

## Molecular mapping in tropical maize (*Zea mays* L.) using microsatellite markers. 2. Quantitative trait loci (QTL) for grain yield, plant height, ear height and grain moisture

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A previous genetic map containing 117 microsatellite loci and 400 F<sub>2</sub> plants was used for quantitative trait loci (QTL) mapping in tropical maize. QTL were characterized in a population of 400 F<sub>2,3</sub> lines, derived from selfing the F<sub>2</sub> plants, and were evaluated with two replications in five environments. QTL determinations were made from the mean of these five environments. Grain yield (GY), plant height (PH), ear height (EH) and grain moisture (GM) were measured. Variance components for genotypes (G), environments (E) and G × E interaction were highly significant for all traits. Heritability was 0.69 for GY, 0.66 for PH, 0.67 for EH and 0.23 for GM. Using composite interval mapping (CIM), a total of 13 distinct QTLs were identified: four for GY, four for PH and five for EH. No QTL was detected for GM. The QTL explained 32.73 % of the phenotypic variance of GY, 24.76 % of PH and 20.91 % of EH. The 13 QTLs displayed mostly partial dominance or overdominance gene action and mapped to chromosomes 1, 2, 7, 8 and 9. Most QTL alleles conferring high values for the traits came from line L-14-4B. Mapping analysis identified genomic regions associated with two or more traits in a manner that was consistent with correlation among traits, supporting either pleiotropy or tight linkage among QTL. The low number of QTLs found, can be due to the great variation that exists among tropical environments.

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The development of high-density linkage maps based on molecular markers in maize and other major crops have allowed the investigations on the genetic basis of quantitative traits, commonly referred to as quantitative trait loci (QTL). Coupled with statistical procedures, along with the availability of computer software (LANDER and BOTSTEIN 1989; ZENG 1994; BASTEN et al. 1994, 1999), these maps provide information on the location and genetic effects of genomic regions affecting economically important quantitative traits. In maize, studies have reported several chromosome regions for QTLs, such as: resistance to biotic and abiotic stresses, morphological characters and grain yield (STUBER et al. 1992; EDWARDS et al. 1992; KOESTER et al. 1993; BEAVIS et al. 1994; AJMONE-MARSAN et al. 1995; LEE 1995).

Grain yield is one of the most important traits for maize breeding programs, but its evaluation and improvement are difficult and expensive to assess due to its complex biology, environmental interactions, and low heritability (HALLAUER and MIRANDA FILHO 1988). These characteristics have made grain yield the primary trait of interest for QTL mapping studies for marker-assisted selection (TANKSLEY 1993; LEE 1995). However, these studies for the detection of QTLs have been carried out mainly with temperate germplasm. There are fewer similar studies with tropical germplasm (BOHN et al. 1997; GROH et al. 1998; KHAIRALLAH et al. 1998). Tropical maize germplasm have a broad genetic base with greater variability than temperate synthetic materials (LANZA et al.

1997), and are exposed to a wide range of environmental stress, higher in the tropics than in temperate zones (RIBAUT et al. 1997). Analysis of QTL on tropical maize germplasm could identify novel genomic regions that have not yet been defined by alleles with quantitative effects.

Restriction fragment length polymorphisms (RFLP) have become the most widely used molecular marker in the genetic analysis of quantitative traits in maize (COE et al. 1995). However, the use of RFLPs in QTL analysis represents excessive labor and costs for the genotyping of large populations. The development of the polymerase chain reaction (PCR) (MULLIS and FALLONA 1987) has made the arising of highly informative markers for genetic mapping, including microsatellite sequences (LITT and LUTY 1989), possible.

