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Molecular Marker-Facilitated Investigations of Quantitative Trait Loci in Maize. II. Factors Influencing Yield and Its Component Traits

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Abstract
Because traits such as grain yield are polygenically inherited and strongly influenced by environment, determination of genotypic values from phenotypic expression is not precise and improvement strategies are frequently based on low heritabilities. Increased knowledge of the genetic factors involved in the expression of yield should enhance the improvement of this trait. The objectives of this study were to identify and locate genetic factors (i.e., quantitative trait loci, QTL's) associated with grain yield and 24 yield-related traits in two F_2populations of maize (*Zea mays* L.) using isozyme marker loci. (The populations were generated by selfing the F_1, hybrids CO159 ✕ Tx303 and T232 ✕ CM37.) In addition, assessments of the types and magnitudes of gene effects expressed by these QTL's were made. About two-thirds of the associations among 17 to 20 marker loci and the 25 quantitative traits were significant with a large proportion of these at $P < 0.001$. Proportions of variation accounted for by genetic factors associated with individual marker loci varied from less than 1% to more than 11%. Although individual marker loci accounted for relatively small proportions of the phenotypic variation for these yield-related traits, differences between mean phenotypic values of the two homozygous classes at certain loci were occasionally more than 16% of the population mean. Also, different genomic regions contributed to yield through different subsets of the yield-related traits. Predominant types of gene action varied among loci and among the 25 quantitative traits. For plant grain yield, top ear grain weight, and ear length, the gene action was primarily dominant or overdominant. However, mainly additive gene action was implicated for ear number, kernel row number, and second ear grain weight. Results from these studies should prove to be useful for manipulating QTL's in marker-facilitated selection programs

Keywords
Quantitative genetics, Grain yield, Zea mays L., Gene action, Genetic factors, Genetic variation, Marker loci associations

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Molecular Marker-Facilitated Investigations of Quantitative Trait Loci in Maize. II. Factors Influencing Yield and Its Component Traits[1]

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ABSTRACT

Because traits such as grain yield are polygenically inherited and strongly influenced by environment, determination of genotypic values from phenotypic expression is not precise and improvement strategies are frequently based on low heritabilities. Increased knowledge of the genetic factors involved in the expression of yield should enhance the improvement of this trait. The objectives of this study were to identify and locate genetic factors (i.e., quantitative trait loci, QTL's) associated with grain yield and 24 yield-related traits in two F_2 populations of maize (*Zea mays* L.) using isozyme marker loci. (The populations were generated by selfing the F_1 hybrids CO159 × Tx303 and T232 × CM37.) In addition, assessments of the types and magnitudes of gene effects expressed by these QTL's were made. About two-thirds of the associations among 17 to 20 marker loci and the 25 quantitative traits were significant with a large proportion of these at $P < 0.001$. Proportions of variation accounted for by genetic factors associated with individual marker loci varied from less than 1% to more than 11%. Although individual marker loci accounted for relatively small proportions of the phenotypic variation for these yield-related traits, differences between mean phenotypic values of the two homozygous classes at certain loci were occasionally more than 16% of the population mean. Also, different genomic regions contributed to yield through different subsets of the yield-related traits. Predominant types of gene action varied among loci and among the 25 quantitative traits. For plant grain yield, top ear grain weight, and ear length, the gene action was primarily dominant or overdominant. However, mainly additive gene action was implicated for ear number, kernel row number, and second ear grain weight. Results from these studies should prove to be useful for manipulating QTL's in marker-facilitated selection programs.

Additional index words: **Quantitative genetics, Grain yield, *Zea mays* L., Gene action, Genetic factors, Genetic variation, Marker loci associations.**

In maize (*Zea mays* L.) and other plant species, the genetic bases of quantitative traits, such as yield and most of its component traits, are normally assumed to be polygenic in nature largely because the phenotypic expressions of these traits form continuous distributions. Typically, estimates of genotypic effects associated with these traits are expressed as an average value across the genome. With the development of molecular markers (isozymes, and, more recently, restriction fragment length polymorphisms, RFLP's), the capabilities are now available for discriminating individual gene effects. Thus, numbers and genomic distribution of genetic factors (quantitative trait loci, QTL's) involved in the expression of yield and other quantitatively inherited traits can now be elucidated. Molecular marker techniques also provide the means for investigating the types and magnitudes of gene effects attributed to these QTL's.

The theoretical basis for interpreting the association of marker loci with QTL's has been outlined by Mather and Jinks (1971), Tanksley, et al. (1982), Soller and Beckmann (1983), and Edwards et al. (1987). The theory exploits the fact that the marker locus serves to identify, or "mark", the chromosomal region in its vicinity and enables that region to be followed in inheritance studies. Alternative homologous chromosomal regions characterized by alternative alleles at the marker locus can be replicated extensively in different individuals and compared for quantitative trait effects, while other chromosomal regions in the same individuals and the environmental factors affecting them are permitted to vary at random. If adequate markers are available and are distributed appropriately throughout the genome, it is possible to evaluate all chromosomal regions for their effects on numerous quantitative traits of interest. A high level of linkage disequilibrium between the marker loci and QTL's is an essential feature of the approach.

Earlier studies to examine the association of specific isozyme loci with grain yield in maize involved monitoring allelic frequency changes at a large number of enzyme loci in different cycles of recurrent selection experiments. In several long-term recurrent selection experiments in North Carolina, allelic frequencies at

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eight isozyme loci showed significant changes greater than would be expected with drift acting alone and were highly correlated with improvements due to selection for increased grain yield (Stuber and Moll, 1972; Stuber et al., 1980).

Based on these earlier results by Stuber et al., it was hypothesized that manipulation of allelic frequencies at the appropriate isozyme loci should produce responses in the correlated quantitative traits in maize. Experimental results indicated that selections based solely on manipulations of allelic frequencies at seven enzyme loci significantly increased grain yield and the highly correlated trait, ear number (Stuber et al., 1982). A somewhat similar study conducted in a population generated from a composite of elite inbred lines produced responses similar to those found for phenotypic selection (Frei et al., 1986b).

In a study designed to assess the value of isozyme markers for predicting single-cross hybrid yield performance among maize inbred lines (Frei et al., 1986a), line pairs were classified into similar and dissimilar isozyme groups. These groups were further subdivided into similar and dissimilar pedigree classes according to commonality of pedigree between lines. In 114 hybrids, grain yield in the dissimilar isozyme class was significantly higher (10%) than in the similar isozyme class. However, the dissimilar pedigree class yielded about 37% more than the similar pedigree class. Frei et al. (1986a) concluded that isozyme marker dissimilarity was significantly associated with higher grain yield, but the utility of these specific markers for predictive purposes was largely limited to lines with similar pedigrees.

The large number of generations of random mating in many of the maize populations used in these earlier studies would have reduced the level of linkage disequilibrium between marker loci and QTL's, and thereby severely restricted the effectiveness of these techniques for evaluating associations of marker loci with quantitative traits. The limited positive results from these and other studies, however, provided the impetus for the investigations reported herein in which associations between marker loci and yield-related traits in two F_2 populations were examined. These investigations differed from the earlier studies in that the F_2 populations (where linkage disequilibrium is maximized) should be much more effective for identifying and locating QTL's (or specific chromosomal segments) associated with the quantitative traits measured. In addition, types and magnitudes of gene effects expressed by these QTL's could be assessed in the F_2's. The quantitative traits evaluated herein included total grain yield and 24 ear and kernel characteristics; thus many more traits were examined than in earlier studies.

