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 F₂ populations of maize (Zea mays L.) using isozyme marker loci. (The populations were generated by selfing the F₁, 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

Disciplines
Agronomy and Crop Sciences | Genetics | Plant Breeding and Genetics

Comments

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

C. W. Stuber, M. D. Edwards, and J. F. Wendel

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 F2 populations of maize (Zea mays L.) using isozyme marker loci. (The populations were generated by selfing the F1 hybrids CO159 × Txs03 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 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), Solier 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

1 Joint contribution from the USDA-ARS and the North Carolina ARS, North Carolina State Univ., Raleigh, NC. This investigation was supported in part by USDA Competitive Research Grant 83-CRCA-1-1273 and in part by Natl. Inst. of Health Res. Grant no. GM 11546 from the Natl. Inst. of General Medical Sciences of the USA. Paper no. 10644 of the Journal Series of the North Carolina ARS, Raleigh, NC. Received 11 Aug. 1986.

2 Research geneticist, USDA-ARS, and professor of genetics, North Carolina State Univ., Raleigh, NC 27695-7614; geneticist, USDA-ARS (now with Pillsbury Company, LeSueur, MN); and assistant professor of botany, Iowa State Univ., Ames, IA 50011.
duced and selfed to generate the two F~_ populations (des-

terials were derived from two U.S. maize inbred lines, Tx303

and T232, and two Canadian lines, CO159 and CM37. The

quantitative traits evaluated herein in-

vestigations differed from the earlier studies in that

studies would have reduced the level of linkage dise-

large number of generations of random mating

Experimenl results indicated that selections based

hypothesized that manipulation of allelic frequencies

second ear over total grain weight per plant.

moisture.

moisture.

upon 100 kernel weight/(100 × kernel volume).

thickness × depth × 1/2 (width + base width).

and cob circumference).

end of kernels (calculated from number of rows of kernels

sured perpendicular to ear length, and measured at embryo

circumference).

kernels (calculated from number of rows of kernels and ear

perpendicular to ear length, and measured at widest end of

row and average row length for the whole ear).

sured parallel to ear length, and measured at widest end of

nus cob diameter (mm).

to cob (cob measured with a fabric tape).

form moisture.

moisture.

moisture.

about 37% more than the similar pedigree class. Frei

class. However, the dissimilar pedigree class yielded

significantly higher (10%) than in the similar isozyme

groups. These groups were further subdivided

line pairs were classified into similar and dissimilar

formance among maize inbred lines (Frei et al., 1986a),

markers for predicting single-cross hybrid yield per-

generated from a composite of elite inbred lines pro-

A somewhat similar study conducted in a population

by Stuber et al., it was

Based on these earlier results by Stuber et al., it was

significantly associated with higher grain

CMT plants grown at Clayton, NC. In the two popu-

15 and 18 segregating isozyme loci, respectively, plus

mations, 15 and 18 segregating isozyme loci, respectively, plus

Second ear weight/total weight--Ratio of grain weight of

Top Ear

Whole Plant

Grain weight--Weight (g) of shelled grain dried to uniform

Ear weight--Weight (g) of grain plus cob dried to uniform

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

Kernels per row--Average number of kernels per row.

Kernel density--Weight per unit volume (mg/mm 3) based

Kernel thickness--Average width (ram) of kernels mea-

Kernel depth--One-half of the unshelled ear diameter mi-

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

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

Ear circumference--Circumference (cm) of ear measured

Kernels base width--Average width (mm) of kernels mea-

Kernel width--Average width (mm) measured

Kernel number--Total number of kernels on all ears of

harvest index--Ratio of shelled grain weight over total

100-kernel weight--Weight (g) of 100 kernels dried to uni-

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

Kernels per row--Average number of kernels per row.

Kernel density--Weight per unit volume (mg/mm 3) based

Kernel thickness--Average width (ram) of kernels mea-

Kernel depth--One-half of the unshelled ear diameter mi-

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

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

Ear circumference--Circumference (cm) of ear measured
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, and this proportion was recorded as an R² 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 R² value, as for the individual traits.

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 F₂ 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 F₂ plants which, obviously, could not be replicated. Any replications would involve a different sample of plants from the F₂ 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)F₂, and CMT, (T₂₃₂ × CM₃₇)F₂, 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 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
Robust than the two Canadian lines, CO159 and CM37. From the USA, Tx303 and T232, were much more distributed throughout the genome.

