Inheritance of the Morphological Differences Between Maize and Teosinte: Comparison of Results for Two F_2 Populations

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ABSTRACT

Molecular marker loci (MMLs) were employed to map quantitative trait loci (QTLs) in an F_2 population derived from a cross of maize (*Zea mays* ssp. *mays*) and its probable progenitor, teosinte (*Z. mays* ssp. *parviglumis*). A total of 50 significant associations (putative QTLs) between the MMLs and nine key traits that distinguish maize and teosinte were identified. Results from this analysis are compared with our previous analysis of an F_2 population derived from a cross of a different variety of maize and another subspecies of teosinte (*Z. mays* ssp. *mexicana*). For traits that measure the architectural differences between maize and teosinte, the two F_2 populations possessed similar suites of QTLs. For traits that measure components of yield, substantially different suites of QTLs were identified in the two populations. QTLs that control about 20% or more of the phenotypic variance for a trait in one population were detected in the other population 81% of the time, while QTLs that control less than 10% of the variance in one population were detected in the other population only 28% of the time. In our previously published analysis of the maize × ssp. *mexicana* population, we identified five regions of the genome that control most of the key morphological differences between maize and teosinte. These same five regions also control most of the differences in the maize × ssp. *parviglumis* population. Results from both populations support the hypothesis that a relatively small number of loci with large effects were involved in the early evolution of the key traits that distinguish maize and teosinte. It is suggested that loci with large effects on morphology may not be a specific feature of crop evolution, but rather a common phenomenon in plant evolution whenever a species invades a new niche with reduced competition.

MAIZE (*Zea mays* ssp. *mays*) and its probable wild ancestor, teosinte (*Z. mays* ssp. *mexicana* or *parviglumis*) differ dramatically in inflorescence morphology despite the fact that they are member of the same biological species (DOEBLEY 1990). Because maize is known only in cultivation while teosinte is a wild plant, it has been proposed that maize is simply a domesticated form of teosinte and that the morphological differences between these taxa are the result of human selection under domestication (BEADLE 1939). In order to define the nature of the genetic events involved in this proposed evolutionary transformation, my colleagues and I used molecular markers to investigate the inheritance of the key morphological traits distinguishing maize and teosinte (DOEBLEY *et al.* 1990; DOEBLEY and STEC 1991). This work provided a detailed picture of the inheritance of the key traits including estimates of the minimum number of QTLs (quantitative trait loci) affecting each trait, the chromosomal locations of these loci, and the magnitude of the effect of each QTL. In the present paper, we report the results from a second experiment in which we again mapped QTLs controlling the morphological differences between maize and teosinte. This experiment employed different maize and teosinte parents, a larger number of F_2 progeny, and more molecular markers. The primary purpose of this experiment was to ask if the results of our first analysis were general or specific to the genotypes we studied. As will be shown, the results of this second experiment are largely congruent with our previous analysis, providing further evidence that the principal genes controlling the dramatic morphological differences between maize and teosinte are largely restricted to five regions of the genome.

MATERIALS AND METHODS

Plant materials: Maize race Reventador (Nay 15) was crossed as the female parent to Balsas teosinte, *Z. mays* ssp. *parviglumis* (*Iltis & Cochrane 81*). A single F_1 plant was grown and self-pollinated. Two hundred-ninety F_2 plants were grown in a winter nursery (1989–1990) on Kauai Island, Hawaii. Race Reventador, a primitive landrace, was chosen as the maize parent because elite maize types are not appropriate for mapping genes involved in the origin of maize since their second generation hybrids with teosinte will simultaneously segregate for the genes differentiating primitive from elite maize (BEADLE 1972, 1980). Balsas teosinte was chosen as the teosinte parent because it is the type of teosinte most likely to be the progenitor of maize (DOEBLEY 1990). The maize and teosinte parents were grown for comparison to the F_2 population. Ten plants of the maize parent were grown in the same winter nursery as

TABLE 1

List of morphological traits analyzed

Trait	Description
CUPR (cupules per rank)	No. of cupules in a single rank
DISA (disarticulation score)	Tendency of ear to shatter (1 to 10 scale)
GLUM (glume score)	Hardness of the outer glume (1 to 10 scale)
LBIL	Average length of internodes in the primary lateral branch
LIBN	No. of branches in primary lateral inflorescence
PEDS (pedicellate spikelet)	Percentage of cupules lacking the pedicellate spikelet
PROL (prolificacy)	No. of ears on the lateral branch
RANK (rank)	No. of rows of cupules
STAM (staminate score)	Percentage of male spikelets in primary lateral inflorescence

the F_2 population. Seed of the teosinte parent failed to germinate that year. Subsequently, eighteen plants of the teosinte parent were grown in a winter nursery (1991–1992) on Molokai Island, Hawaii. In this same nursery, ten additional plants of the maize parent were grown.