MATERIALS AND METHODS

Plant materials, isozyme marker loci, and experimental techniques utilized for this investigation were identical to those described by Edwards et al. (1987). Experimental materials were derived from two U.S. maize inbred lines, Tx303 and T232, and two Canadian lines, CO159 and CM37. The F_1 hybrids, CO159 × Tx303 and T232 × CM37, were produced and selfed to generate the two F_2 populations (designated as COTX and CMT, respectively) used to investigate associations between marker loci and yield-related traits.

Descriptions of the traits (grain yield and 24 yield-related traits) measured on individual plants in this investigation are as follows.

Whole Plant

Grain weight—Weight (g) per plant of all shelled grain dried to uniform moisture.

Ear number—Number of ears per plant with at least 1 g of grain.

Ear weight—Weight (g) of all ears (grain plus cob) dried to uniform moisture.

Kernel number—Total number of kernels on all ears of the plant.

Grain index—Ratio of shelled grain weight over ear weight per plant.

Harvest index—Ratio of shelled grain weight over total plant weight (grain plus cob plus stover).

Top Ear

Grain weight—Weight (g) of shelled grain dried to uniform moisture.

Ear weight—Weight (g) of grain plus cob dried to uniform moisture.

Row number—Number of rows of kernels on the ear.

Kernels per row—Average number of kernels per row.

100-kernel weight—Weight (g) of 100 kernels dried to uniform moisture.

Ear circumference—Circumference (cm) of ear measured with a fabric tape at widest point of the ear.

Ear length—Length (cm) from butt to tip of ear.

Ear length/ear diameter—Ratio of length over diameter.

Percent cob diameter—Percent of ear diameter attributed to cob (cob measured with a fabric tape).

Kernel depth—One-half of the unshelled ear diameter minus cob diameter (mm).

Kernel thickness—Average width (mm) of kernels measured parallel to ear length, and measured at widest end of kernels (calculated from the average number of kernels per row and average row length for the whole ear).

Kernel width—Average width (mm) of kernels measured perpendicular to ear length, and measured at widest end of kernels (calculated from number of rows of kernels and ear circumference).

Kernel base width—Average width (mm) of kernels measured perpendicular to ear length, and measured at embryo end of kernels (calculated from number of rows of kernels and cob circumference).

Kernel volume—Estimated volume (mm^3) based upon thickness × depth × 1/2 (width + base width).

Kernel density—Weight per unit volume (mg/mm^3) based upon 100 kernel weight/(100 × kernel volume).

Grain index—Ratio of shelled grain weight over ear weight.

Second Ear

Grain weight—Weight (g) of shelled grain dried to uniform moisture.

Ear weight—Weight (g) of grain plus cob dried to uniform moisture.

Second ear weight/total weight—Ratio of grain weight of second ear over total grain weight per plant.

Field evaluations were made on 1776 COTX plants and 1930 CMT plants grown at Clayton, NC. In the two populations, 15 and 18 segregating isozyme loci, respectively, plus two morphological loci each, were used as markers. These

marker loci are distributed on 8 of the 10 chromosomes in each population and are within about 20 centimorgan (cM) of nearly 40 to 45% of the genome (Fig. 1).

For each genotypic class at each marker locus, a mean was computed for each of the 25 quantitative traits. Then, for each marker locus and each trait, a single factor analysis of variance was computed to evaluate the significance of the variation among marker-locus genotypic class means. Then F tests were used as the measures of significance, and significant F values were interpreted to indicate segregation of genotypes at a yield-related locus (or loci) that was linked to the marker locus. The variation attributed to each marker locus was considered as a proportion of the total variation for each trait, and this proportion was recorded as an R^2 value.

Additive and dominance effects attributed to the yield-related loci were estimated from contrasts among the marker-locus genotypic class means (Edwards et al., 1987). The ratio (d/a) of the estimated dominance effect over the estimated additive effect was used to measure the degree of dominance. Because the distribution of d/a ratios was continuous, no discrete classifications for type of genetic effect were evident. The following classifications, however, were judged by the authors to be reasonable: A (additive) = 0 to 0.20; *PD* (partial dominance) = 0.21 to 0.80; *D* (dominance) = 0.81 to 1.20; *OD* (overdominance) = >1.20.

Principal component analyses (using correlation matrices) were employed to explore the multiple relationships of specific marker loci with a subset of the yield-related traits: ear number, kernel number, whole plant grain index, row number, kernels per row, 100-kernel weight, ear circumference, ear length, percent cob diameter, kernel depth, and ratio of second ear weight to total weight. The proportion of the total variation for each principal component that could be attributed to each marker locus was computed and recorded as an R^2 value, as for the individual traits.

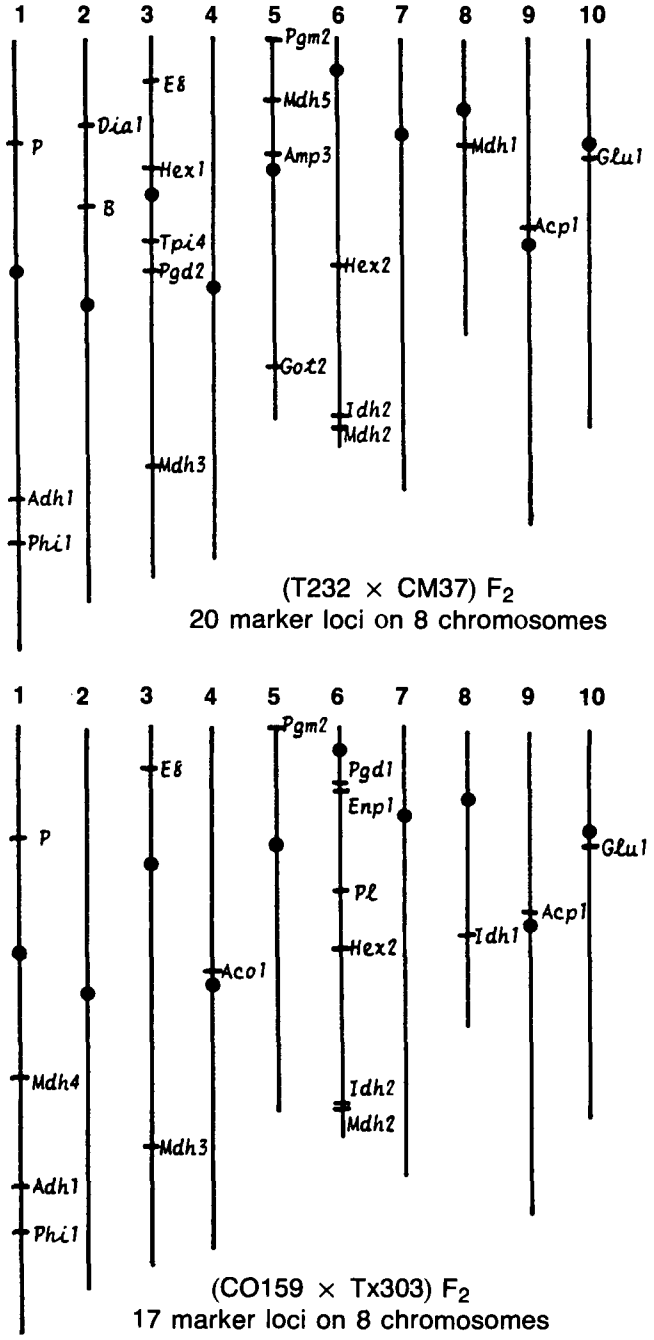

Fig. 1. Distributions of the 20 and 17 marker loci segregating in the F_2 populations of T232 × CM37 (CMT) and CO159 × TX303 (COTX), respectively.