Associated with grain yield and yield-related traits were reflected effects of the same underlying factors (Fig. 6). Tightly linked pairs on chromosome 1, cases, may have reflected the effects of the same QTL(s). Loci were on the same chromosome arm and, in some populations, however, only about one-half of the marker showed significant associations in CMT. In both populations, significant associations were at P < 0.001, viz., 180 were significant. About two-thirds of these statistically significant associations were at P < 0.001, viz., 180 were significant. About two-thirds of these statistically significant associations were at P < 0.001, viz., 180 were significant.

Table 1. Mean values of 25 yield-related traits measured on individual plants in (CO159 x Tx303)F2 and 1930 individual plants in (CO159 x Tx303)F2 (T232 x CM37)F2.

Phenotypic Expression of Yield and Yield-Related Traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>COTX</th>
<th>CMT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole plant grain index</td>
<td>0.81</td>
<td>0.83</td>
</tr>
<tr>
<td>Harvest index</td>
<td>0.45</td>
<td>0.50</td>
</tr>
<tr>
<td>Kernel number</td>
<td>465.64</td>
<td>407.26</td>
</tr>
<tr>
<td>Ear length/ear diameter</td>
<td>2.84</td>
<td>3.68</td>
</tr>
<tr>
<td>Ear length</td>
<td>14.07</td>
<td>15.42</td>
</tr>
<tr>
<td>Ear circumference</td>
<td>15.74</td>
<td>13.23</td>
</tr>
<tr>
<td>100-kernel weight</td>
<td>27.71</td>
<td>31.76</td>
</tr>
<tr>
<td>Kernels per row</td>
<td>27.67</td>
<td>25.25</td>
</tr>
<tr>
<td>Row number</td>
<td>15.65</td>
<td>12.58</td>
</tr>
<tr>
<td>Ear weight</td>
<td>141.92</td>
<td>118.06</td>
</tr>
<tr>
<td>Grain weight</td>
<td>118.66</td>
<td>99.68</td>
</tr>
<tr>
<td>Kernel density</td>
<td>8</td>
<td>8</td>
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<tr>
<td>Kernel thickness</td>
<td>13</td>
<td>13</td>
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<tr>
<td>Kernel depth</td>
<td>17</td>
<td>19</td>
</tr>
<tr>
<td>Kernel volume</td>
<td>9</td>
<td>12</td>
</tr>
<tr>
<td>Kernel base width</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>Kernel width</td>
<td>10</td>
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<tr>
<td>Kernel depth</td>
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<td>19</td>
</tr>
<tr>
<td>Ear length/ear diameter</td>
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</tr>
<tr>
<td>Ear weight</td>
<td>141.92</td>
<td>118.06</td>
</tr>
<tr>
<td>Grain weight</td>
<td>118.66</td>
<td>99.68</td>
</tr>
</tbody>
</table>

Table 2. Number of segregating marker loci that showed significant associations with the 25 yield-related traits in CMT, the maximum number is 500.