Quantitative trait analysis: The differences in inflorescence morphology between maize and teosinte are complex. Previously, we described these differences and defined a system of measurement for quantifying the variance for these differences in maize-teosinte hybrid populations (DOEBLEY and STEC 1991; see also DOEBLEY 1992). This system includes the measurement of nine traits that circumscribe the key differences (Table 1). For the present study, these nine traits were measured as described by DOEBLEY and STEC (1991) except that RANK was measured on the primary lateral inflorescence instead of the secondary lateral inflorescence.

Molecular marker loci (MMLs): Each of the 290 F_2 plants was assayed for its genotype at 82 MMLs (see Figure 1). DNAs were extracted as described by SAGHAI-MAROOF *et al.* (1984) with a slightly modified extraction buffer (100 mM Tris-HCl, 2% mixed alkyltrimethylammonium bromide, 700 mM NaCl, 20 mM EDTA, 1% 2-mercaptoethanol, 1% sodium bisulfite, pH 8.0). Approximately 10 μg of each DNA sample were digested with restriction endonucleases (*Bam*HI, *Eco*RI, *Eco*RV or *Hin*dIII) according to manufacturer's instructions (BRL), size-fractionated in 0.8% agarose electrophoretic gels (100 mM Tris-acetate, 1 mM EDTA, pH 8.1), and transferred to Magna (MSI) nylon membranes without HCl nicking (MANIATIS, FRITSCH and SAMBROOK 1982). Plasmid clones of low-copy-number nuclear DNA sequences of maize were available from Brookhaven National Laboratory (BURR *et al.* 1988), Pioneer Hi-Bred International (BEAVIS and GRANT 1991), Native Plants Incorporated (HELENTJARIS, WEBER and WRIGHT 1988), and University of Missouri-Columbia (COE, HOISINGTON and NEUFFER 1990). Cloned inserts were separated from the plasmid vector in low-melting-point agarose electrophoretic gels and labelled with [^{32}P]dCTP as described by FEINBERG and VOGELSTEIN (1983), except that the labeling reactions were allowed to proceed for 5 hr at 37°. Unincorporated [^{32}P]dCTP was separated from the labeled probe in spun columns (MANIATIS, FRITSCH and SAMBROOK 1982). Nylon filters were prehybridized for 15 min in QuikHyb solution (Stratagene Inc.), then the heat-denatured labeled probe was added to the hybridization vessel, and the hybridization allowed to proceed for 1–1.5 hr at 68°. Following hybridization, the filters were washed two times for 15 min at room temperature in 2 × SSC (0.03 M sodium citrate, 0.3 M NaCl)/0.1% SDS and once for 30 min at 60° in 0.1 × SSC/0.1% SDS. The filters were then wrapped in plastic, and exposed to x-ray film for 18 hr to 8 days.

Statistical analysis: Skewness and kurtosis were calculated for each trait to determine the extent to which they deviated from normality. To correct non-normally distributed traits, transformations were performed to reduced skewness and kurtosis as follows: log of CUPR, LBIL, LIBN, and PROL; square root of STAM; square of GLUM; and cubic root of PEDS. DISA and RANK were not transformed.

Single factor regression was used to estimate the R^2 values for associations between MMLs and morphological traits, and multivariate regression was used to estimate the total proportion of the phenotypic variance (multilocus R^2) simultaneously explained by all observed QTLs (EDWARDS, STUBER and WENDEL 1987). In cases where a trait showed a significant R^2 for two adjacent MMLs, R^2 was recalculated for that chromosomal segment after excluding individuals with detectable recombination events within that segment (KNAPP, BRIDGES and BIRKES 1990). The probability level (P) for rejecting the null hypothesis of no association between a MML and a morphological trait was 0.01.

Interval mapping of QTLs was performed using the computer program MAPMAKER-QTL version 0.9 (LANDER and BOTSTEIN 1989). In these analyses, the LOD score threshold value was set to 2.4 based on Figure 4 of LANDER and BOTSTEIN (1989). MAPMAKER-QTL provides estimates of the percentage of the phenotypic variance explained (PVE) by a QTL (or group of QTLs). These values are equivalent to R^2 values from regression analyses. MAPMAKER-QTL was also used to compare the likelihoods of models involving two QTLs on a single chromosome versus alternative models involving a single QTL.

MMLs were checked for normal Mendelian segregation using LINKAGE-1 version 3.50 (SUITER, WENDEL and CASE 1983). A linkage map for the MMLs was assembled using MAPMAKER version 2.0 (LANDER *et al.* 1987).