RESULTS AND DISCUSSION

Although evaluations were made in only a single environment, this was judged to be adequate to meet the objective, which was to assess the associations of marker loci with quantitative traits in two specific F_2 populations. We recognize that measurements on quantitative traits would be affected by interaction with the specific environment in which the evaluations were made; however, we did not attempt to extrapolate these results to other environments. In addition, measurements were made on individual F_2 plants which, obviously, could not be replicated. Any replications would involve a different sample of plants from the F_2 populations used. It should be noted, however, that results from these single environment studies were used as the basis for marker-facilitated selection studies evaluated in three environments in the following year. Several quantitative traits were very effectively manipulated in these selection studies even though the selections were based on results from the single environment (Stuber and Edwards, 1986).

Mean values for shelled grain yield (grain weight) and the 24 yield-related traits are presented for COTX, (CO159 × Tx303)F_2, and CMT, (T232 × CM37)F_2, in Table 1. Although the two populations had identical grain yields, they differed in how the yield was attained through the various yield component traits. The CMT population had 21% (0.3 per plant) more ears than COTX. The top ears of CMT weighed 17% less and the second ears weighed 169% more than the corresponding COTX ears. However, CMT had fewer (12.5% less) but heavier (14.6% greater) kernels than COTX. Other traits such as row number and kernel volume also differed between the two populations.

Numbers of Detected Factors Influencing the Expression of Grain Yield and Yield-Related Traits

Numbers and proportions of segregating marker loci that showed significant associations with yield-related trait expression are presented in Table 2. For the 17

Table 1. Mean values of 25 yield-related traits measured on 1776 individual plants in (CO159 × Tx303)F_2 and 1930 individual plants in (T232 × CM37)F_2.

Yield-related trait	(CO159 × Tx303)F_2 COTX	(T232 × CM37)F_2 CMT
	Whole plant	
Grain weight (g)	127.95	127.53
Ear number	1.40	1.70
Ear weight (g)	156.38	151.38
Kernel number	465.64	407.26
Grain index	0.81	0.83
Harvest index	0.45	0.50
	Top ear	
Grain weight (g)	118.66	99.68
Ear weight (g)	141.92	118.06
Row number	15.65	12.58
Kernels per row	27.67	25.25
100-kernel weight (g)	27.71	31.76
Ear circumference (cm)	15.74	13.23
Ear length (cm)	14.07	15.42
Ear length/ear diameter	2.84	3.68
% cob diameter	66.00	64.00
Kernel depth (mm)	8.61	7.60
Kernel thickness (mm)	4.99	6.09
Kernel width (mm)	10.13	10.66
Kernel base width (mm)	6.67	6.83
Kernel volume (mm^3)	360.98	403.12
Kernel density (mg/mm^3)	0.77	0.80
Grain index	0.84	0.84
	Second ear	
Grain weight (g)	9.25	27.80
Ear weight (g)	12.37	33.31
Second ear weight/total weight	0.06	0.19

marker loci in COTX, 282 (66%) of the 425 comparisons were statistically significant. Likewise, for the 20 marker loci in CMT, 360 (72%) of the 500 comparisons were significant. About two-thirds of these statistically significant associations were at $P < 0.001$, viz., 180 (64%) of 282 in COTX and 247 (69%) of 360 in CMT (Tables 3 and 4).

The significant marker locus-quantitative trait associations indicate that marker loci were linked to QTL's that influence the expression of each of these traits. The average number of significant associations identified for individual traits was 11.3 for COTX and 14.4 for CMT; the range was 6 to 17 and 8 to 19 in COTX and CMT, respectively. The proportion of significant associations with grain yield and the 24 yield-related traits was greater in the CMT than in the COTX population. For grain weight, ear weight, kernel row number, kernels per row, ear circumference, ear length, and kernel base width, 17 to 19 of the 20 marker loci showed significant associations in CMT. In both populations, however, only about one-half of the marker loci showed significant associations with ear number, whole plant grain index, harvest index, kernel density, and top ear grain index.

As indicated in Tables 3 and 4, some of the marker loci were on the same chromosome arm and, in some cases, may have reflected the effects of the same QTL(s). Tightly linked pairs on chromosome 1 (*Adh1-Phi1*) and chromosome 6 (*Pgd1-Enp1* and *Idh2-Mdh2*) likely reflected effects of the same underlying factors (Fig. 1). In both populations, however, factors significantly associated with grain yield and yield-related traits were distributed throughout the genome.

When grown in North Carolina, the parental lines from the USA, Tx303 and T232, were much more robust than the two Canadian lines, CO159 and CM37.

Table 2. Number of segregating marker loci that showed significant ($P < 0.05$) associations with the 25 yield-related traits and the number from each parent for which the contributing factor showed a positive response in COTX, (CO159 × Tx303)F_2 and CMT, (T232 × CM37)F_2.

Yield-related trait	(CO159 × Tx303)F_2 No. significant†	No. positive Tx303	No. positive CO159	(T232 × CM37)F_2 No. significant‡	No. positive T232	No. positive CM37
		Whole plant				
Grain weight	13	9	4	18	15	3
Ear number	10	10	0	9	7	2
Ear weight	13	9	4	18	15	3
Kernel number	16	12	4	15	14	1
Grain index	9	4	5	8	7	1
Harvest index	9	3	6	11	7	4
		Top ear				
Grain weight	13	9	4	19	14	5
Ear weight	13	9	4	19	14	5
Row number	12	9	3	17	9	8
Kernels per row	11	5	6	18	14	4
100-kernel weight	8	4	4	13	7	6
Ear circumference	16	10	6	19	10	9
Ear length	10	5	5	19	13	6
Ear length/ear diameter	6	3	3	14	7	7
% cob diameter	16	4	12	14	2	12
Kernel depth	17	12	5	15	11	4
Kernel thickness	13	5	8	16	5	11
Kernel width	10	2	8	13	7	6
Kernel base width	8	0	8	17	5	12
Kernel volume	9	7	2	13	8	5
Kernel density	8	1	7	9	6	3
Grain index	9	4	5	8	6	2
		Second ear				
Grain weight	11	11	0	12	12	0
Ear weight	12	11	1	12	12	0
Second ear weight/total weight	10	9	1	14	11	3
Mean	11.3	6.7	4.6	14.4	9.5	4.9
		Total§				
No.	282	167	115	360	238	122
Percent	(66)	(39)	(27)	(72)	(48)	(24)

† Number significant of 17 total marker loci segregating in COTX.
‡ Number significant of 20 total marker loci segregating in CMT.
§ For COTX, the maximum number of significant associations is 425; for CMT, the maximum number is 500.