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. positive</th>
<th>Total £</th>
<th>CMT No.</th>
<th>CMT %</th>
<th>COTX No.</th>
<th>COTX %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain weight</td>
<td>9</td>
<td>13</td>
<td>13</td>
<td>72</td>
<td>9</td>
<td>48</td>
</tr>
<tr>
<td>Second ear weight/total weight</td>
<td>0</td>
<td>10</td>
<td>10</td>
<td>0</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>Ear weight</td>
<td>13</td>
<td>17</td>
<td>15</td>
<td>9</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>Grain weight</td>
<td>9</td>
<td>13</td>
<td>13</td>
<td>72</td>
<td>9</td>
<td>48</td>
</tr>
<tr>
<td>Harvest index</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>54</td>
<td>9</td>
<td>54</td>
</tr>
<tr>
<td>Grains index</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>54</td>
<td>9</td>
<td>54</td>
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<tr>
<td>Kernel number</td>
<td>16</td>
<td>16</td>
<td>16</td>
<td>96</td>
<td>16</td>
<td>96</td>
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<td>17</td>
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<td>13</td>
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<td>Kernel thickness</td>
<td>13</td>
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<td>Kernel depth</td>
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<td>Kernel volume</td>
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<td>12</td>
<td>12</td>
<td>72</td>
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<td>72</td>
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<tr>
<td>Kernel base width</td>
<td>8</td>
<td>5</td>
<td>5</td>
<td>31</td>
<td>5</td>
<td>31</td>
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<tr>
<td>Kernel width</td>
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<td>10</td>
<td>10</td>
<td>63</td>
<td>10</td>
<td>63</td>
</tr>
<tr>
<td>Kernel depth</td>
<td>17</td>
<td>19</td>
<td>19</td>
<td>114</td>
<td>19</td>
<td>114</td>
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<tr>
<td>Ear length/ear diameter</td>
<td>2.84</td>
<td>3.68</td>
<td>3.68</td>
<td>100</td>
<td>2.84</td>
<td>100</td>
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<tr>
<td>Ear length</td>
<td>14.07</td>
<td>15.42</td>
<td>15.42</td>
<td>100</td>
<td>14.07</td>
<td>100</td>
</tr>
<tr>
<td>Ear circumference</td>
<td>15.74</td>
<td>13.23</td>
<td>13.23</td>
<td>100</td>
<td>15.74</td>
<td>100</td>
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<tr>
<td>100-kernel weight</td>
<td>27.71</td>
<td>31.76</td>
<td>31.76</td>
<td>100</td>
<td>27.71</td>
<td>100</td>
</tr>
<tr>
<td>Kernels per row</td>
<td>27.67</td>
<td>25.25</td>
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<td>88</td>
<td>27.67</td>
<td>88</td>
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<tr>
<td>Row number</td>
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<td>12.58</td>
<td>12.58</td>
<td>80</td>
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<tr>
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<td>88</td>
<td>141.92</td>
<td>88</td>
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<tr>
<td>Grain weight</td>
<td>118.66</td>
<td>99.68</td>
<td>99.68</td>
<td>81</td>
<td>118.66</td>
<td>81</td>
</tr>
</tbody>
</table>

These results clearly demonstrated that highly favorable alleles for these yield-related traits were associated with the positive response to selection in the parental lines. In CMT, 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.
Table 3. Probability level of significant associations between each of 17 segregating marker loci and 25 yield-related traits, percent of total variation ($R^2 \times 100$) 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) F2.

<table>
<thead>
<tr>
<th>Segregating marker locus</th>
<th>Yield-related trait</th>
<th>P</th>
<th>Mdh4</th>
<th>Adhl</th>
<th>Phil</th>
<th>Est8</th>
<th>Mdh3</th>
<th>Acol</th>
<th>Pgm2</th>
<th>Pgdl</th>
<th>Enpl</th>
<th>Hex2</th>
<th>Idh2</th>
<th>Mdh2</th>
<th>Idhl</th>
<th>Acpl</th>
<th>Glul</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Whole plant</td>
<td></td>
<td>C</td>
<td>C</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
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<td>T</td>
</tr>
<tr>
<td>Grain weight</td>
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<td>3.50</td>
<td>2.64</td>
<td>1.59</td>
<td>1.39</td>
<td>0.89</td>
<td>0.92</td>
<td>0.69</td>
<td>1.06</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
<td>T</td>
</tr>
<tr>
<td>Ear number</td>
<td>1.82</td>
<td>0.43</td>
<td>0.35</td>
<td>0.73</td>
<td>0.65</td>
<td>0.38</td>
<td></td>
<td></td>
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<td>T</td>
<td>T</td>
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<tr>
<td>Ear weight</td>
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<td>1.50</td>
<td>0.83</td>
<td>0.88</td>
<td>0.82</td>
<td>0.63</td>
<td>0.95</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td>T</td>
<td>T</td>
<td>T</td>
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<td>T</td>
</tr>
<tr>
<td>Kernel number</td>
<td>0.37</td>
<td>1.17</td>
<td>3.89</td>
<td>3.27</td>
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<td>1.96</td>
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<td>0.90</td>
<td>0.61</td>
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<td>T</td>
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*,**,** Denotes significance levels of F tests at 0.05, 0.01, and 0.001 probability levels, respectively.

Table 4. Probability level of significant associations between each of 20 segregating marker loci and 25 yield-related traits, percent of total variation \( R \times 100 \) 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 \((T232 \times CM37)F_1\).