RESULTS

Linkage and segregation: Figure 1 shows the linkage map for the 82 MMLs employed in this study. There is a MML within 15 map units of most positions in the genome with the exceptions of the distal portions of chromosome arms *4S* and *7S*. Comparison of the amount of recombination between adjacent markers in the Reventador maize × ssp. *parviglumis* teosinte population (R×P; this paper) and the Chapalote maize × ssp. *mexicana* teosinte population (C×M; DOEBLEY and STEC 1991) reveals greater recombination in the R×P population (Table 2). For 15 sets of adjacent markers that could be compared between the two populations, there are 10 cases in which the difference in the amount of recombination between the two populations exceeds twice the standard error.

For nine of these 10 cases, there is greater recombination in the R×P population.

Fifteen of the 82 MMLs show segregation ratios that differ significantly from Mendelian expectations (1:2:1) for a codominant locus (Table 3). MMLs showing distorted segregation are restricted to four regions of the genome. Eight of the nine markers on chromosome *4* have segregation distortion with a deficiency of the homozygous maize (*MM*) genotype and an excess of the homozygous teosinte (*TT*) genotype. A region on chromosome *8* near *NPI426* also shows strong segregation distortion with a deficiency of maize homozygotes (*MM*) and an excess of heterozygotes (*MT*). There are four additional MMLs that show significant ($P < 0.05$) segregation distortion. Four such significant results would be expected by chance alone given that 82 tests of segregation distortion were performed.

Quantitative traits: The R×P population analyzed in this paper is based on different parents than the C×M population analyzed by DOEBLEY and STEC (1991). The teosinte parents of both populations have the typical teosinte conditions of the key traits. Both teosinte parents have ears with four to five cupules along a single rank (CUPR = 4–5), fully disarticulating ears (DISA = 10), highly indurate glumes (GLUM = 10), long internodes in the lateral branches (LBIL = 17–22 cm), only a single spikelet in each cupule of the ear (PEDS = 1.0), many small secondary ears along each lateral branch (PROL = 8 to 9), the cupules arranged in two ranks (RANK = 2.0), and primary lateral inflorescences that are male or staminate (STAM = 1.0) (Table 4). Similarly, both maize parents possess the typical maize conditions for the key traits including ears with numerous cupules along a single rank (CUPR > 37), ears that remain fully intact at maturity (DISA = 1), relatively soft glumes (GLUM = 1), very short internodes in the lateral branch (LBIL < 1.0 cm), two spikelets in each cupule of the ear (PEDS = 0.0), few or no secondary ears along the lateral branch (PROL ≤ 1.0), multiple ranks of cupules in the ear (RANK > 5.0), and primary lateral inflorescences that are fully female (STAM = 0.0) (Table 4).

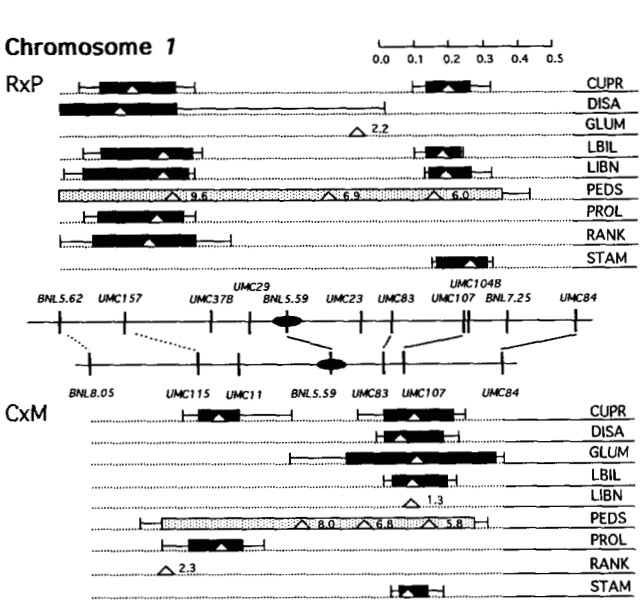
Although both populations were based on crosses of a typical teosinte by a typical primitive maize, the two F_2 populations show different patterns of segregation for at least some of the key traits (Figure 2; Table 4). RANK is strongly bimodally distributed in the C×M population, whereas it is weakly bimodal in the R×P population and has a mean closer to the teosinte parental value. STAM is strongly bimodal in C×M with a mean near the mid-parent value, and unimodal and skewed in R×P with a mean closer to the maize parent value. LBIL is strongly skewed in the R×P population with a mean near the maize parent value, although it is more normally distributed with a mean closer to the mid-parent value in the C×M population. PEDS is highly skewed in both populations, but more so in the C×M population. CUPR and PROL are approximately normally distributed in both populations, but with means closer to the teosinte parental value.