In COTX, however, the parental origin of the positive factor was CO159 in 4.6 (41%) of the mean (11.2) significant associations identified. Likewise, in CMT, CM37 contributed the factor for a positive response in 4.8 (33%) of the mean (14.4) identified associations. These results clearly demonstrated that highly favorable genetic factors may be found in lines that perform poorly because they are grown out of their range of adaptation. In addition, the results exemplify why the phenotypic appearance of a line in a specific environment frequently belies its genotypic potential for trait performance.

Individual Marker Locus Associations with Phenotypic Expression of Yield and Yield-Related Traits

The number of plants measured in each population was adequate to detect factors contributing as little as 0.2% of the phenotypic variation in these yield-related traits. However, effects detected by marker loci diminish relative to the true effect at the QTL as a function of the distance (recombination frequency) between the marker locus and the QTL (Edwards et al.,

Table 3. Probability level of significant associations between each of 17 segregating marker loci and 25 yield-related traits, percent of total variation (R^2 × 100) accounted for by each marker locus, and parent (T = Tx303 and C = CO159) that contributed the factor showing a positive response for that trait in (CO159 × Tx303) F_2.

Yield-related trait	Segregating marker locus																
	1S†	1L			3S	3L	4S	5S	6L						8L	9L	10L
	P	*Mdh4*	*Adh1*	*Phi1*	*Est8*	*Mdh3*	*Aco1*	*Pgm2*	*Pgd1*	*Enp1*	Pl	*Hex2*	*Idh2*	*Mdh2*	*Idh1*	*Acp1*	*Glu1*
Whole plant																	
Grain weight		*** 1.03 C	*** 3.50 C	*** 2.64 C		*** 1.59 T	*** 1.39 T	*** 0.89 T	*** 0.92 T	** 0.69 T	*** 1.06 T	*** 1.06 T			*** 1.75 T	*** 1.30 T	** 0.61 C
Ear number	*** 1.82 T	* 0.43 T		* 0.35 T					** 0.73 T	** 0.65 T	* 0.38 T	* 0.57 T	* 0.36 T		*** 5.24 T	*** 2.42 T	
Ear weight		** 0.56 C	*** 2.64 C	*** 1.99 C		*** 1.50 T	** 0.83 T	*** 0.88 T	*** 0.82 T	** 0.63 T	*** 0.95 T	*** 1.10 T			*** 3.06 T	*** 1.45 T	* 0.49 C
Kernel number	* 0.37 T	*** 1.17 C	*** 3.89 C	*** 3.27 C		*** 1.01 T	*** 1.96 T	*** 0.80 T	*** 0.90 T	** 0.61 T	*** 1.24 T	*** 1.48 T	** 0.66 T	** 0.67 T	*** 1.44 T	*** 1.38 T	*** 1.02 C
Grain index		*** 1.15 C	*** 3.83 C	*** 2.97 C			*** 1.44 T	* 0.41 T					* 0.36 T	* 0.44 T	*** 2.29 C	*** 0.97 C	
Harvest index		*** 3.50 C	*** 7.06 C	*** 6.15 C			*** 1.67 T	** 0.58 T	* 0.50 T						*** 4.00 C	** 0.80 C	*** 0.95 C
Top ear																	
Grain weight		*** 1.68 C	*** 4.86 C	*** 3.92 C		*** 1.35 T	*** 1.15 T	*** 0.94 T	*** 0.95 T	** 0.73 T	*** 0.77 T	*** 0.93 T			** 0.79 T	*** 1.05 T	** 0.72 C
Ear weight		*** 1.41 C	*** 4.78 C	*** 3.98 C		*** 1.42 T	*** 0.93 T	*** 0.87 T	*** 0.94 T	*** 0.76 T	*** 0.73 T	*** 0.92 T			*** 1.13 T	*** 1.09 T	** 0.62 C
Row number			*** 1.06 C	*** 1.56 C	** 0.66 T	*** 2.18 T		*** 0.90 C	** 0.59 T	** 0.68 T	*** 1.47 T	*** 3.88 T	*** 1.58 T	*** 1.16 T	* 0.47 T		
Kernels per row		*** 2.21 C	*** 4.96 C	*** 4.01 C			*** 1.93 T	*** 1.58 T	* 0.49 T		* 0.26 T	*** 1.04 C			*** 0.99 C	*** 0.98 T	*** 1.12 C
100-kernel weight	* 0.38 C	* 0.36 T				*** 1.12 T	*** 1.91 C					** 0.60 C			* 0.39 T	* 0.45 C	*** 1.31 T
Ear circumference	* 0.39 T	*** 1.10 C	*** 2.46 C	*** 3.47 C		*** 1.48 T	** 0.94 C	* 0.39 C	*** 2.35 T	*** 2.57 T	*** 1.72 T	*** 1.67 T	** 0.71 T	** 0.64 T	* 0.45 T	*** 0.88 T	*** 0.90 C
Ear length	*** 1.26 C	** 0.59 C	*** 2.39 C	*** 1.54 C		** 0.62 T	* 0.53 T	*** 0.95 T				*** 0.97 C			*** 4.27 T		* 0.40 T
Ear length/ ear diameter	*** 2.26 C					** 0.63 C		** 0.71 T				*** 1.25 C			*** 4.54 T		** 0.71 T
% Cob diameter	*** 1.29 C	* 0.39 T	*** 1.04 C	*** 1.25 C	*** 0.97 C		*** 3.45 C	*** 1.29 C	*** 1.14 C	*** 1.20 C	*** 1.89 C	*** 1.65 C	*** 1.65 C	*** 1.41 C	*** 2.67 T	* 0.47 T	*** 0.98 T
Kernel depth	*** 1.19 T	** 0.83 C	*** 1.11 C	*** 1.13 C	* 0.53 T	** 0.82 T	*** 1.59 T	** 0.67 T	*** 2.14 T	*** 2.31 T	*** 2.51 T	*** 2.23 T	*** 1.71 T	*** 1.47 T	*** 1.42 C	** 0.61 T	*** 1.05 C
Kernel thickness	*** 1.79 C	** 0.83 T	*** 2.00 T	*** 1.74 T			** 0.99 C	** 0.63 C	* 0.46 C		** 0.68 C	** 0.73 C	** 0.77 C	*** 0.92 C	*** 2.15 T		*** 2.03 T
Kernel width					** 0.80 C	*** 1.49 C	*** 0.99 C	*** 0.97 T			** 0.44 C	*** 2.78 C	*** 0.84 C	* 0.54 C	** 0.66 C	* 0.45 T	
Kernel base width	** 0.46 C				*** 1.68 C	*** 1.51 C	*** 2.06 C				*** 1.46 C	*** 4.27 C	*** 2.00 C	*** 1.51 C			
Kernel volume	** 0.46 C	*** 1.58 T	*** 1.27 T	*** 1.25 T			** 0.90 C		* 0.53 T	** 0.63 T					* 0.43 T		*** 1.17 T
Kernel density		*** 1.63 C	*** 1.94 C	*** 1.59 C		** 0.83 T			*** 1.15 C	*** 1.55 C		** 0.81 C				* 0.58 C	
Grain index		*** 1.08 C	*** 3.33 C	*** 2.51 C			*** 1.33 T	** 0.54 T						* 0.37 T	*** 2.28 C	*** 0.83 T	* 0.39 C
Second ear																	
Grain weight	*** 1.49 T	*** 1.09 T				* 0.38 T	* 0.58 T	** 0.67 T			** 0.43 T	** 0.86 T	** 0.63 T	** 0.64 T	*** 4.15 T	*** 2.36 T	
	***	***	*	*		*		***			*	**	*	*	***	***	

(continued on next page)

Table 3. Continued.

