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Molecular-marker-facilitated studies of morphological traits in maize. II: Determination of QTLs for grain yield and yield components

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Abstract Genetic factors controlling quantitative inheritance of grain yield and its components have not previously been investigated by using replicated lines of an elite maize (*Zea mays* L.) population. The present study was conducted to identify quantitative trait loci (QTLs) associated with grain yield and grain-yield components by using restriction fragment length polymorphism (RFLP) markers. A population of 150 random $F_{2:3}$ lines was derived from the single cross of inbreds Mo17 and H99, which are considered to belong to the Lancaster heterotic group. Trait values were measured in a replicated trial near Ames, Iowa, in 1989. QTLs were located on a linkage map constructed with one morphological and 103 RFLP loci. QTLs were found for grain yield and all yield components. Partial dominance to overdominance was the primary mode of gene action. Only one QTL, accounting for 35% of the phenotypic variation, was identified for grain yield. Two to six QTLs were identified for the other traits. Several regions with pleiotropic or linked effects on several of the yield components were detected.

Key words Restriction fragment length polymorphism (RFLP) · Quantitative trait loci (QTLs) · Plant breeding

Introduction

Investigations on the genetic basis of quantitative traits have been facilitated by the discovery and application of molecular markers. Restriction fragment length polymorphisms (RFLPs) have been used in many plant species to dissect genetic factors underlying quantitative traits in segregating populations. In maize, Edwards et al. (1987) and Stuber et al. (1987) studied morphological and yield-related traits by using isozyme markers and trait measurements made in populations of F_2 plants created by crossing very divergent inbred parents. Several traits have recently been studied in maize by using more saturated maps consisting of RFLP loci. These include thermotolerance (Ottaviano et al. 1991), low-phosphorous stress tolerance (Reiter et al. 1991), plant height (Beavis et al. 1991), resistance to *Exserohilum turcicum* (Freymark et al. 1993), resistance to second-generation corn borer (*Ostrinia nubilalis* Hübner) (Schön et al. 1993), morphological differences distinguishing maize from teosinte (Doebley et al. 1990), and several morphological and grain-yield component traits of F_2 plants (Edwards et al. 1992).

Breeders consider grain yield to be the most important trait in maize inbred development (Bauman 1981), but low heritability makes it one of the most difficult traits to evaluate and improve (Hallauer and Miranda 1988). Yield components such as kernel weight and ear length are correlated with grain yield and have higher heritabilities than grain yield itself (Hallauer and Miranda 1988). Knowledge of the interdependent nature of these traits has been limited to estimates of correlations and genetic effects over the entire genome. With molecular markers, our understanding of the genetic factors controlling these traits can be improved because these factors can be identified within specific regions of the genome, and their effects estimated individually (Stuber et al. 1987).

In the present study, grain yield and yield components were investigated in an elite population of 150 $F_{2:3}$ lines. By using replicated progeny, the standard error of the QTL genotype mean is reduced, and fewer progeny are needed to detect QTLs with the efficiency of a larger population (Cowen 1988; Knapp and Bridges 1990). The population size we use is representative of sample sizes used by breeders (Bauman 1981).

Materials and methods

Experimental methods, $F_{2:3}$ lines, RFLP marker loci, and statistical analysis were as described in Veldboom et al. (1994). One-hundred

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and fifty $F_{2:3}$ lines were derived from the cross of elite inbreds Mo17 and H99. These inbreds are considered to be part of the Lancaster Sure Crop heterotic group (Melchinger et al. 1991). The 150 lines, plus six entries of a bulk of all 150 lines, were evaluated in two replications of a 12×13 lattice design at the Agronomy and Agricultural Engineering Research Farm near Ames, Iowa, in 1989. The single-row plots were 5.5 m long with 0.76-m spacing between rows. Plots were machine-planted at a density of 76,500 kernels ha^{-1} on 20 April 1989 and were thinned at the six- to eight-leaf stage to a density of 57,400 plants ha^{-1}. Fertility and cultivation regimes were consistent with optimum maize production for this region. The growing season at Ames had below-normal precipitation (seventh driest year on record) and was preceded by a drought at the location in 1988 (the driest year on record). However, below-normal temperature and timely rains during pollination permitted complete growth and development.