Despite differences in how the traits segregated in the two populations, the structure of the correlation matrices for the traits is similar (Table 5). For example, STAM, LBIL and LIBN show strong positive correlations with one another in both populations. Similarly, PEDS and CUPR show strong negative correlations in both populations.

QTL mapping in the R×P population: A total of 50 independent significant associations between the MMLs and the quantitative traits were detected by regression analysis (Table 6). Each of these associations represents a putative QTL. Each trait shows between four and seven significant associations with R^2 values that range from 3.3 to 49.2%. Of these 50 significant associations, 46 were also detected by interval mapping. The estimates of the proportions of the phenotypic variance explained by the QTLs are similar whether based on regression or interval mapping, although the values (PVE) from interval mapping are generally larger (Table 6). The directions of the effects of the QTLs generally fit the *a priori* expectation that the teosinte alleles at the MMLs should be associated with teosinte-like phenotypes and the maize alleles with maize-like phenotypes. There are, however, six exceptions to this result, most of which involve QTLs with small effects.

The proportion of phenotypic variation explained by all QTLs affecting a single trait was estimated by calculating multilocus R^2 and by interval mapping with multiple QTL models (Table 7). For most traits, approximately 50% or more of the phenotypic variation is explained. The portion of the phenotypic variance not explained by the QTLs could be explained by environment, epistasis, and QTLs too small to be detected by our analyses.

Comparison of the two populations: A principal goal of this research was to determine whether or not the same QTLs affecting the traits occur in both F_2 populations. We considered a QTL for a trait in one population to be putatively the same as a QTL for that trait in the other population if there was overlap in their one-LOD support intervals from interval mapping. Deciding when QTLs were putatively the same in the two populations is complicated by the fact that different MMLs were used in the two populations. In practice, however, this was not a serious problem since most QTLs fell within a few restricted regions of the genome, and there was clear overlap in their one-LOD support intervals (Figure 1). Nevertheless, de-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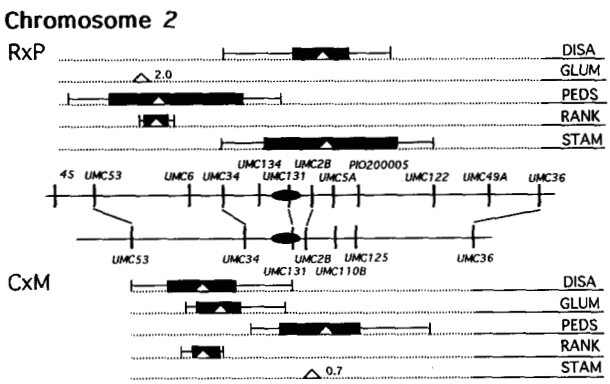
CxM
CUPR
DISA
GLUM
LBIL
LIBN
PEDS
PROL
RANK
STAM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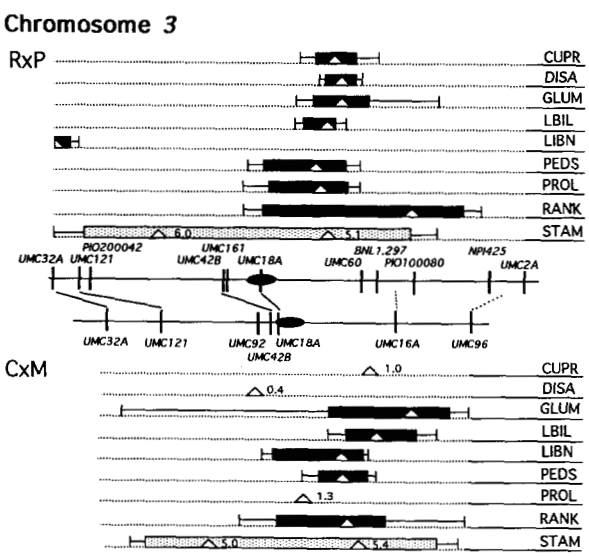
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CUPR
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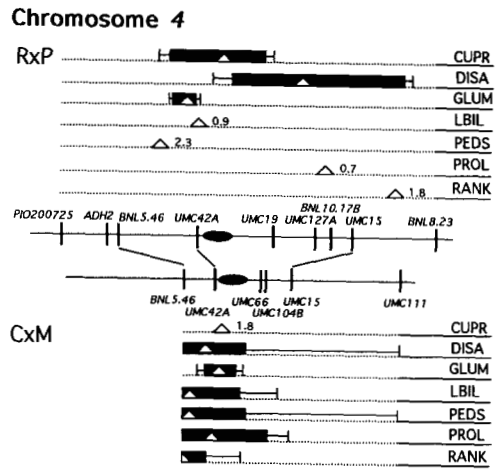
PEDS
PROL
RANK
STAM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CxM
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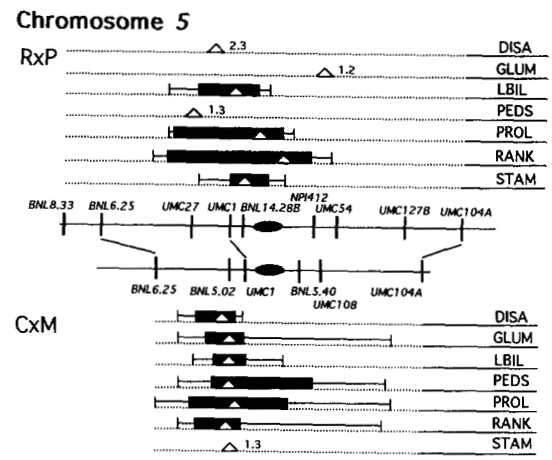
PROL
RANK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CxM
DISA
GLUM
LBIL
PEDS
PROL
RANK
STAM