Yield-related trait	Segregating marker locus																	
	1S†	1L			3S	3L	4S	5S	6L						8L	9L	10L	
	P	*Mdh4*	*Adh1*	*Phi1*	*Est8*	*Mdh3*	*Aco1*	*Pgm2*	*Pgd1*	*Enp1*	PI	*Hex2*	*Idh2*	*Mdh2*	*Idh1*	*Acp1*	*Glu1*	
Ear weight	1.65	1.41	0.46	0.49		0.44		0.85			0.37	0.79	0.43	0.45	5.32	2.91		
	T	T	T	T		T		T			T	T	T	C	T	T		
	***	***	*	***				**				**	**	**	***	***		
Second ear weight/ total weight	1.70	1.36	0.51	0.89				0.65				0.60	0.57	0.59	4.55	2.69		
	T	T	T	T				T				T	T	C	T	T		

*,**,*** Denotes significance levels of F tests at 0.05, 0.01, and 0.001 probability levels, respectively. † Chromosome arm.

Table 4. Probability level of significant associations between each of 20 segregating marker loci and 25 yield-related traits, percent of total variation (R^2 × 100) accounted for by each marker locus, and parent (T = T232 and C = CM37) that contributed the factor showing a positive response for that trait in (T232 × CM37)F_2.

Yield-related trait	Segregating marker locus																		
	1S†	1L		2S		3S		3L			5S			5L	6L			8L	9L	10L
	P	*Adh1*	*Phi1*	*Dia1*	B	*Est8*	*Hex1*	*Tpi4*	*Pgd2*	*Mdh3*	*Pgm2*	*Mdh5*	*Amp3*	*Got2*	*Hex2*	*Idh2*	*Mdh2*	*Mdh1*	*Acp1*	*Glu1*
Whole plant																				
Grain weight	***	***	***	***		**	***	*	***	***	***	***	***		***	*	*	***	***	**
	1.69	1.82	2.06	5.08		0.61	2.59	0.30	3.78	0.74	3.18	4.06	4.04		0.89	0.32	0.37	4.50	1.77	0.62
	T	T	T	T		T	T	T	T	T	T	T	T		T	C	C	T	T	C
Ear number		**	***	***	*				***	***	*						*	*		
		0.71	0.88	4.13	0.23				0.78	2.14	0.40						0.47	0.33		
		T	T	T	T				T	T	C						C	T		
Ear weight	***	***	***	***		*	***	**	***	***	***	***	***		***	*	*	***	***	**
	2.10	1.62	1.66	5.46		0.44	2.13	0.48	4.26	0.80	2.54	3.29	3.30		0.81	0.35	0.40	4.83	2.31	0.60
	T	T	T	T		T	T	T	T	T	T	T	T		T	C	C	T	T	C
Kernel number	***	***	***	***			***	*	***	***	***	***	***		**			***	***	***
	1.44	1.87	2.06	3.90			2.27	0.29	3.09	0.97	1.17	2.14	2.05		0.74			5.14	0.82	1.60
	T	T	T	T			T	T	T	T	T	T	T		T			T	T	C
Grain index			*			**	***		***	*	***	***	***							
			0.39			0.55	0.87		0.78	0.47	1.37	1.73	1.50							
			T			C	T		T	T	T	T	T							
Harvest index		***	***	***	**		**	*	***	***	*		***		***					
		1.88	1.78	1.08	0.52		0.96	0.23	1.02	1.24	0.44		0.78		0.92					
		T	T	C	C		T	T	T	T	C		C		T					
Top ear																				
Grain weight	***	***	***	***	*	***	***		***	***	***	***	***	***	*	*	*	***	***	***
	2.50	1.08	1.31	1.78	0.24	0.75	1.44		2.35	1.21	8.55	8.62	8.12	0.80	0.45	0.46	0.35	2.94	1.61	0.85
	T	T	T	T	C	T	T		T	C	T	T	T	T	T	C	C	T	T	C
Ear weight	***	***	***	***	*	**	***		***	***	***	***	***	***	*	*	*	***	***	***
	3.24	0.90	1.10	2.09	0.35	0.51	1.19		2.75	1.41	7.27	7.37	6.74	0.75	0.43	0.47	0.39	3.03	2.16	0.88
	T	T	T	T	C	T	T		T	C	T	T	T	T	T	C	C	T	T	C
Row number	***			*	*		***	***	***	***	***	***	***	**	***	**	**	***	***	***
	5.49			0.42	0.25		1.43	1.71	3.67	1.14	2.94	2.30	4.32	0.55	2.12	0.69	0.56	0.95	1.07	4.88
	T			C	C		T	T	T	T	T	T	T	C	C	C	C	T	C	C
Kernels per row		***	***	***		***	*	*	***	***	***	***	***	*	***	*	*	***	***	***
		1.94	1.83	1.79		0.97	0.27	0.22	1.14	2.08	3.15	3.85	2.34	0.39	1.62	0.43	0.33	3.29	1.65	1.18
		T	T	T		C	T	C	T	C	T	T	T	T	T	T	T	T	T	C
100-kernel weight		***	***	**		**				**	***	***	***			*	*	**	***	***
		0.98	0.88	0.59		0.61				0.56	2.02	1.19	1.87			0.47	0.38	0.65	2.35	3.84
		C	C	T		T				C	T	T	T			C	C	C	T	T
Ear circumference	***		**	***	***	*	***	**	***	**	***	***	***	***	***	***	***	***	*	***
	4.08		0.57	1.11	0.94	0.47	0.66	0.36	1.69	0.56	8.31	7.85	11.30	1.25	1.37	1.74	1.14	1.61	0.40	1.09
	T		C	C	C	T	T	T	T	C	T	T	T	T	C	C	C	T	C	C
Ear length	***	***	***	***	***	*	**		***	***	***	***	***	**	*	*	*	***	***	**
	1.52	1.80	2.14	2.84	0.83	0.40	0.48		1.16	2.31	4.24	2.78	1.65	0.72	0.39	0.32	0.32	1.93	2.42	0.71
	T	T	T	C	C	C	T		T	C	T	T	T	C	T	T	T	T	T	C
Ear length/ ear diameter		***	***	***				*	**	***	***		***	***	***	***	***	*	***	
		2.01	2.76	1.14				0.25	0.66	2.00	0.95		1.22	1.04	1.30	1.33	1.22	0.42	2.25	
		T	T	C				C	C	C	C		C	C	T	T	T	T	T	
% Cob diameter		**		***	***	***	***	***	***		***	***	***	*				***	***	**
		0.69		2.93	1.28	0.80	1.95	2.06	2.97		2.22	2.79	3.73	0.38				0.81	3.21	0.64
		T		C	C	C	C	C	C		C	C	C	T				C	C	C
Kernel depth	***	**	*	***		***	***	***	***		***	***	***			**	*	***	***	
	1.11	0.58	0.48	0.77		0.98	2.00	1.82	3.22		6.33	6.79	9.88			0.59	0.46	1.46	1.77	
	T	C	C	T		T	T	T	T		T	T	T			C	C	T	T	
Kernel thickness	*	**		***		**		***	***	***	**	***	***	***	***	**	*	***		**
	0.29	0.56		1.90		0.66		0.65	0.83	1.58	0.53	1.94	1.78	0.92	1.45	0.55	0.44	1.99		0.66
	T	C		C		T		T	T	T	C	C	C	C	C	C	C	C		C
Kernel width	***	*	*	*		*	***	***	***	***				***	***				***	***
	2.73	0.50	0.33	0.42		0.50	1.21	1.43	2.41	2.17				2.14	1.45				1.48	5.57
	C	T	T	T		C	C	C	C	C				T	T				T	T
	***	**	*	**	*	***	***	***	***	***	***	***	***	***	**			*		***

