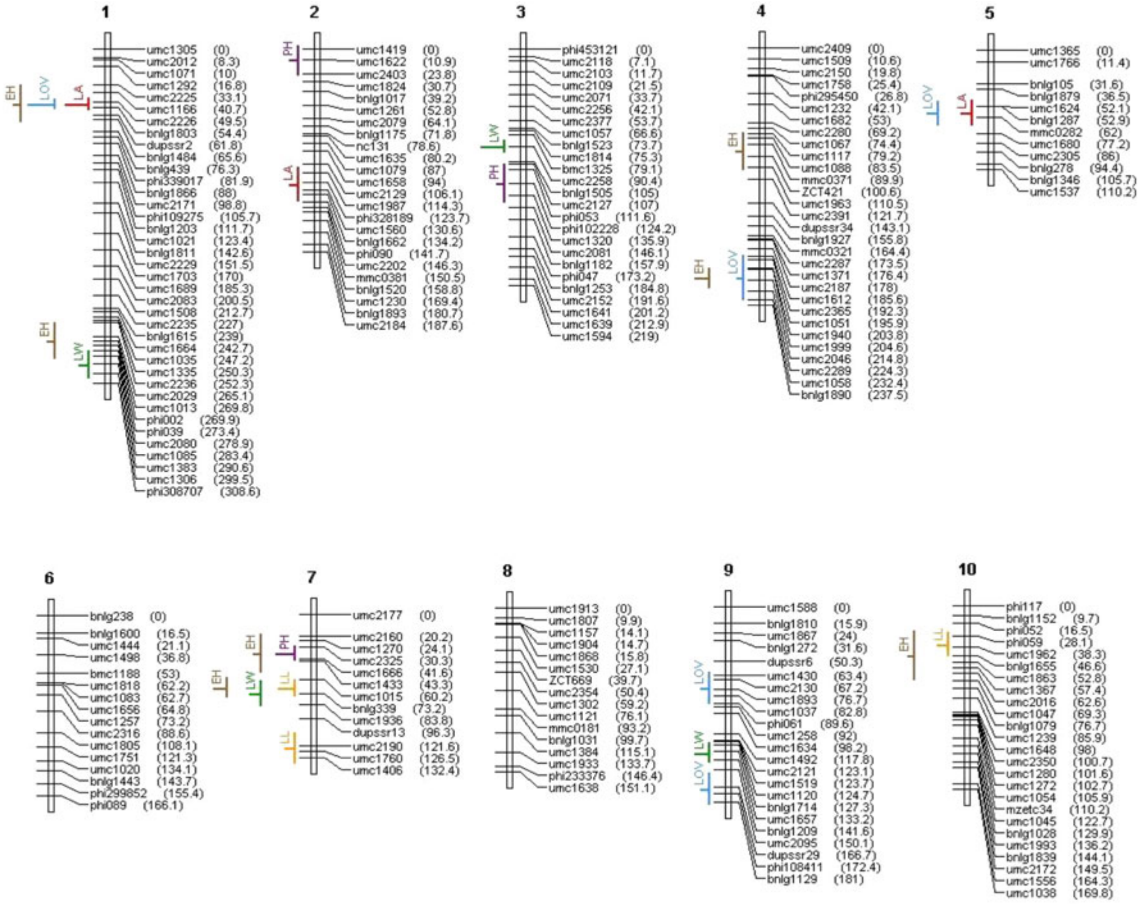

Fig. 2 The QTL detected for leaf angle, leaf orientation value, leaf value, leaf length, leaf width, plant height and ear height

from 8.7 to 20.4%. The QTL on chromosome 9 had an additive effect, while the other three QTL on chromosomes 1, 3, and 7 showed partial dominance. All the alleles for narrower LW were contributed by Yu82 (P_1), except for one QTL on chromosome 1.

The three QTL related to PH were identified on chromosomes 2, 3, and 7, and accounted for 30.3% of the phenotypic variance, with individual effects ranging from 6.5 to 16.0%. The QTL on chromosome 3 and 7 showed partial dominance, while one QTL on chromosome 2 showed over-dominance. All alleles associated with increased PH were contributed by P_1, except one QTL on chromosome 7 contributed by P_2.

The seven QTL for EH mapped on chromosomes 1, 4, 7, and 10 accounted for 55.5% of the phenotypic variance, with individual effects ranging from 5.1 to 12.1%. Of these seven QTL, five showed partial dominance, one, qEH4a on chromosome 4, showed an additive effect. The QTL qEH4b accounted for 11.9% of variance and showed dominance. Alleles related to increased EH were contributed by P_2 for six out of these seven QTL.

Discussion

Maize plant architecture is an important agronomic trait and has long attracted attention of breeders for achieving ideal plant architecture to improve grain yield, focusing especially on leaf architecture and angle, internode elongation, and tassel morphology. One of our interests was to investigate genetic controls underlying leaf angle and leaf orientation value for maize architecture improvement. A few QTL for leaf angle and leaf orientation value have been detected in previous studies (Mickelson et al. 2002; Yu et al. 2006; Lu et al. 2007), but chromosome regions on which the QTL have been located vary across studies. In this study, we have identified major QTL affecting leaf angle and leaf orientation value in 229 $F_{2:3}$ families derived from compact and expanded inbred line cross and evaluated in three environments. Among these QTL, three for leaf angle were detected on chromosomes 1, 2, and 5 and individual effects ranged from 7.3 to 20.4%, while five QTL for leaf orientation value were detected on chromosomes 1, 4, 5, and 9 and individual effects ranged from 5.6

to 23.2%. As far as genetic effects and actions were concerned, their additive effects were more important than dominant effects (additivity and partial dominance in general, Table 3).