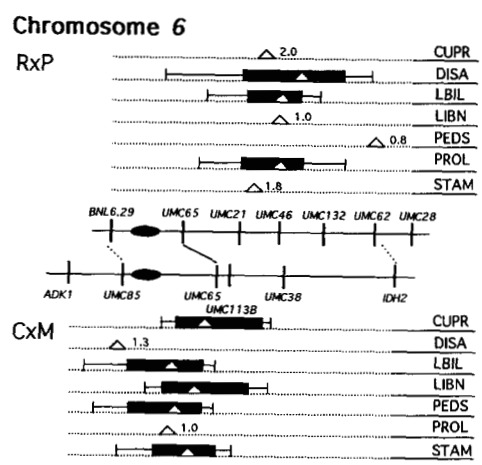
Chromosome 6
RxP
CxM
CUPR
DISA
LBIL
LIBN
PEDS
PROL
STAM

FIGURE 1

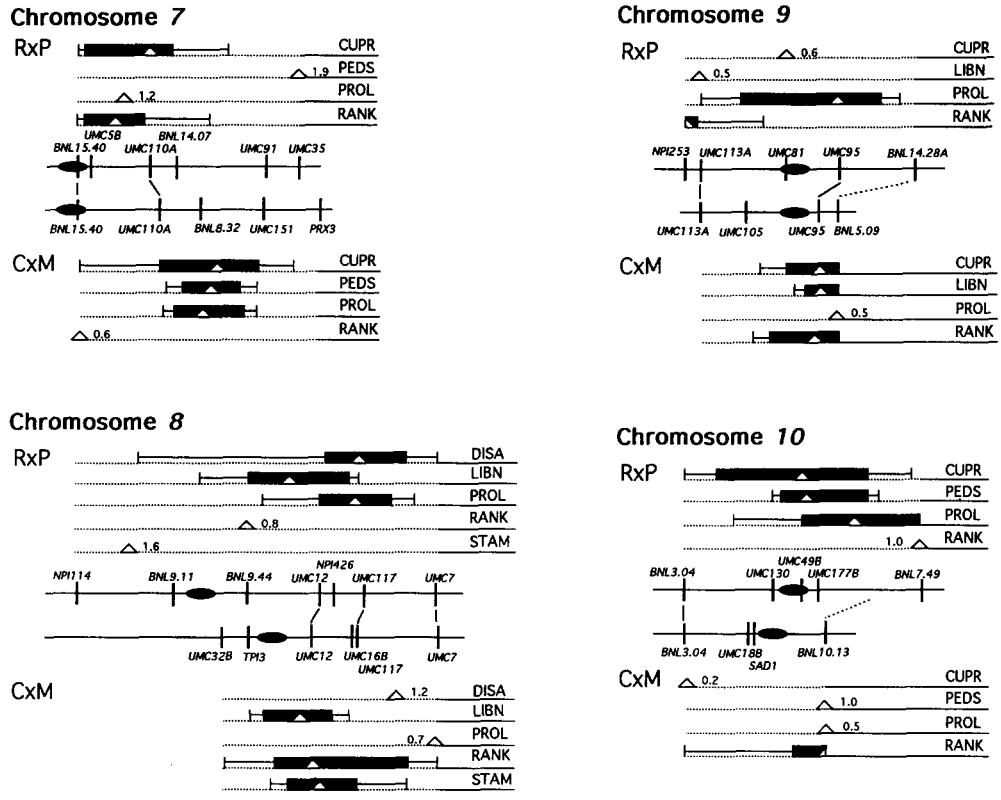

FIGURE 1.—Chromosome maps showing the positions of QTLs detected in the R×P and C×M F_2 populations. QTL positions are indicated by the white triangles with their one-LOD (black cylinders) and two-LOD (whiskers) support intervals. In some cases, the LOD-scores were high along most of the length of the chromosome, suggesting that more than a single QTL was present, but making it difficult to accurately map the QTLs. In these cases, the stippled cylinder indicates LOD > 3.0 and the whiskers LOD > 2.0. The positions and LOD-scores of peaks within these regions are shown. Where a QTL was identified in one population but not the other, the highest peak (although statistically insignificant, LOD < 2.4) is indicated for the other population. The names of the molecular marker loci and the positions of the centromeres (black ovals) are shown on the chromosomes. Diagonal lines show exact (solid line) and approximate (dashed line) points of alignment between the chromosome maps for the two populations. Trait acronyms are explained in Table 1. Scale is recombination units.