Using a great number of PCR primers for maize microsatellites obtained through both database searches and random screening of genomic libraries, and available at MAIZE DATA BANK (2001), a genetic map in a tropical maize  $F_2$  population was recently developed (SIBOV et al. 2003). Following, 400  $F_{2:3}$  lines from the cross of two tropical maize inbred lines with replicated trials, across five environments were evaluated. The objectives of this study were (i) the detection of QTLs for grain yield, plant height, ear height and grain moisture in tropical maize germplasm that show consistency in expression across environments using the composite interval mapping (CIM) approach and the genetic map presented by SIBOV et al. (2003); (ii) determine the number, genomic positions, and gene effects of QTLs involved in the variation of grain yield (GY), plant height (PH), ear height (EH) and grain moisture (GM) in this material.

## MATERIAL AND METHODS

### *Plant material*

The mapping population used to obtain the genetic map, made up of 400  $F_2$  plants (SIBOV et al. 2003), was used to mapping QTLs. So as to increase the number of available seeds and allow the installation of experiments with increased experimental precision, 400  $F_{2:3}$  lines were obtained, by selfing these individual  $F_2$  plants, and the  $F_{2:3}$  lines were sib-mated by using 30 plants of each line.

### *Field trials*

Field trials were conducted at the Research Farms of the Departamento de Genética, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo (ESALQ/USP) in Piracicaba, SP (Southeast

Brazil) in 1999 and 2000. The  $F_{2:3}$  lines were evaluated in field experiments in five environments: Areão (1999 and 2000), Caterpillar (1999 and 2000), and Experimental area of the Department of Genetics (2000). Each site-year combination was treated as an environment in subsequent statistical analysis. The 400  $F_{2:3}$  lines were grown in four  $10 \times 10$  lattice design with two replications each. In order to cover the differences in the field area, the position of each one of the lattice replications was randomized. Thus, this disposal did not require that the replication of each lattice be placed side by side. Plots consisted of single rows, 0.8 m apart and 4 m long. Plots were overplanted and later thinned to a final plant density of 10 plants  $m^2$  with a total of 20 plants per row, corresponding to a planting density of 62,500 plants per hectare. At each location, plot size and management were in accordance with local practice.

Shortly after flowering, plant height (PH) and ear height (EH) were measured on five plants per plot: PH: as the distance (cm) from the ground to the point of insertion of the flag leaf; EH: as the distance (cm) from the ground to the node of attachment of the primary ear. After the plots were harvested, grain yield (GY) and grain moisture (GM) were measured: GY: the total weight (g) of hand harvested, shelled grain adjusted to 150 g  $kg^{-1}$  grain moisture; GM: moisture of a 200 g kernel sample from shelled grain from the total area of the plot measured by electronic equipment and converted to g  $H_2O kg^{-1}$ .

### *Field data analysis*

For all traits, means, standard deviations, and skewness of trait distribution were calculated. Grain moisture was log-transformed because it was not normally distributed. Analyses of variance were performed on the data from each environment. For each trait, adjusted means of the five trials were averaged to obtain trait values for the mean of the environments, which were used in the QTL analysis. From the combined analysis of variance across environments, estimates of variance components  $\sigma_g^2$  (genotypic variance),  $\sigma_{g \times e}^2$  (genotype-by-environment interaction variance) and  $\sigma_e^2$  (error variance) of  $F_{2:3}$  lines and their confidence intervals lines were calculated using the method of moments. Broad sense heritabilities ( $h^2$ ) were estimated as described by HALLAUER and MIRANDA FILHO (1988). Exact 90% confidence intervals of  $h^2$  were calculated according to KNAPP et al. (1985). All these analyses were performed using the SAS software (SAS INSTITUTE, 2001).

### *QTL mapping*

Microsatellite assays and the linkage analysis of the marker were previously described in SIBOV et al.

(2003). The same linkage map was used here. QTLs were mapped based on the adjusted means across the environment by the composite interval mapping method (CIM) proposed by ZENG (1993, 1994), using the QTLCartographer 1.15 version software (BASTEN et al. 1994, 1999). CIM is an extension of interval mapping (LANDER and BOTSTEIN 1989) and tests the hypothesis that an interval flanked by two adjacent markers contains a QTL affecting the trait, while statistically accounting for the effects of additional segregating QTL outside the tested interval, using multiple regression. The likelihood-ratio (LR) test statistic used is  $-2\ln(L_0/L_1)$ , where  $L_0/L_1$  is the ratio of the likelihood under the null hypothesis (there is no QTL in the interval) and the alternative hypothesis (there is a QTL in the interval).