(continued on next page)

Table 4. Continued.

Yield-related trait	Segregating marker locus																		
	1S†	1L		2S		3S		3L			5S			5L	6L		8L	9L	10L
	P	*Adh1*	*Phi1*	*Dia1*	B	*Est8*	*Hex1*	*Tpi4*	*Pgd2*	*Mdh3*	*Pgm2*	*Mdh5*	*Amp3*	*Got2*	*Hex2*	*Idh2*	*Mdh2*	*Mdh1*	*Acp1*	*Glu1*
Kernel base width	2.32 C	0.67 T	0.34 T	0.71 C	0.22 C	0.84 C	2.58 C	3.03 C	4.74 C	1.77 C	0.90 C	0.59 C	1.44 C	2.50 T	0.73 T			0.50 C		3.31 T
Kernel volume		*** 0.89 C	** 0.62 C			* 0.50 T		*** 0.69 T	** 0.71 T		*** 1.38 T	** 0.55 T	*** 1.81 T			*** 0.89 C	** 0.78 C	** 0.56 C	*** 1.92 T	*** 2.79 T
Kernel density		*** 1.20 T	*** 0.96 T	*** 1.36 T				*** 1.10 C	*** 1.24 C				* 0.50 C		* 0.51 T	* 0.44 T	** 0.59 T			
Grain index						** 0.52 C	*** 0.63 T		** 0.62 T	* 0.34 T	*** 1.55 T	*** 1.69 T	*** 1.64 T						* 0.38 C	
								Second ear												
Grain weight		*** 1.10 T	*** 1.36 T	*** 6.55 T	*** 1.04 T	* 0.45 T	*** 1.38 T	* 0.29 T	*** 2.12 T	*** 3.42 T					*** 0.81 T			*** 2.02 T	** 0.60 T	
Ear weight		*** 1.10 T	*** 1.20 T	*** 6.78 T	*** 1.03 T	* 0.40 T	*** 1.12 T	** 0.37 T	*** 2.22 T	*** 3.37 T					*** 0.77 T			*** 2.27 T	** 0.72 T	
Second ear weight/ total weight		*** 0.83 T	*** 1.04 T	*** 5.49 T	*** 1.07 T	* 0.36 T	*** 0.78 T	* 0.22 T	*** 1.42 T	*** 4.15 T	*** 1.13 C	** 0.57 C	** 0.49 C		** 0.60 T			*** 1.06 T		

*,**,*** Denotes significance levels of F tests at 0.05, 0.01, and 0.001 probability levels, respectively. † Chromosome arm.

1987). Therefore, the true magnitude of the variation explained by the detected factors cannot be determined without further information, and estimates of variation explained by individual marker loci must be viewed as conservative.

For the primary trait, grain weight per plant, individual marker loci explained as much as 5.1% of the total phenotypic variation in CMT. This significant association occurred with *Dia1* on chromosome 2S. Genotypic classes at *Pgm2*, *Mdh5*, and *Amp3* on chromosome 5S accounted for 6 to more than 11% of the variation in ear circumference, kernel depth, top ear grain weight, and top ear total weight (Tables 4 and 5). Markers were less effective in predicting trait expression in COTX for the yield-related traits with a maximum of about 5% explained by factors associated with *Idh1* on chromosome 8L. The traits strongly associated with this marker were ear number, harvest index, second ear weight, total ear weight, and ear length (Tables 3 and 6). Although two-thirds or more of the associations of marker loci with yield-related traits were significant, in a preponderance of these associations individual marker loci accounted for less than 2.0% of the phenotypic variation of the traits in the COTX population. Even in CMT, which showed a stronger association of markers with yield-related traits, single marker loci accounted for less than 2.0% of the phenotypic variation in more than one-half of the associations evaluated.

Although individual marker loci accounted for relatively small proportions of phenotypic variation for the yield-related traits studied, differences between mean phenotypic values of the two homozygous classes at certain marker loci were occasionally more than 16% of the population mean (Tables 5 and 6). In CMT, for example, whole plant grain weight differences between the two homozygous classes for four unlinked marker loci (*Dia1*, *Pgd2*, *Amp3*, and *Mdh1*) were each slightly more than 20 g/plant (16% of the mean grain yield in this F_2 population). The T232 type homozygous class yielded the greatest for all four of these marker loci. However, these loci each accounted for only about 4 to 5% of the total phenotypic variation. Although the whole plant grain weight differences associated with these four marker loci were the same, the loci differed in their associations with yield-component traits. The data suggested that ear number, kernel number, and second ear grain weight might account for a major portion of the whole plant grain weight differences associated with *Dia1*. In fact, the T232 type homozygous class averaged 16% more ears, 18% more kernels, and 124% heavier second ears than the CM37 type homozygous class at *Dia1*. Kernel number, row number, kernel depth, and second ear grain weight were largely responsible for grain yield differences noted for the *Pgd2* marker locus. Kernel number, top ear grain weight, row number, ear circumference, and kernel depth contributed largely to grain yield differences for the *Amp3* locus. For the *Mdh1* locus, kernel number, kernels per row, and second ear grain weight appeared to be the major components associated with yield differences at this locus.

In COTX (Table 6), the grain yield difference associated with the two homozygous classes at *Adh1* was 20 g/plant (16% of the population mean). For two other loci, *Mdh3* and *Idh1*, differences between the two homozygous classes were about 10% of the population mean. It should be noted that the CO159 type homozygous class for *Adh1* was the higher yielding whereas the Tx303 type homozygous class was the higher yielding for the *Mdh3* and *Idh1* marker loci. The three loci, *Adh1*, *Mdh3*, and *Idh1*, however, accounted for only 3.50, 1.59, and 1.75% of the total phenotypic variation for grain yield, respectively. Kernel number, top ear grain weight, and kernels per row were largely responsible for the whole plant grain yield difference noted at the *Adh1* locus. Differences in harvest index were also strongly associated with this locus. Differences in grain yield associated with *Mdh3* appeared to arise from small effects on several yield components in-

Table 5. Mean values of homozygous and heterozygous marker classes, percent of variation ($R^2 \times 100$) associated with respective marker loci, and type of gene action for several grain yield and yield-related traits in CMT, (T232 × CM37)F_2. Marker loci are *Dia1* (chromosome 2S), *Pgd2* (chromosome 3L), *Amp3* (chromosome 5), and *Mdh1* (chromosome 8L).