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<td>2.97</td>
<td>2.22</td>
<td>2.79</td>
<td>3.73</td>
<td>0.38</td>
<td>0.81</td>
<td>3.21</td>
</tr>
<tr>
<td>Kernel depth</td>
<td>1.11</td>
<td>0.58</td>
<td>0.48</td>
<td>0.77</td>
<td>0.98</td>
<td>2.00</td>
<td>1.82</td>
<td>3.22</td>
<td>6.33</td>
<td>6.79</td>
<td>9.88</td>
<td>0.59</td>
<td>0.46</td>
</tr>
<tr>
<td>Kernel thickness</td>
<td>0.29</td>
<td>0.56</td>
<td>1.90</td>
<td>0.66</td>
<td>0.65</td>
<td>0.83</td>
<td>1.58</td>
<td>0.53</td>
<td>1.94</td>
<td>1.78</td>
<td>0.92</td>
<td>1.45</td>
<td>0.55</td>
</tr>
<tr>
<td>Kernel width</td>
<td>2.73</td>
<td>0.50</td>
<td>0.33</td>
<td>0.42</td>
<td>0.50</td>
<td>1.21</td>
<td>1.43</td>
<td>2.41</td>
<td>2.17</td>
<td>2.14</td>
<td>1.45</td>
<td>1.48</td>
<td>5.57</td>
</tr>
</tbody>
</table>
| (continued on next page)
Table 4. Continued.

<table>
<thead>
<tr>
<th>Trait</th>
<th>CO159</th>
<th>CMT</th>
<th>COTX</th>
<th>Tx303</th>
<th>CM37</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kernel volume</td>
<td>0.89</td>
<td>0.82</td>
<td>0.67</td>
<td>0.71</td>
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</tr>
<tr>
<td>Kernel base width</td>
<td>2.32</td>
<td>0.67</td>
<td>0.34</td>
<td>0.71</td>
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<tr>
<td>Yield-related yield</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ear number</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harvest index</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Total ear weight</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Second ear weight</td>
<td></td>
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<tr>
<td>Ear weight</td>
<td>1.10</td>
<td>1.20</td>
<td>6.78</td>
<td>1.03</td>
<td>0.40</td>
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<tr>
<td>Grain weight</td>
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<tr>
<td>Kernel density</td>
<td>1.20</td>
<td>0.96</td>
<td>1.36</td>
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<tr>
<td>Top ear total weight</td>
<td></td>
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</tr>
<tr>
<td>Total plant grain weight</td>
<td>16%</td>
<td></td>
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<tr>
<td>Individual marker loci</td>
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<td></td>
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<tr>
<td>Maximum phenotypic variation</td>
<td></td>
<td></td>
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</tbody>
</table>

Note: The table continues with similar entries for other traits and marker loci. The text mentions that associations individual marker loci accounted for less than 2.0% of the phenotypic variation of the traits in more than one-half of the yield-related traits studied. Differences between the CO159 type homozygous class for four unlinked marker loci accounted for 6 to more than 11% of the variation in ear circumference, kernel depth, top ear length (Tables 3 and 6). Although two-thirds or more of the mean grain weight were largely responsible for grain yield differences at this locus. Differences in harvest index were also strongly associated with this locus. Differences in harvest index were considered conservative, as the true magnitude of the variation from small effects on several yield components increase in more than one-half of the yield-related traits with a maximum of about 5% explained by factors associated with these four marker loci were the same, and the associations evaluated.

*,**,** Denotes significance levels of F tests at 0.05, 0.01, and 0.001 probability levels, respectively.
<table>
<thead>
<tr>
<th>Ear circumference (cm)</th>
<th>Marker</th>
<th>Gene</th>
<th>Type of gene action</th>
<th>$R^2 \times 100$</th>
</tr>
</thead>
<tbody>
<tr>
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</tr>
</tbody>
</table>

**Significance levels:** (0.05, 0.01, 0.001, respectively) of F tests.
rental lines are quite different in the two populations.

Yield-related traits are shown for the two F2 populations.

Adjusted directional additive or dominance effects for a principal component might be found that would account for only 2.46% of the variation in ear number, and second ear weight suggested that strong associations in CMT markers and the quantitative traits. For example, the 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 result in an overestimation of the dominance/additive effect. The directionality of dominance effects, however, is uninfluenced by parental origin of alleles and effects, both in type and magnitude. This is advantageous for the plant breeder, however, as it allows for averaging of associations across all of the genomic regions represented by the marker loci as well as other regions.
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.