We used Model 6 of the Zmapqtl module of QTL Cartographer, scanning intervals of 1 cM between markers and putative QTLs with a window size of 10 cM. The number of marker cofactors for background control was set by forward-backward stepwise regression. A genome-wide critical threshold value for the experiment wise type I error rate ( $\alpha = 0.10$ ) was set for each trait independently, by randomly permuting 1000 times the means among genotypes and using the empirical permutation false positive rate (CHURCHILL and DOERGE 1994). Stringent controls on type I error greatly increase the probability of rejecting a true QTL (a type II error). Thus, an alpha level of 0.10 was chosen to reduce the probability of a type II error. The estimation of the position, genetic effects and percentage of phenotypic variation of the QTL were carried out at the significant LR peak in the region under consideration.

The phenotypic variance explained by a single QTL was estimated by the square of the partial correlation coefficient ( $R^2$ ). Estimates of the  $R^2$  value, the addi-

tive and dominance effects of a QTL were also estimated by the Zmapqtl module. The total proportion of phenotypic variance explained were obtained by fitting a model including all QTL for the respective trait simultaneously, according to the procedures described by BOHN et al. (1996). The sign of the estimates was used to identify the favorable alleles contributed by each parent. For QTL main effects, positive and negative signs of the estimates indicate that L-14-4B and L-08-05F, respectively, contributed towards higher value alleles for the trait. Average levels of dominance of each QTL and across all QTL were calculated as the  $|d|/|a|$  ratio, with dominance effects,  $d$ , being the dominance effects estimated for the  $F_2$  population. Gene action was determined on the basis of the average level of dominance by using the criteria of STUBER et al. (1987): additive (A) = 0 to 0.20; partial dominance (PD) = 0.21 to 0.80; dominance (D) = 0.81 to 1.20; and overdominance (OD) > 1.20.

## RESULTS

### Field data analysis

For all the evaluated character, the confidence intervals and the coefficients of variation showed that the estimates for means, variance components and heritabilities of the  $F_{2,3}$  lines were obtained with good accuracy (Table 1). The means for GY, PH and EH were continuously distributed as expected for a quantitative trait, but GM had significant deviations from a normal distribution and the data was log-transformed. In combined analyses across environments, GY, PH and EH had highly significant differences among the lines and highly significant genotype  $\times$  environment interactions. But GM showed limited vari-

Table 1. Estimates of means, variance components and heritabilities of the  $F_{2,3}$  lines for grain yield (GY), plant height (PH), ear height (EH) and grain moisture (GM), taken from the corrected means of all trials.

Parameters	Grain yield (g/plant)	Plant height (cm)	Ear height (cm)	Grain moisture (gH <sub>2</sub> O/Kg)
Means <sup>a</sup>	57.69 $\pm$ 13.58	171.72 $\pm$ 9.84	85.60 $\pm$ 6.82	10.76 $\pm$ 0.70
$F_{2,3}$ lines				
Variances <sup>b</sup>				
$\sigma_g^2$	82.29	62.19	27.52	0.0103
	[67.84; 105.69]	[50.77; 77.96]	[22.54; 34.35]	[0.0096; 0.0110]
$\sigma_g^2 \times e$	93.09	78.18	29.78	0.0442
	[80.23; 109.32]	[68.39; 90.26]	[25.64; 35.01]	[0.0437; 0.0448]
$\sigma_e^2$	184.39	160.00	73.05	0.25
C.V.(%)	23.54	7.37	9.98	4.65
Heritabilities <sup>c</sup>	0.69	0.66	0.67	0.23
$h^2$ (90 % I.C)	[0.63; 0.73]	[0.60; 0.71]	[0.621; 0.72]	[0.15; 0.28]

<sup>a</sup> With standard errors.