Grain yield and yield-component traits were measured on a plot basis as follows:

Grain yield (GY) is the total weight (g) of hand harvested, shelled grain dried at 60°C for 7 days and converted to Mg ha^{-1}.
Kernel weight (KWT) is the weight (g) of a 300-kernel sample from total shelled grain.
Ear number per plant (ENP) is the total number of ears in a plot divided by the number of plants in the plot.
Ear length (EL) is the average length (cm) of ten primary ears.
Ear diameter (ED) is the average diameter (cm) of ten primary ears.
Cob diameter (CD) is the average diameter (cm) of ten cobs.
Kernel depth (KD) is the calculated depth (cm) obtained by (ED − CD)/2.
Kernel row number (KR) is the average number of kernel rows of ten primary ears.

Statistical analysis of field data and QTL analysis were both performed as described in Veldboom et al. (1994). All entry means were adjusted for lattice block effects according to Cochran and Cox (1957) if the block effects were significant. Simple phenotypic correlations were calculated between traits on the basis of adjusted entry means.

An RFLP linkage map was created by using 103 RFLP and one morphological marker, *P1*, as described in detail in Veldboom et al. (1994). QTLs were determined by interval mapping by using MAPMAKER-QTL (Ver. 0.9) (Lander and Botstein 1989). Genetic effects and the percentage of phenotypic variation attributable to individual putative QTLs were estimated at the peaks of significant regions when the genome was evaluated by using the unconstrained genetic model. Because $F_{2:3}$ progeny were used for trait evaluation, the estimates of dominance effects of genotypic means from heterozygous F_2 plants are expected to be reduced by half. In this instance, estimates of dominance effects were doubled in accordance with established procedures (Mather and Jinks 1971). Average levels of dominance were calculated as the ratio d/a with the dominance effects, d, being those 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. Because the effects of the QTLs were estimated in the same experiment in which the QTLs were found significant, it is realized that the effects will be biased upwards (Lande and Thompson 1990). Additionally, the total percentage of variation associated with molecular markers for each trait was determined in a multiple model that included all significant QTLs (Lander and Botstein 1989).

Results

Analysis of field data

The means for GY and yield components of the $F_{2:3}$ lines were tested for normality of distribution by using the Shapiro and Wilk (1965) W statistic. Most traits fit a normal distribution, but ENP and EL had significant deviations from a normal distribution. The distribution of ENP was skewed toward lines with fewer ears per plant, and EL was skewed toward longer ears.

Mid-parent heterosis and transgressive segregation were evident for each trait in which the parental values were available for comparison (Table 1). Mo17 had larger trait values than H99 for each yield component except KR. This is reflected in the much greater GY of Mo17. Highly-significant differences were found between $F_{2:3}$ lines for all traits. Broad-sense heritabilities were relatively large for each trait (Table 1). Because the measurements were taken in only one environment, these heritabilities were biased upward due to the genetic variance component also containing the estimate of genotype-by-environment interaction.

All yield-component traits were highly significantly correlated with GY (Table 2). Most traits have highly significant correlations with the other yield components except for ENP, which was correlated only with GY and EL. ED and CD were highly correlated ($r_p = 0.77$); however, KD, which was derived from these two traits, was significantly correlated with only ED. Significant correlations were mostly positive except for KWT and KR, which had a low, negative correlation.

Estimation of QTL

QTLs were determined based on the linkage map described in Veldboom et al. (1994) (Fig. 1). Significant associations with RFLP markers were found for all traits (Fig. 2; Table 3). GY with one, and ENP with two, had the fewest genomic regions identified as QTLs. The other traits each had four to six significant QTLs. These associations, evaluated in a multiple QTL model for each trait, accounted for 35 to 71% of the phenotypic variation of the traits.