Yield-related trait	Marker locus	Marker classes: CM37 homozygote	Hetero-zygote	T232 homozygote	R^2 (× 100)	Gene action†
		Whole plant				
Grain weight (g)	*Dia1*	110.7	133.0	131.3	5.08***	D
	Pgd2	113.3	131.3	132.8	3.78***	D
	Amp3	113.8	130.3	135.2	4.04***	PD
	Mdh1	114.7	132.6	135.0	4.50***	PD
Ear number	*Dia1*	1.53	1.73	1.78	4.13***	PD
	Pgd2	1.63	1.70	1.74	0.78***	PD
	Amp3	1.73	1.69	1.68	0.17	
	Mdh1	1.66	1.71	1.72	0.33*	D
Kernel number	*Dia1*	358.9	421.1	421.4	3.90***	D
	Pgd2	365.5	416.9	424.6	3.09***	D
	Amp3	374.5	416.3	421.0	2.05***	PD
	Mdh1	363.6	421.5	441.4	5.14***	PD
Harvest index (ratio)	*Dia1*	0.51	0.51	0.49	1.08***	PD
	Pgd2	0.49	0.51	0.51	1.02***	PD
	Amp3	0.50	0.51	0.49	0.78***	OD
	Mdh1	0.50	0.50	0.51	0.06	
		Top ear				
Grain weight (g)	*Dia1*	95.3	103.2	96.8	1.78***	OD
	Pgd2	92.3	102.7	100.8	2.35***	OD
	Amp3	87.1	101.5	108.1	8.12***	PD
	Mdh1	92.7	102.6	103.4	2.94***	D
Row number	*Dia1*	12.76	12.59	12.43	0.42*	A
	Pgd2	12.04	12.58	13.00	3.67***	A
	Amp3	12.07	12.56	13.11	4.32***	A
	Mdh1	12.35	12.64	12.86	0.95***	A
Kernels per row	*Dia1*	24.08	25.98	24.86	1.79***	OD
	Pgd2	24.54	25.91	24.75	1.14***	OD
	Amp3	23.67	25.77	25.74	2.34***	D
	Mdh1	23.66	25.79	26.35	3.29***	PD
100-kernel weight (g)	*Dia1*	31.30	32.05	31.61	0.59***	OD
	Pgd2	31.43	31.87	31.85	0.20	
	Amp3	31.04	31.69	32.57	1.87***	A
	Mdh1	31.97	31.89	31.07	0.65**	D
Ear circumference (cm)	*Dia1*	13.24	13.31	13.07	1.11***	OD
	Pgd2	13.01	13.27	13.33	1.69***	PD
	Amp3	12.75	13.24	13.65	11.30***	A
	Mdh1	13.05	13.29	13.36	1.61***	PD
Ear length (cm)	*Dia1*	15.34	15.72	14.93	2.84***	OD
	Pgd2	15.10	15.63	15.34	1.16***	OD
	Amp3	14.97	15.56	15.58	1.65***	D
	Mdh1	15.00	15.58	15.66	1.93***	PD
		Second ear				
Grain weight (g)	*Dia1*	15.42	29.69	34.57	6.55***	PD
	Pgd2	20.99	28.59	31.84	2.12***	PD
	Amp3	26.60	28.77	27.07	0.13	
	Mdh1	21.95	29.94	31.47	2.02***	PD
Second ear weight/ total weight	*Dia1*	0.12	0.20	0.23	5.49***	PD
	Pgd2	0.16	0.19	0.21	1.42***	PD
	Amp3	0.21	0.19	0.17	0.49**	A
	Mdh1	0.16	0.20	0.21	1.06***	PD

*,**,*** Significance levels (0.05, 0.01, 0.001, respectively) of F tests to determine associations of marker loci with quantitative trait loci.
† A = additive, PD = partial dominance, D = dominance, OD = overdominance.

Table 6. Mean values of homozygous and heterozygous marker classes, percent of variation ($R^2 \times 100$) associated with respective marker loci, and type of gene action for several grain yield and yield-related traits in COTX, (CO159 × Tx303)F_2. Marker loci are *Adh1* (chromosome 1L), *Mdh3* (chromosome 3L) and *Idh1* (chromosome 8L).

Yield-related trait	Marker locus	Marker classes: CO159 homozygote	Hetero-zygote	Tx303 homozygote	R^2 (× 100)	Gene action†
		Whole plant				
Grain weight (g)	*Adh1*	133.2	132.7	112.8	3.50***	D
	Mdh3	118.0	131.4	131.2	1.59***	D
	Idh1	117.7	132.2	130.0	1.75***	OD
Ear number	*Adh1*	1.37	1.39	1.43	0.17	
	Mdh3	1.37	1.40	1.42	0.15	
	Idh1	1.23	1.42	1.53	5.24***	PD
Kernel number	*Adh1*	483.7	484.1	408.8	3.89***	D
	Mdh3	437.6	473.3	478.5	1.01***	PD
	Idh1	433.0	480.4	469.3	1.44***	OD
Harvest index (ratio)	*Adh1*	0.48	0.46	0.40	7.06***	PD
	Mdh3	0.44	0.45	0.45	0.12	
	Idh1	0.47	0.46	0.41	4.00***	PD
		Top ear				
Grain weight (g)	*Adh1*	124.8	123.3	102.8	4.86***	D
	Mdh3	110.4	121.5	121.1	1.35***	D
	Idh1	113.8	122.1	116.3	0.79**	OD
Row number	*Adh1*	15.84	15.73	15.28	1.06***	PD
	Mdh3	15.25	15.61	16.12	2.18***	A
	Idh1	15.42	15.68	15.82	0.47*	PD
Kernels per row	*Adh1*	28.81	28.68	24.40	4.96***	D
	Mdh3	26.96	28.11	27.45	0.34	
	Idh1	27.45	28.39	26.34	0.99***	OD
100-kernel weight (g)	*Adh1*	27.74	27.64	27.83	0.03	
	Mdh3	26.99	28.12	27.64	1.12***	OD
	Idh1	27.29	27.77	28.05	0.39*	PD
Ear circumference (cm)	*Adh1*	15.85	15.81	15.44	2.46***	D
	Mdh3	15.52	15.80	15.83	1.48***	PD
	Idh1	15.64	15.80	15.70	0.45*	OD
Ear length (cm)	*Adh1*	14.29	14.21	13.56	2.39***	PD
	Mdh3	13.91	14.22	13.93	0.62**	OD
	Idh1	13.47	14.16	14.54	4.27***	PD
		Second ear				
Grain weight (g)	*Adh1*	8.30	9.41	9.93	0.11	
	Mdh3	7.48	9.80	10.09	0.38*	PD
	Idh1	3.89	9.97	13.69	4.15***	PD
Second ear weight/ total weight	*Adh1*	0.06	0.06	0.07	0.51*	PD
	Mdh3	0.06	0.06	0.06	0.13	
	Idh1	0.03	0.07	0.09	4.55***	PD

*,**,*** Significance levels (0.05, 0.01, 0.001, respectively) of F tests to determine associations of marker loci with quantitative trait loci.
† A = additive, PD = partial dominance, D = dominance, OD = overdominance.

cluding kernel number, row number, kernel weight, ear circumference, and kernel width. For *Idh1*, ear number, ear length, and second ear grain weight appeared to be the major contributing yield component traits. In fact, the Tx303 type homozygous class averaged 0.30 ears more per plant than the CO159 type homozygous class at the *Idh1* marker locus. Harvest index also showed a significant association with *Idh1*.