<sup>b</sup> In Squared units, with confidence intervals (95 %)

<sup>c</sup> Exact 90 % confidence intervals of  $h^2$  were calculated according to KNAPP et al. (1985).

ability and the genotypic variance was 25 times lower than the error variance. Because the measurements were taken in five environments with two replications, the estimated broad-sense heritabilities were high due to the decrease in both the experimental errors and genotype-by-environment interaction. These heritabilities estimated from the mean environment for the 400  $F_{2:3}$  lines, were high for GY ( $h^2 = 0.69$ ), PH ( $h^2 = 0.66$ ) and EH ( $h^2 = 0.67$ ) and low for GM ( $h^2 = 0.23$ ) indicating the low genetic variability for this trait (Table 1).

#### QTL analysis

The gene actions, the directions of response and the QTLs detected using CIM for the traits are listed in Table 2 and illustrated in Fig. 1. For 1000 permutations, a genome-wide critical threshold value for each

trait was calculated ( $\alpha = 0.10$ ). These values were 16.01 for GY, 16.31 for PH, 15.78 for EH and 32.44 for GM. Determinations of QTL in the mean of the five environments yielded 13 “stable” QTLs which affected GY, PH and EH. The parent lines were not significantly different for GM, the trait did not segregate in the mapping population and no QTLs were mapped. The mapped QTL were located on chromosomes 1, 2, 7, 8, and 9.

#### Grain yield

For GY, 4 QTLs were detected on chromosomes 2 (*Gy2*), 7 (*Gy7*) and 8 (*Gy8a*, *Gy8b*) (Fig. 1, Table 2). These 4 QTLs together explain 32.73 % of the phenotypic variation. Individual QTL accounted for 5.22–11.18 % of the phenotypic variation. For two of the QTLs (*Gy8a* and *Gy8b*), alleles from L-08-05F con-

Table 2. Chromosomic location, effects and types of individual gene action of QTLs for grain yield (GY), plant height (PH) and ear height (EH) taken from the adjusted means of the  $F_{2:3}$  lines evaluated in five environments.

QTL	QTL position			LR <sup>b</sup>	Genetic effect <sup>c</sup>			Gene action <sup>d</sup>		
	Bin <sup>a</sup>	cM	Marker Interval		R <sup>2</sup>	a	d	d / a	Type	Direction
Grain yield										
<i>Gy2</i>	2.03–2.04	52.88	umc1845-bnlg0166	28.20	11.18	85.47	–96.76	1.13	D	L-14
<i>Gy7</i>	7.04–7.05	125.20	dupssr13-umc1154	26.38	8.35	80.39	61.39	0.76	DP	L-14
<i>Gy8a</i>	8.03–8.05	57.94	phi0115-bnlg1176	23.23	5.22	–77.62	–6.54	0.08	A	L-08
<i>Gy8b</i>	8.05–8.06	74.70	bnlg1176-bnlg1607	23.39	7.98	–91.46	29.30	0.32	DP	L-08
			Total <sup>e</sup> :		32.73		Total <sup>f</sup> :	0.67	DP	
Plant height										
<i>Ph1a</i>	1.04–1.05	79.38	bnlg2238-umc2025	17.55	5.87	–0.42	–5.08	12.08	SD	L-08
<i>Ph1b</i>	1.07–1.08	153.38	bnlg0615-phi0037	18.48	4.27	3.25	–0.54	0.17	A	L-14
<i>Ph2</i>	2.03–2.04	53.88	umc1845-bnlg0166	21.23	8.76	3.49	–4.29	1.23	SD	L-14
<i>Ph7</i>	7.04–7.05	117.20	dupssr13-umc1154	18.70	5.86	2.86	2.81	0.98	D	L-14
			Total:		24.76		Total:	3.56	SD	
Ear height										
<i>Eh1</i>	1.07–1.08	150.38	bnlg0615-phi0037	17.38	3.73	1.98	0.56	0.28	DP	L-14
<i>Eh7a</i>	7.01	35.70	umc1632-umc1409	16.95	3.66	1.69	–1.11	0.66	DP	L-14
<i>Eh7b</i>	7.03–7.04	91.70	bnlg0434-dupssr13	17.05	4.82	2.04	–0.41	0.20	A	L-14
<i>Eh7c</i>	7.04–7.05	119.20	dupssr13-umc1154	19.47	5.61	2.21	0.44	0.20	A	L-14
<i>Eh9</i>	9.02–9.03	1.01	umc1893-bnlg0430	16.11	3.09	–0.84	–2.42	2.89	SD	L-08
			Total:		20.91		Total:	0.69	DP	