Two key genome regions controlling leaf angle and leaf orientation were identified from our study. The QTL on chromosome 1 displayed the largest additive effect, and another QTL on chromosome 5 showed the largest partial dominance for leaf angle and leaf orientation value. All QTL were contributed by Yu82 for decreasing leaf angle and increasing leaf orientation value.

The important QTL associated with LA on chromosome 1

An important QTL, qLA1, for LA was identified in the 1.02 region of chromosome 1 (close to umc2226). A decrease by 2.0° was observed for the compact alleles at the qLA1 loci. Yu et al. (2006) also found QTL for LA in the bin 1.02 region of chromosome 1 (close to bnlg1429), which had additive effect and explained 14% of the phenotypic variance in $F_{2:3}$ families derived from H21 × Mo17 cross. Our and Yu's results suggest that qLA1 for LA in the bin 1.02 region of chromosome 1 is a major effect QTL in different genetic backgrounds and environments. Furthermore, QTL associated with LOV and EH were also detected in this region, "compact alleles" increasing LOV by 2.5 and decreasing EH by 3.3 cm. These results together suggest there might be crucial genes for these traits in this region. According to Sakamoto et al. (2006), this region is synthenic to a rice region which contains an ortholog of the rice *osdwarf4-1*. The *osdwarf4-1*shows slight dwarfism and erect leaves without undesirable phenotypes. *OsDWARF4* is a homolog of *A. thaliana DWARF4*, which encodes a cytochrome P450 and catalyzes C-22 hydroxylation, the rate-limiting step of brassinosteroid biosynthesis (Sakamoto et al. 2006). Thus, *osdwarf4-1* gene appears as a good candidate for qLA1. To identify if qLA1 is in fact orthologous to *osdwarf4-1*, a gene-specific marker should be developed and used to confirm co-segregation between the QTL and orthologous gene of *osdwarf4-1* in a large mapping population. This work is currently underway in our lab (see below).

Another important QTL associated with LA on chromosome 5

The other important QTL, qLA5, for LA was identified on chromosome 5 between bnlg1287 and mmc0282. A decrease by 1.4° was observed for the compact allele at the qLA5 loci. Mickelson et al. (2002) also detected one QTL for LA on chromosome 5 (nearest marker bnl5.02) with LOD scores of 9.90 and 10.98 evaluated in two environments using the IBMRIL population. Lu et al. (2007) also found QTL for LA on chromosome 5 (interval between umc1822 and phi048), explaining 8.65% of the phenotypic variance in $F_{2:3}$ families derived from Ye478 × D340 cross. In addition, a QTL associated with LOV was also detected in this region, with compact alleles increasing LOV by 2.2. The consistent identification of a QTL on chromosome 5 by different researchers suggested that this region includes a crucial gene(s).

Yabby15 gene involved in leaf development was located in the vicinity of qLA5 according to information of the maizeGDB database. *Yabby15* was one of the maize *yabby* gene family expressed on the adaxial side of incipient and developing leaf primordia. A genetic pathway involving *yabby* genes integrated positional information within the shoot apical meristem and led to adaxial/abaxial patterning and mediolateral outgrowth of the leaf (Juarez et al. 2004). This suggests *Yabby15* was required for the specification of the adaxial/upper leaf surface (regulating leaf angle). Further fine mapping and identification of a gene specific marker are essential to confirm whether the QTL is *Yabby15*. Positional cloning can be done using near-isogenic lines (NILs) constructed using main effect QTL identified for LA to further explore mechanisms of leaf angle regulation and validate the identity of the gene controlling the trait.

QTL application of maize plant architecture improvement

Crop plants with desirable architecture are excellent targets for genetic selection to enhance grain yields. One of the greatest successes of the Green Revolution, which led to major increases in production per unit area, was based on the modification of plant architecture (Khush 2001). Li (2001) has also developed the idea that improving plant architecture is a powerful way to increase planting density and further enhance production per unit area. In China, a commercial hybrid DH3719 associated with narrow leaf angle, at planting densities of 102,075 plants/ha, set a record high yield of 21,043 kg/ha under the conditions of short summer season (Yang et al. 2007). Erect leaves enhance light capture for photosynthesis, serve as nitrogen reservoirs for grain filling and enable more dense plantings with a higher leaf area index, and then increase yield (Sinclair et al. 1999). Therefore, a complementary strategy for plant productivity improvement is to develop varieties displaying more erect leaves. In this study, we detected QTL for LA, LOV, and EH located in clusters within a 4.8 cM interval in the chromosome 1.02 region. These QTL explain 20.4% of the phenotypic variance in LA, favorable alleles being contributed by Yu82. Therefore, the QTL for LA and LOV in this study could facilitate MAS for maize architecture improvement to create hybrids with ideal plant architecture that are more appropriate for high-density planting. We selected for all favorable (compact plant architecture) alleles identified and developed a plant with 19.82° leaf angle and 70.06 leaf orientation value in a BC2F2 population of Yu82 × Shen137 (Yu82 as donor) genetic background. The plant was selected in a BC2F2 population of 1,328 plants, where the recovery rate of Shen137 genetic background reached 98.4% using foreground selection based on markers umc1166 and umc2226 and background selection with 100 markers, in the field trial during the spring of 2008. The inbred line with compact plant architecture and Shen137 genetic background was developed from this plant. Hybrids with optimized plant architecture derived from this inbred line are being tested with regard to yield in different environments. In addition, recombinant plants from BC2F2 population were backcrossed with Shen137 and then selfed to develop BC3F3 population. The QTL is presently delimited to an interval of 0.7 Mb according to the fine mapping of BC3F3 population with the markers developed from the target region (Chen Y., personal communication) Therefore, the results of this study may provide valuable information for the further identification and characterization of genes responsible for leaf angle and leaf orientation.

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