TABLE 2

Recombination between adjacent loci in two populations

Adjacent Markers[a]	Population C×M[b]	Population R×P[b]
*BNL5.59-UMC83**	16.7 ± 1.8	31.0 ± 2.5
*UMC83-UMC107**	6.2 ± 1.1	20.6 ± 2.0
UMC107-UMC84	29.8 ± 2.5	31.3 ± 2.5
UMC53-UMC34	32.6 ± 2.7	34.7 ± 2.6
UMC34-UMC131	13.9 ± 1.7	16.5 ± 1.7
*UMC131-UMC2B**	3.8 ± 0.9	6.3 ± 1.1
*UMC32-UMC121**	15.2 ± 1.8	7.4 ± 1.2
*UMC121-UMC42B**	30.2 ± 2.6	40.5 ± 2.9
*UMC42B-UMC18**	2.8 ± 0.7	10.3 ± 1.4
*BNL5.46-UMC42A**	9.0 ± 1.3	23.3 ± 2.1
*UMC42A-UMC15**	20.4 ± 2.0	37.3 ± 2.7
*BNL6.25-UMC1**	26.0 ± 2.4	34.8 ± 2.7
BNL15.40-UMC110	23.7 ± 2.3	19.7 ± 1.9
UMC117-UMC7	23.7 ± 2.2	19.6 ± 1.9
*UMC113-UMC95**	30.8 ± 2.6	36.3 ± 2.7

[a] An asterisk (*) indicates that the percent recombination in the two populations differs by more than two standard errors.

[b] Values, percent recombination ± standard error, were calculated with the computer software program Linkage-1 (SUITER, WENDEL and CASE 1983).

TABLE 3

Loci showing segregation distortion

Chromosome	Locus[a]	Genotype[b] *MM*	*MT*	*TT*
2	*BNL8.45**	64	164	58
2	*UMC34**	73	124	90
2	*UMC5A**	77	124	88
4	*PIO200725**	52	147	88
4	*ADH2***	37	137	116
4	*BNL5.46***	36	130	121
4	*UMC42A***	31	144	114
4	*UMC19**	45	140	99
4	*UMC127A***	51	135	96
4	*BNL10.17B**	51	128	85
4	*UMC15**	55	144	88
8	*UMC12A***	47	167	75
8	*NPI426***	47	167	74
8	*UMC117***	53	172	65
9	*NPI253**	77	153	51

[a] $P < 0.05$; ** $P < 0.01$.

[b] The number of individuals in each of the three genotypic classes is shown. *M* = maize allele; *T* = teosinte allele.