<sup>a</sup> Bin locations are designated by an X.Y code, where X is the linkage group containing the bin and Y is the location of the bin within the linkage group (GARDNER et al. 1993).

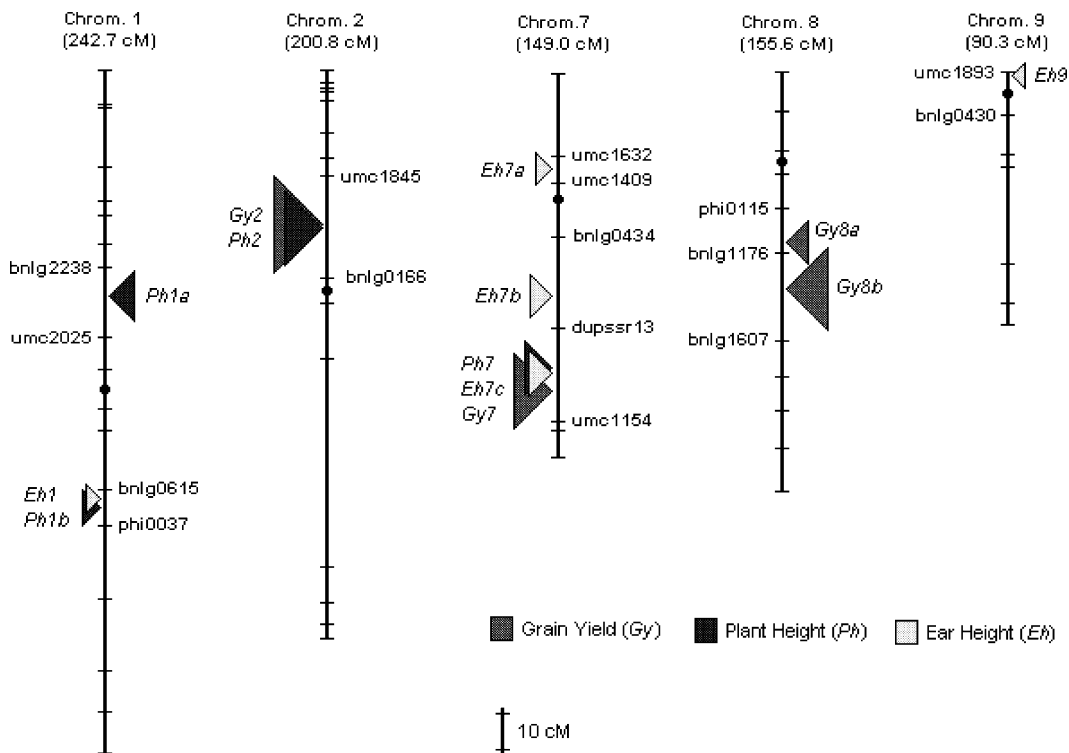
<sup>b</sup> Likelihood ratio test statistic.

<sup>c</sup> Additive (a): effect of the substitution of the L-08-05F allele by the L-14-4B allele. A negative value indicates that the L-08-05F allele diminishes the value of the trait. Dominance (d): effect of the L-08-05F allele on the L-14-4B allele. Positive values indicate that the heterozygote possess upper phenotypic values than the average of the two homozygotes. Negative values indicate that the heterozygote possess inferior phenotypic values than the average of the two homozygotes.