The amount of phenotypic variation attributable to individual QTLs ranged from 6% to 41%, and most (67%) of the QTLs accounted for greater than 10% of the phenotypic variation. Only one region was associated with GY (Table 3), but this region accounted for 35% of the phenotypic variation of that trait. The means for GY were 5.56 Mg ha^{-1} for the Mo17/Mo17 class, 5.02 Mg ha^{-1} for the Mo17/H99 class, and 3.02 Mg ha^{-1} for the H99/H99 class. This region was also significantly associated with most yield components. Mo17 alleles increased trait values and generally contributed the largest effects for most yield-component QTLs. The only exception was CD in which H99 alleles increased the trait value at four of six loci. For each yield component, alleles with significant effects were derived from both parents.

Gene action at QTLs was partial dominance to overdominance for yield components (Table 3). Regions characterized by additive effects were less common. Dominance effects usually increased the value of GY and yield components. No association was found between heterozygosity across all loci and GY (data not shown). Only ENP

Table 1 Means, genetic-variance component estimates, and heritabilities of $F_{2:3}$ lines for grain yield and yield components

Item	Trait			
	GY (Mg ha^{-1})	KWT (g/300)	ENP	EL (cm)
Means				
Mo17[a]	4.37	93.0	1.0	18.3
H99[a]	1.76	56.5	0.9	13.1
$F_{2:3}$ lines	4.86	77.6	1.1	18.6
Range				
$F_{2:3}$ lines	(0.87–8.18)	(51.6–100.6)	(0.6–1.7)	(11.6–22.3)
Variance components ($F_{2:3}$ lines)				
$\sigma_g^2 \pm$ SE	1.74±0.23**	105.2±13.1**	0.0259 ±0.087**	2.72±0.70**
σ^2	0.478	16.39	0.0204	0.620
Heritability ($F_{2:3}$ lines)				
h^{2b}	0.88	0.93	0.72	0.90
90% C. I. on h^2	(0.84, 0.91)	(0.90, 0.95)	(0.63, 0.79)	(0.86, 0.92)

Item	Trait			
	ED (cm)	CD (cm)	KD (cm)	KR
Means				
Mo17	–	–	–	11.0
H99	–	–	–	11.3
$F_{2:3}$ lines	4.0	2.6	0.7	11.7
Range				
$F_{2:3}$ lines	(2.9–4.5)	(2.1–3.0)	(0.4–0.9)	(10.0–14.0)
Variance components ($F_{2:3}$ lines)				
$\sigma_g^2 \pm$ SE	0.122±0.015**	0.0263±0.0070**	0.0058±0.0017**	0.568±0.153**
σ^2	0.0109	0.0075	0.0025	0.181
Heritability ($F_{2:3}$ lines)				
h^{2b}	0.92	0.88	0.82	0.86
90% C. I. on h^2	(0.89, 0.94)	(0.84, 0.91)	(0.77, 0.87)	(0.82, 0.90)

[a] Data for Mo17 and H99 obtained from the 1989 Iowa State University Experimental Corn Trials (Russell et al. 1989) grown at the same location and planted 24 April 1989
[b] Knapp et al. (1985)
** Significant at the 0.01 level

Table 2 Phenotypic correlations between traits of Mo17× H99 $F_{2:3}$ lines

Trait	KWT	ENP	EL	ED	CD	KD	KR
GY	0.34**	0.57**	0.74**	0.55**	0.32**	0.52**	0.21**
KWT		– 0.08	0.36**	0.59**	0.29**	0.62**	– 0.21**
ENP			0.46**	0.06	0.03	0.06	0.00
EL				0.28**	0.28**	0.36**	0.10
ED					0.77**	0.75**	0.36**
CD						0.15	0.39**
KD							0.15

*, **Significant at the 0.05 and 0.01 levels, respectively

had dominance deviations that decreased the value for the trait at all loci.