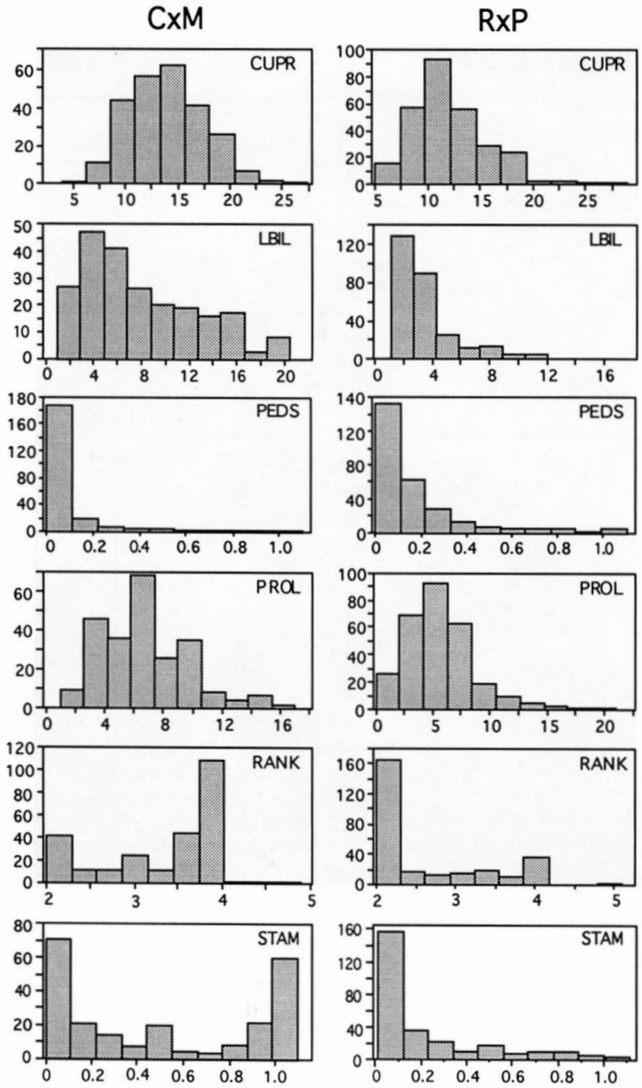

FIGURE 2.—Histograms depicting the frequency distributions of six traits distinguishing maize and teosinte in the C×M and R×P F_2 populations. Column heights (*y*-axis) indicate the number of individual plants in each frequency class. The values for the traits are shown along the *x*-axis. Values for CUPR, PROL and RANK are simple counts, *e.g.*, CUPR is the number of cupules along the length of the ear. Values for LBIL are in centimeters. Values for PEDS and STAM are proportions, *e.g.*, PEDS is the proportion of cupules possessing only a single spikelet.

terminations of whether QTLs in the two populations are indeed the same should be considered preliminary.

Results from the two populations are compared visually using column graphs in which the height of each column corresponds to the size of the effect (R^2-value) of the QTL (Figure 3). The columns from the R×P population (above the *x*-axis) are aligned with the columns from the C×M population (below the *x*-axis) when the QTLs were judged putatively the same, as described above. In the case of QTLs for PEDS on chromosome *1*, the columns are not precisely aligned because the QTLs' positions are uncertain (Figure 1). Both populations show effects for PEDS along most of the length of this chromosome, suggesting that more than a single QTL is present, but making it difficult to precisely locate these QTLs. The presence of a second QTL for PEDS on chromosome *1* in the C×M population is marked by an asterisk (*) because it falls just below the level of statistical significance.

Results of QTL mapping in the R×P and C×M populations revealed similar suites of QTLs controlling some traits, but largely different suites of QTLs for other traits (Figures 1 and 3). For CUPR, both populations possess QTLs in similar positions on chromosome arms *1S* and *1L* with a QTL of large effect on *1L*. Otherwise the control of this trait is quite different in the two populations. DISA also shows considerable difference in the distribution of QTLs in the two populations with only a single QTL on chromosome *4* in common. In contrast, GLUM shows a very similar distribution of QTLs in the two populations with both populations possessing a major QTL on chromosome *4* and minor QTLs on chromosomes *1*, *2* and *3*. LBIL shows a largely similar distribution of QTLs in both populations. LIBN and PROL both show dissimilar distributions of QTLs in the two populations, although, for PROL, both populations possess a QTL of large effect on chromosome arm *1S*. PEDS shows a similar distribution of QTLs with both populations possessing major QTLs on chromosomes *1* and *3*. There are QTLs with large effects on RANK on chromosomes *2* and *5* in both populations. There are QTLs for STAM on chromosome arms *1L*, *3S*, and *3L* in both populations.

In comparing the two populations for the size and location of the QTLs (Figures 1 and 3), the agreement is greatest for QTLs of large effects. In 13 of 16 cases (81%) where a QTL for a trait with an R^2 value of 20% or greater was detected in one population, a QTL for that trait was also detected in the same genomic region in the other population. These values are 16 of 29 cases (55%) for QTLs with R^2 values between 10% and 20%, and only 15 of the 53 cases (28%) for QTLs with R^2 values below 10%.

In our previous analysis of the C×M population (DOEBLEY and STEC 1991), we identified five regions of the genome that controlled most of the differences between the maize and teosinte parents. The same five regions were also the most important in the R×P population. In both populations, chromosome arm *1L* has a large effect on LBIL, PEDS and STAM with smaller effects on several other traits (Figures 1 and 3). Chromosome arm *2S* has the largest effect on RANK in both populations. Chromosome arm *3L* affects several traits in both populations, but principally it affects LBIL, PEDS, and STAM. Chromosome *4* (near the centromere) has the largest effect on GLUM with smaller effects on other traits. A region of chromosome *5* has effects on several traits in both

TABLE 4

Mean values for the key morphological traits

Trait	C×M[a]			R×P		
	Maize	Teosinte	F_2	Maize	Teosinte	F_2
CUPR	37.4	5.3	14.1	44.5	4.6	12.1
DISA	1.0	10.0	6.0	1.0	10.0	5.2
GLUM	1.0	10.0	6.6	1.0	10.0	7.7
LBIL	0.7	21.9	7.9	0.7	17.3	3.6
LIBN	0.0	5.8	3.8	0.0	5.2	0.9
PEDS	0.0	1.0	0.09	0.0	1.0	0.17
PROL	1.0	8.4	6.7	0.4	9.3	5.9
RANK	5.6	2.0	3.3	6.4	2.0	2.6
STAM	0.00	0.97	0.49	0.00	0.94	0.21

[a] Values for the maize and teosinte parents of the C×M population differ slightly from those presented by DOEBLEY and STEC (1991) which were taken from herbarium specimens and a published description of race Chapalote (WELLHAUSEN *et al.* 1952).