<sup>d</sup> Gene action was determined on the basis of the average level of dominance calculated as the ratio  $|d|/|a|$  by using the criteria of STUBER et al. (1987): additive (A) = 0 to 0.20; partial dominance (PD) = 0.21 to 0.80; dominance (D) = 0.81 to 1.20; and overdominance (OD) > 1.20.

<sup>e</sup> Total proportion of phenotypic variance explained were obtained by fitting a model including all QTL for the respective traits simultaneously, according to the procedures described by BOHN et al. (1996).

<sup>f</sup> Total gene action of all QTLs detected for the trait: weighed mean between the ratio  $|d|/|a|$  and the phenotypic variance explained by each QTL ( $R^2$ ).



**Fig. 1.** Genetic map of chromosomes 1, 2, 7, 8 and 9 in a population of tropical maize showing the location of the 13 QTLs associated with grain yield (GY), plant height (PH), ear height (EH). The vertex of each triangle point in relation to the chromosomal position with bigger value of the LR test for analyses using CIM. The size of each triangle is proportional to the values of the explained phenotypic variation ( $R^2$ ) for each QTL. The names of the loci that flank the interval where the QTL was detected are only indicated. Triangles to the right of each chromosome indicate contribution of alleles from the L-08-05F parental. Triangles to the left of each chromosome indicate favorable alleles from the L-14-4B parental.

tributed towards an increase of the trait values. For the other two QTLs (*Gy2* and *Gy7*), alleles from L-14-4B were going towards increasing the trait value. Dominance effects reached significance in three QTLs, whereas only 1 QTL (*Gy8a*) displayed additive gene action.

#### Plant height

Four QTLs were mapped for PH on chromosomes 1 (*Ph1a*, *Ph1b*), 2 (*Ph2*) and 7 (*Ph7*) (Fig. 1, Table 2) explaining 24.76 % of phenotypic variation. Individual QTL accounted for 5.86–8.76 % of the phenotypic variation. For three of these QTLs, alleles from L-14-4B were going towards increasing the trait values, whereas for the QTL on chromosome 1 (*Ph1a*), the allele from L-08-05F contributed to the increase of the trait score. The QTLs displayed significant dominant gene action with the QTL on chromosome 1 (*Ph1a*), showing a very large dominance effect. Due to this increased effect, the genetic action for the character was overdominance. Only 1 QTL displayed additive gene effects for PH (*Ph1b*) (Table 2).

#### Ear height

Five QTLs were detected for EH on chromosomes 1 (*Eh1*), 7 (*Eh7a*, *Eh7b*, *Eh7c*) and 9 (*Eh9*) (Fig. 1, Table 2) explaining 20.91 % of the phenotypic variation. Individual QTLs accounted for 3.66–5.61 % phenotypic variation. The majority of the QTLs, alleles from L-14-4B were going towards increasing ear height. For only one of these QTLs, alleles from L-08-05F were going towards increasing the trait values. Additive gene action occurred at two QTLs. The remaining QTLs displayed significant dominant gene effects.

#### QTLs groups

Taken together, only three QTLs (*Ph1a*, *Eh7a* and *Eh9*) were not mapped close to other QTLs (Fig. 1). The remaining 10 QTLs were detected in the same chromosomal regions, forming four groups of QTLs. The highest concentrations of QTLs were found in the dupssr13-umc1154 marker interval in chromosome 7 where QTLs for all three traits were detected. Each group of QTLs has the same parental alleles

contributing to increase trait values. Alleles from L-08-05F contributed to an increase of the trait values for the group on chromosome 8 (*Gy8a-Gy8b*). Due to the proximity of these peaks, it is possible that these two QTLs are really one single QTL. Alleles from L-14-4B contributed to an increase of the trait values for the remaining groups on chromosomes 1 (*Eh1-Ph1b*), 2 (*Gy2-Ph2*) and 7 (*Eh7b-Ph7-Eh7c-Gy7*).