There were 14 genomic regions associated with yield-component traits. Nine regions were associated with more than one trait. The region on 6L (long arm of chromosome six) near locus npi280 was associated with all traits except CD and KR. The region on 8L was associated with KWT, KD, EL, and ED. Alleles from Mo17 were associated with increased values for each of these traits in these two regions. The region on 3L near umc165A was associated with ENP, EL, ED, and KD. Mo17 alleles contributed increased values for three of these traits (ENP, ED, and KD), whereas alleles from H99 positively affected EL. The region on 1S was associated with four traits: EL, CD, KD, and KR. In this region, Mo17 alleles increased EL and CW, and H99 alleles increased KD and KR. Five other regions (1L, 2L, 4L, 5S, and 7L) were significantly associated with two or three traits.

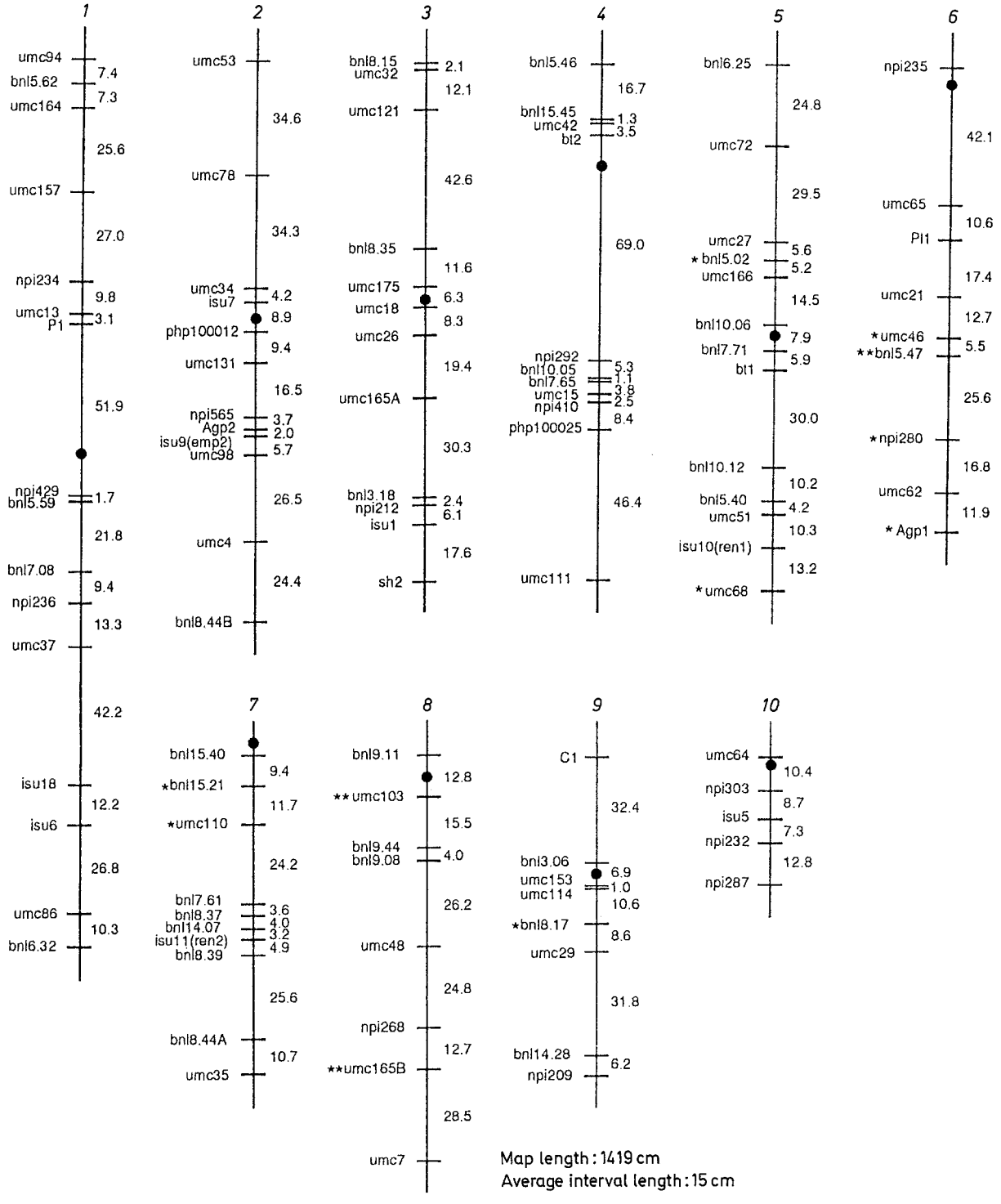

Fig. 1 RFLP map of Mo17×H99 $F_{2:3}$ lines. Distances between probes are given in cM to the right of each chromosome. Probes with significant distortions from Mendelian segregations are marked with an * or ** for the 0.05 and 0.01 levels of significance, respectively

Discussion

Mo17 and H99 differ greatly in GY. GY of the $F_{2:3}$ lines was highly heritable and ranged from half the value of H99 to twice the value of Mo17 (Table 1); yet, only one region on chromosome 6L was found to be significantly associated with this trait. This region accounted for 35% of the phenotypic variation and represented a 2.5 Mg ha^{-1} difference in parental marker classes. This same region accounted for a large proportion of the variation for almost