The significant associations of certain marker loci with an array of yield component traits suggested that the underlying genetic factor(s) might be producing similar effects in several of these yield-related traits. This led to the hypothesis that a linear combination of traits could be found, through a procedure such as principal component analysis, that would more clearly represent the composite effects of the underlying factor(s). If the hypothesis is accepted, then markers linked to these factor(s) should be more strongly associated with the principal component value than with the individual yield-related trait values.

Results of the principal component analyses, how-

ever, did not simplify the relationships among the markers and the quantitative traits. For example, the strong associations in CMT of *Dial* with ear number, kernel number, and second ear weight suggested that a principal component might be found that would account for a greater proportion of the whole plant grain yield differences associated with this locus than any individual related trait. These three yield-related traits did, in fact, show high positive loadings in the second principal component (results not shown). However, genotypic classes at *Dial* accounted for only 2.46% of the variation in this principal component, which is less than for any of the three individual traits (Table 4). Also in CMT, *Amp3* showed strong associations with kernel number, row number, ear circumference and kernel depth; these traits had high positive loadings in the first principal component. Although factors associated with *Amp3* accounted for 9.16% of the variation in this principal component, this locus alone accounted for 11.30 and 9.88% of the variation in ear circumference and kernel depth, respectively.

Principal component analysis provides a statistical averaging of associations across all of the genomic regions represented by the marker loci as well as other unmarked regions affecting trait expressions. The failure of principal component analyses to reveal stronger associations with marker loci than individual traits implies that the average associations arise from numerous genomic regions with very different individual effects, both in type and magnitude. This is advantageous for the plant breeder, however, as it allows for selection among specific marked regions for genotypes with desirable effects on combinations of traits.

Types of Gene Action Associated with Yield and Yield-Related Traits

As indicated by Edwards et al. (1987) estimates of gene action associated with specific marker loci likely reflect the effects of multiple, rather than single, QTL's. In such cases, the contrasts used to estimate types of gene action are sums of recombination-frequency-adjusted directional additive or dominance effects for several contributing QTL's. The additive contrast may, therefore, underestimate the sum of individual additive effects due to opposing positive and negative effects. The directionality of dominance effects, however, is uninfluenced by parental origin of alleles and may be largely unidirectional for traits such as grain yield that consistently exhibit heterosis. For such traits, linkage of multiple QTL's to a marker locus may often result in an overestimation of the dominance/additive ratio associated with individual marker loci. Also, findings of overdominance probably are caused by pseudo-overdominance, i.e., the complementary action of linked loci in repulsion (Crow, 1952). A low level of partial dominance is all that is necessary to give an apparent estimate of overdominance in this case.

Summaries of the number of marker loci exhibiting different types of gene action for grain yield and seven yield-related traits are shown for the two F_2 populations in Tables 7 and 8. Also, types of gene action associated with several individual marker loci are given in Tables 5 and 6. Although the pedigrees for the parental lines are quite different in the two populations

Table 7. Number of marker loci† exhibiting different types of gene action for eight grain yield and yield-related traits in COTX, (CO159 × Tx303)F_2.

	Traits							
Type of gene action‡	Whole plant			Top ear				Second ear
	Grain wt.	Ear no.	Kernel no.	Grain wt.	Row no.	Circum-ference	Length	Grain wt.
A		2			3	1		2
PD	1	3	4	1	8	4	3	4
D	3	2	7	3		3	1	1
OD	8	1	3	8		6	5	2
R^2 (Add)§	0.48	0.78	0.66	0.42	0.91	0.57	0.50	0.68

† For the 15 marker loci segregating 1:2:1.
‡ A = additive, PD = partial dominance, D = dominance, OD = overdominance.
§ R^2 (Add) = average proportion of variance attributable to additive effects for those marker loci showing significant associations with the respective quantitative trait.

Table 8. Number of marker loci† exhibiting different types of gene action for eight grain yield and yield-related traits in CMT, (T232 × CM37)F_2.

	Traits							
Type of gene action‡	Whole plant			Top ear				Second ear
	Grain wt.	Ear no.	Kernel no.	Grain wt.	Row no.	Circum-ference	Length	Grain wt.
A		3			9	4		2
PD	4	2	7	2	3	3	4	7
D	5	2	3	2			3	
OD	5	1	1	11		7	8	
R^2 (Add)§	0.60	0.82	0.76	0.34	0.96	0.63	0.44	0.91

† For the 15 marker loci segregating 1:2:1.
‡ A = additive, PD = partial dominance, D = dominance, OD = overdominance.
§ R^2 (Add) = average proportion of variance attributable to additive effects for those marker loci showing significant associations with the respective quantitative trait.

studied, the types of gene action for the eight traits evaluated are very similar for the two populations (Tables 7 and 8). Both populations showed mostly dominance or overdominance for whole plant grain weight, top ear grain weight, and ear length. Likewise, mainly additive gene action was implicated for ear number, row number, and second ear grain weight in both populations. Ear circumference appeared to be governed by a range of gene action from additive to dominance. Although types of gene action were similar for the two populations, there were considerable differences among the various yield-related traits.

CONCLUSIONS

These investigations in the two F_2 populations, COTX and CMT, demonstrated that isozyme marker loci can be effective in identifying and locating many quantitative trait loci (or genomic regions) affecting the expression of grain yield and 24 yield-related traits. Although about two-thirds of the associations of marker loci with these traits were significant, in more than one-half of the significant relationships the marker loci accounted for less than 2% of the variation of the 25 traits. Some individual marker loci accounted for more than 10% of the trait variation, and differences between phenotypic values of the two homozygous classes

at certain loci exceeded 16% of the population mean. Thus, genetic factors (QTL's or specific genomic regions) that have major effects on grain yield and yield-related traits were detected. These results demonstrated the value of this type of investigation for identifying and locating factors that should be useful for marker-facilitated improvement programs, including intrapopulation selection or transfer of desired factors to other germplasm. Studies involving marker-facilitated breeding approaches are underway and will be reported in subsequent papers.

Results from these investigations provide the impetus for new avenues of research for the quantitative geneticist and plant breeder. Multiple-trait associations with genomic regions are complex and studies are necessary to determine whether these associations can be explained by pleiotropy or by groups of linked factors. In addition, the stability of these identified factors when transferred to other genetic backgrounds and when evaluated in varying environments requires investigation. We are currently conducting studies in several of these areas.

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