## DISCUSSION

In this study, a total of 13 QTLs were identified for GY, PH and EH in tropical maize lines through the use of the mean across environments by replicated field trials and evaluations in five environments. Results for the detection of QTLs in maize (VELDBOOM and LEE 1996a,b; AUSTIN and LEE 1998) showed that the use of the average phenotypic value of the characters in different tested environments was an efficient approach to QTL detection, therefore considering only the most stable ones. According to KNAPP et al. (1990), the means across environments reduces the standard error of the values of the evaluated traits, increasing the precision and the power of mapping QTLs. In maize, several studies reported that QTL effects for grain yield, ear height and plant height are largely independent of the environment, despite the presence of significant genotype by environment interaction (STUBER et al. 1992; RAGOT et al. 1995; COCKERHAM and ZENG 1996; MELCHINGER et al. 1998). However, this does not seem to be the case, as the number of mapped QTLs was small, possibly due to the fact that the only QTLs found were those that show great effect and are very stable.

The estimates of the heritabilities for GY, PH and EH were relatively high, reflecting the use of averages of lines and the great amount of replications and environments tested, reducing the variance components of genotype-by-environment interaction and experimental error. Moreover, low heritabilities for GM can also be explained by the absence of genetic variability for this trait. The observed differences among the trials for GM should have been caused mainly by experimental errors, providing strong influence in the estimate of the variability and the accuracy in the detection of QTLs.

The L-08-05F and L-14-4B parental lines have contrasting traits for plant and ear height, kernel type, maturity and yield. L14-4B has a higher plant stature, higher yield and a late maturity cycle compared to inbred L-08-05F. These differences were noted in the results, due to the fact that L-14-4B contributed with alleles that increased the trait value

at 9 of the 13 QTL for GY, PH and EH (Table 2). Gene action for all QTLs, for the traits evaluated, was mainly dominance effects. Of these QTLs, 31 % exhibited partial dominance, 15 % dominance, 23 % overdominance, and the remainder 31 % exhibited additive effects. The PH and EH traits usually have high heritability and additive gene action or partial dominance for QTL affecting these traits. The specific gene action affecting these traits depends on the materials and experimental conditions employed (VELDBOOM et al. 1994; RAGOT et al. 1995; AUSTIN and LEE 1996; KHAIRALLAH et al. 1998). Gene action for EH is in agreement with former studies, but overdominant gene action for PH was surprising. This result is due mainly to a QTL (*Ph1a*) which had dominance effects several times greater than the corresponding additive effects (Table 2). This kind of gene action may reflect the effects of several QTLs within the genomic interval under study, a situation that would tend to result in overestimation of dominance.

In diverse studies for the mapping of QTLs, individual QTLs explained the great percentage of the phenotypic variation, with a range from 25 % to 35 % (RAGOT et al. 1995; STUBER et al. 1992; AJMONE-MARSAN et al. 1995; VELDBOOM and LEE 1994; BEAVIS et al. 1994; JIANG et al. 1999). QTLs with sharp effects were not detected in this study, possibly because only stable QTLs across environments are being mapping in this research. For all the characters, the majority of the QTLs detected had small effects, explaining less than 10 % of the phenotypic variation. Only a QTL for GY had a higher effect, explaining 11.18 % of the variation. In all, the ratio of the phenotypic variation explained by all the QTLs detected for each character was 32.73 % for GY, 24.76 % for PH and 20.91 % for EH. The phenotypic variation not explained by the QTLs detected in this population can be due to: 1) the QTLs in regions not mapped in the genome; 2) QTLs with small effect not detected; 3) epistatic effect between QTLs.