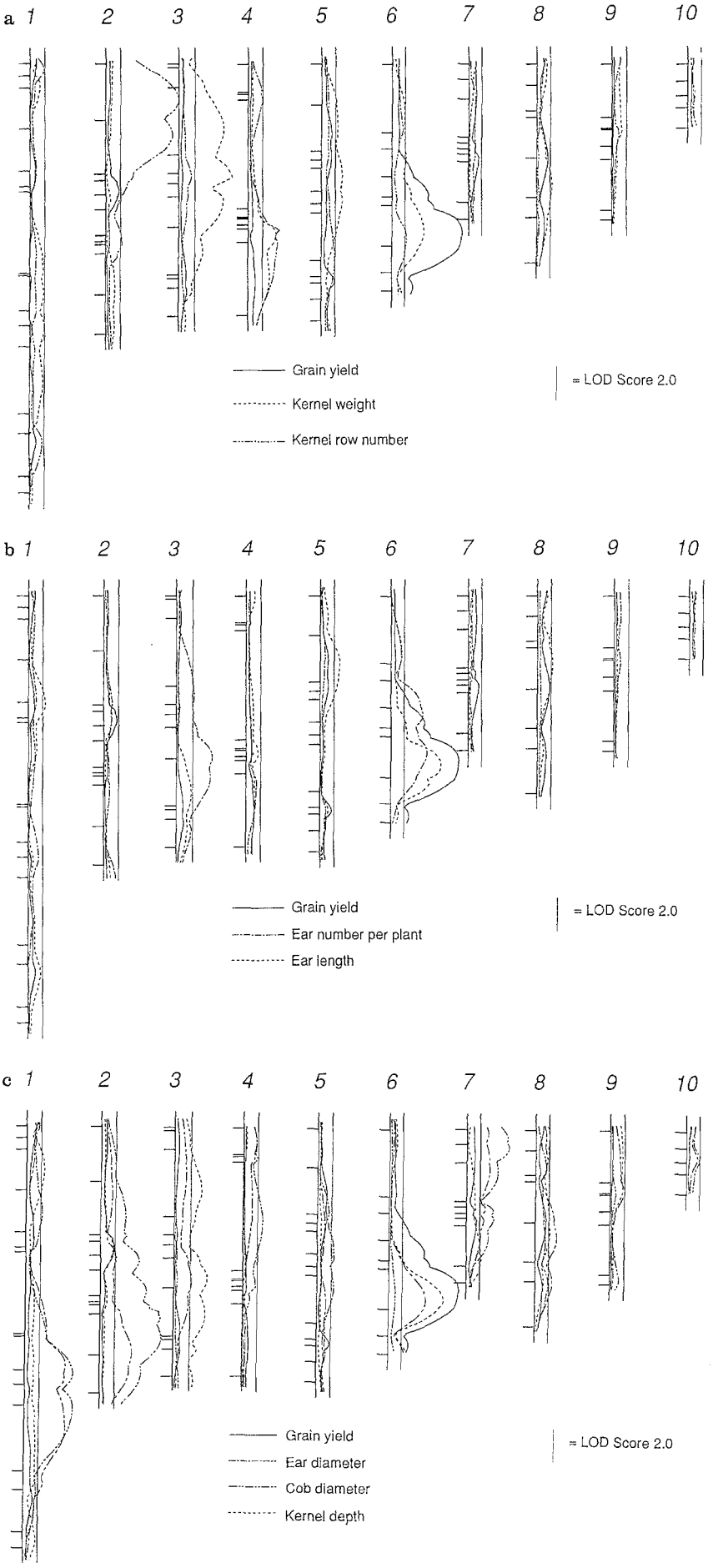

Fig. 2a QTL likelihood plots of GY, KWT, and KR. **b** QTL likelihood plots of GY, ENP, EL. **c** QTL likelihood plots of GY, ED, CD, KD

Table 3 Genomic locations, genetic effects, and percentage of phenotypic variation of QTLs of yield-component traits

Chromosome region	Nearest RFLP locus	Distance[a] (cM)	Max. LOD score	% Var	Genetic effects[b]			Gene action[c]	Direction[d]
					a	d	d/a		
Grain yield					– Mg ha^{-1} –				
6L	npi280	– 10	10.7	35	– 1.27	1.47	– 1.16	D	Mo17
Total[e]			10.7	35					
Kernel weight					– g 300^{-1} kernels –				
1L	npi236	0	2.4	7	3.6	5.6	1.56	OD	H99
3	umc175	0	8.1	22	– 7.3	0.9	– 0.12	A	Mo17
4L	npi410	0	4.3	12	5.1	3.7	0.73	PD	H99
5S	umc166	6	2.9	11	– 4.7	5.2	1.10	D	Mo17
6L	npi280	– 12	4.7	19	– 6.0	12.6	– 2.10	OD	Mo17
8L	npi268	– 9	2.3	9	– 3.5	– 8.0	2.29	OD	Mo17
Total			27.3	63					
Ear number plant^{-1}					– number plant^{-1} –				
3L	umc165A	– 5	5.4	19	0.12	– 0.07	– 0.58	PD	H99
6L	bn15.47	10	5.7	24	– 0.15	– 0.01	0.05	A	Mo17
Total			11.5	39					
Ear length					– cm –				
1S	npi234	2	2.7	9	– 0.77	0.41	– 0.53	PD	Mo17
3L	umc165A	16	2.2	11	0.73	1.72	2.36	OD	H99
5S	umc27	– 8	3.0	14	– 0.59	2.58	– 4.37	OD	Mo17
6L	npi280	– 8	8.0	35	– 1.39	3.58	– 2.58	OD	Mo17
8L	bn19.08	12	2.1	10	– 0.85	1.00	– 1.18	D	Mo17
Total			20.1	64					
Ear diameter					– cm –				
1L	umc37	10	6.1	24	0.18	0.08	0.44	PD	H99
2L	umc4	– 8	4.7	21	– 0.16	0.15	– 0.93	D	Mo17
3L	umc165A	– 9	2.6	10	– 0.12	– 0.06	0.50	PD	Mo17
6L	npi280	– 4	5.7	19	– 0.16	0.30	– 1.88	OD	Mo17
7L	umc110	6	3.4	16	0.15	0.18	1.20	D	H99
8L	umc48	8	3.3	13	– 0.14	– 0.05	0.36	PD	Mo17
Total			26.6	71					
Cob diameter					– cm –				
1S	npi234	– 13	2.2	10	– 0.06	0.13	– 2.17	OD	Mo17
1L	bn17.08	0	7.3	20	0.11	0.10	0.91	D	H99
2L	umc98	8	9.3	34	– 0.14	0.02	– 0.14	A	Mo17
4	npi292	– 31	3.1	29	0.11	0.22	2.00	OD	H99
5L	Bt1	8	2.3	10	0.07	0.10	1.43	OD	H99
7L	bn115.21	4	6.4	21	0.10	0.22	2.20	OD	H99
Total			24.7	67					
Kernel depth					– cm –				
1S	umc157	– 12	2.5	10	0.04	0.02	0.50	PD	H99
3L	umc165A	– 9	5.1	19	– 0.06	0.01	0.17	A	Mo17
6L	npi280	– 4	8.5	30	– 0.06	0.14	– 2.33	OD	Mo17
7L	bn18.44A	– 10	2.1	9	0.02	– 0.09	– 4.50	OD	H99
8L	umc48	6	2.2	8	– 0.04	– 0.02	0.50	PD	Mo17
Total			18.0	52					
Kernel rows					– number –				
1S	bn15.52	0	2.3	7	0.05	0.83	16.6	OD	H99
2S	umc78	– 11	11.2	41	– 0.67	– 0.72	1.07	D	Mo17
4S	Bt2	0	2.1	6	0.29	0.17	0.59	PD	H99
4L	umc15	0	4.8	14	– 0.45	0.10	– 0.22	PD	MO17
Total			19.3	53					