Genomic regions significantly involved with the evaluated features were detected in five out of the ten chromosomes of the maize. An important consideration in the detection of QTLs is if the location and the estimated effect of a QTL detected in a population can be observed in other populations (LEE 1995). The direct matching of results of the mapping of QTLs between different studies becomes difficult, due to the differences in methodology, in the size and the type of the mapped populations, to the lack of common marker loci and to different tested environments (LEE 1995; BEAVIS 1994). Moreover, tropical germplasm was used in this work, while in the majority of the other works in maize used crossings be-

tween temperate germplasms. However even considering these limitations, some QTLs had been detected next to mapped regions, in other studies. For GY, between 2.03 and 2.04 bins, BEAVIS et al. (1994), RIBAUT et al. (1997) and MELCHINGER et al. (1998) also found QTLs. Various authors also found QTLs (BEAVIS et al. 1994; AUSTIN and LEE 1996; RIBAUT et al. 1997; MELCHINGER et al. 1998), in the region between 7.04 and 7.05 bins and also between bins 8.03 and 8.05 (BEAVIS et al. 1994; AGRAMA and MOUSSA 1996; AUSTIN and LEE 1996; RIBAUT et al. 1997; MELCHINGER et al. 1998). For PH, the QTLs mapped closer were also located by other authors on chromosome 1 (BEAVIS et al. 1991; KOESTER et al. 1993; SCHON et al. 1994; VELDBOOM et al. 1994; BERKE and ROCHEFORD 1995; VELDBOOM and LEE 1996; LUBBERSTEDT et al. 1997; MELCHINGER et al. 1998; KHAIRALLAH et al. 1998) and on chromosome 2 (BEAVIS et al. 1991; VELDBOOM et al. 1994; LUBBERSTEDT et al. 1997; KHAIRALLAH et al. 1998; MELCHINGER et al. 1998). For EH, QTLs were found by other authors on chromosomes 1 and 7 (VELDBOOM and LEE 1996), and 9 (BEAVIS et al. 1991). These results seem to confirm the fact that the QTLs are normally located in clusters which contain genes that control development (KHAVKIN and COE 1998), and that these QTLs mapped here can represent regions which are common to various populations, which is extremely important to genetic improvement, as these QTLs can be successfully used in assisted selection programs. It is important to stress here that also in this case these QTLs are extremely stable, justifying even more their use and importance in assisted selection programs.

The distribution of the QTLs for the genoma showed a high concentration of QTLs in few chromosomal regions. Such a concentration in the distribution of QTLs have already been observed in previous studies (ABLER et al. 1991; STUBER et al. 1992; VELDBOOM and LEE 1994; AUSTIN and LEE 1998). PH and EH possess two common genomic regions in chromosomes 1 and 7 (Fig. 1). These morphologic characters were also mapped in regions very close to the QTLs for GY in chromosome 2 (*Gy2-Ph2*) and 7 (*Ph7-Eh7c-Gy7*). GY, PH and EH are positively correlated (HALLAUER and MIRANDA FILHO 1988), which is in agreement with what has been observed, as the QTLs of these characters were mapped in genomically similar regions. According to AASTVEIT and AASTVEIT (1993), there are three primary causes of correlation among traits: pleiotropy, linkage, and environmental effects. If the same QTL controls more than one different character or if each QTL is specific for a determined character, is something that is not clear. Only future studies, using more elaborated

statistical analyses, such as those presented by JIANG and ZENG (1995), will allow us to distinguish between these hypothesis. This type of research is very important, as the distinction between linkage and pleiotropy as a cause of correlation between characters can help decision making in improvement programs. If the cause of the correlation is linkage between QTLs, strategies can be adopted which allow it to be broken. In the case of pleiotropy, it is not possible to eliminate the effect for the QTL under debate. The mapping of QTLs in the mean environment (some replications and years), allowed the identification of QTLs with an effect on the production of grains, height of the plant and height of the ear in tropical maize germplasm. The QTLs consistently detected were identified in environments favoring their use in future programs for marker-assisted selection (MAS), if the objective is selecting stable QTLs. However, new methods of analysis will be necessary to increase the power of resolution of QTL mapping, incorporating more precise tests for the testing against pleiotropy vs linkage, the quantification of epistatic effects and the obtention of interaction estimates between QTLs and environments. If these questions are answered, the study of the quantitative characters will provide safe tools to answer basic questions on the genetic base of these traits in maize in general, and in tropical germplasm in particular.

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