[a] The distance is measured from the nearest RFLP marker to the maximum LOD peak of a QTL. A positive distance is given for QTLs located toward the terminal end of the long arm of the chromosome from the marker, and a negative distance is given for QTLs located toward the terminal end of the short arm

[b] Additive effects are associated with the allele from H99. A negative value means that the H99 allele decreases the value of the trait

[c] Gene action is determined from the ratio d/a

[d] Direction of response is the parent whose additive value of a marker allele increased the value of the trait

[e] Totals are the LOD score and the percent of phenotypic variation accounted for in a multiple model of all QTLs

all traits measured in this population, including flowering and plant and ear heights (Veldboom et al. 1994). Alleles from Mo17 contributed to increased values for all traits associated with this region except flowering. Factors for increased growing-degree-days-to-flowering (or lateness) were contributed by H99. QTLs for flowering were more closely associated with bnl5.47, and the QTLs for the other traits were more closely associated with npi280, 25 cM from bnl5.47 (Fig. 1). Therefore, at least two different linked QTLs may influence these traits. It seems likely that a QTL in this region could have pleiotropic effects on all yield-related traits, including plant and ear height, with a separate QTL controlling flowering traits.

Eighty-eight percent of the phenotypic variation of GY was due to genetic factors (Table 1). Even though 35% of the phenotypic variation of GY is accounted for by the region on 6L, almost 50% of the phenotypic variation due to genetic factors or 60% (1–0.35/0.88) of the genetic variation remains unaccounted for. Each remaining locus affecting GY must, individually, account for less than 6% of the variation because this was the minimum amount of variation distinguishable from experimental error in this study. If most genetic factors controlling GY have effects indistinguishable from experimental error, then it is easy to understand why selection for GY is so difficult.

Although direct comparisons could not be made, some QTLs detected in our study were located in regions reported by Edwards et al. (1992). These included 6L for GY; 1S, 6L, and 8L for EL; and 4S for KR. So far, identification of QTLs seems limited to the population and environments in which they were detected, but comparison of several studies may confirm the existence of loci that are important to traits of interest for specified reference populations.

Correlation and compensation among traits

GY was significantly correlated with all traits measured in this study (Table 2). The highest correlations were between GY and traits that also have QTLs on chromosome 6L, but correlations still occurred between GY and yield components that do not have any detected QTLs in common. It is generally accepted that genes affecting yield components have pleiotropic effects on yield (Hallauer and Miranda 1988). Therefore, it is possible that loci affecting these yield components also affect yield but to a degree that is not detectable at our level of resolution. If each of the 14 yield component QTLs had an effect on GY, the average effect at any one locus would be less than our minimum level of detection; i.e., 6% of the phenotypic variation. Most likely, other loci for yield components, whether or not detected in this study, exist, which also would have an effect, though small, on GY.

Breeders have observed compensation among yield-component traits (Salazar and Hallauer 1986). Compensation is evident when one trait, such as EL, increases, while another trait, such as ED, decreases. In this study, a negative correlation was observed between KWT and KR. One region on 4L had QTLs for these traits with divergent additive effects. In general, as segments containing alleles from H99 are incorporated in this region, KWT and KR should respectively increase and decrease.

Gene action and direction of response

Gene action was partial dominance to overdominance for all traits. Dominance deviations generally increased the value of the trait independent of the direction of response for the additive effects. Several QTLs exhibited overdominance or "pseudo-overdominance", indicating possible linkage of two or more genes in repulsion (Moll et al. 1964). Overdominance was observed by Edwards et al. (1987) and by Veldboom et al. (1994).

Even though Mo17 is the parent with greater values for almost all traits measured, H99 did have significant positive contributions to each trait except yield. For KD and KR, alleles from H99 accounted for the smallest percentage of variation by individual loci. For other traits, H99 contributed alleles with larger effects, but Mo17 generally contributed alleles that accounted for the largest amount of phenotypic variation. The contribution of favorable alleles from the parent with the smaller value for a trait is at variance with the underlying assumptions of many theories and methods such as the estimation of factors controlling a trait (Lande 1981) and the generation-means analysis (Hayman 1958) to determine additive and dominance effects. Breeders, though, make use of the contribution of favorable alleles from both parents as evidenced by the observation of transgressive segregation in crosses and the ability to cross "good" × "good" parents and obtain improved progeny.

Detection of QTLs

ENP and EL had significant deviations from normality. Normality of distribution is one of the assumptions for interval estimations in MAPMAKER-QTL (Lander and Botstein 1989). Because no transformations to normalize the data could be found, the data were used as recorded though with the realization that a decrease in sensitivity and the ability to estimate effects could result. Previous studies having non-normal distributions of traits have been reported (Doebley et al. 1990; Paterson et al. 1991), and simulation studies have shown that maximum-likelihood estimates with the use of flanking markers are robust to the effects of non-normality of distribution (Knott and Haley 1992). In this instance, sensitivity for detecting QTLs could have been reduced for ENP because only two regions were identified. However, five regions were detected for EL.

Measurements made on individual plants, as used by Edwards et al. (1987), Stuber et al. (1987), Doebley et al. (1990), and Edwards et al. (1992), are subject to greater error. For most traits, values for each $F_{2:3}$ line in this study were based on measurements made on ten competitive

plants within a row of plants grown in a replicated experiment. This should improve the precision of $F_{2:3}$ line-means by reducing the standard error and, therefore, more accurately estimate the true value of each genotype in this environment (Cowen 1988). Using means based on replicated evaluations of progeny will reduce the error in fitting the model used by MAPMAKER-QTL and increase the ability to detect true differences associated with the genotypic marker classes.

The present study reports on data obtained in a single environment with inbred progeny. Paterson et al. (1991) found that few QTLs in tomato were detected in more than one environment. The lines in our study will be analyzed in two more environments (similar locations but different years representing stress and non-stress growing conditions), and the stability of QTLs across environments will be determined for inbred and hybrid progeny. These putative QTLs will also be compared with QTLs that are detected by averaging the effects of all environments as reported by Beavis et al. (1991).

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