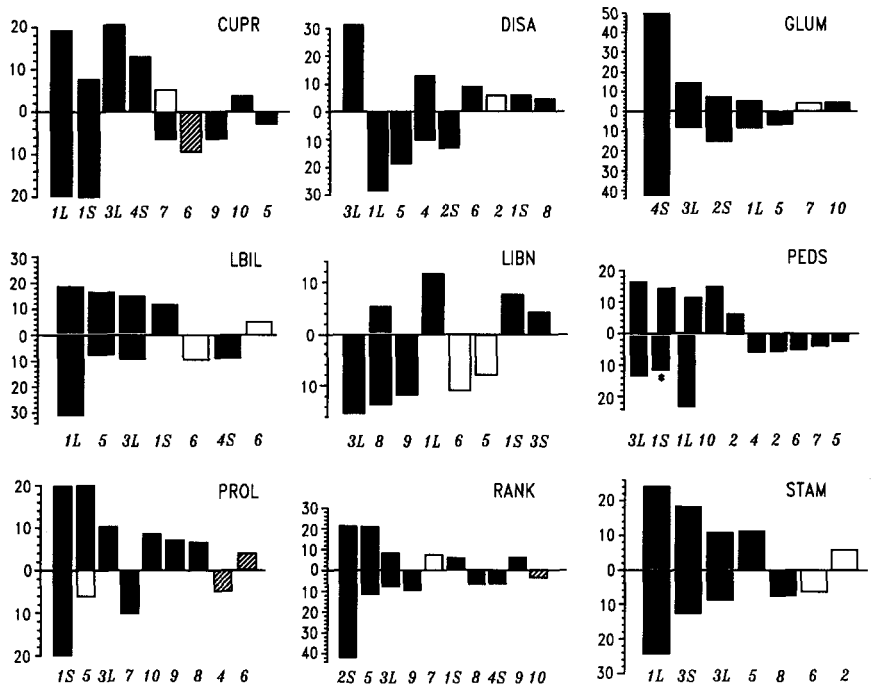

FIGURE 3.—Column graphs showing the number and magnitude of significant associations between molecular marker loci and morphological traits. Results from the R×P population are shown above and the C×M population below the x-axis. The heights of the columns represent the R^2 values from the regression analysis expressed as a percentage (Table 6; DOEBLEY and STEC 1991). The number below each column is the chromosome or chromosome arm on which the effect was detected. The columns from the two populations are aligned above/below one another if they putatively represent the same QTL (see text for discussion of column alignment for PEDS). Columns are white if the effect of the QTL was in the wrong direction (*i.e.*, a teosinte QTL that makes the plant more maize-like or vice versa), and they are striped if there was apparent overdominance. A key to the acronyms for the traits can be found in Table 1.

TABLE 5

Correlation coefficients (r) among the traits

	CUPR	DISA	GLUM	LBIL	LIBN	PEDS	PROL	RANK	STAM
CUPR	—	−0.42	−0.41	−0.22	−0.19	−0.51	−0.30	0.12	−0.24
DISA	−0.28	—	0.30	0.19	0.10	0.40	0.25	−0.13	0.19
GLUM	−0.33	0.50	—	0.01	0.19	0.30	0.12	−0.24	0.10
LBIL	−0.22	0.30	0.35	—	0.47	0.33	0.54	−0.27	0.57
LIBN	−0.10	0.13	0.22	0.47	—	0.26	0.33	−0.14	0.58
PEDS	−0.48	0.27	0.44	0.26	0.23	—	0.37	−0.26	0.26
PROL	0.02	0.02	0.13	0.22	0.23	0.02	—	−0.37	0.38
RANK	0.14	−0.20	−0.40	−0.06	−0.09	−0.28	−0.10	—	−0.21
STAM	−0.25	0.24	0.37	0.75	0.65	0.35	0.15	−0.17	—

Values for the R×P population are in the upper triangle and those for the C×M population are in the lower triangle. Values of r are significant at the $P < 0.05$ level if $r \geq |0.12|$ in the R×P population or $r \geq |0.14|$ in the C×M population.

TABLE 6

Associations between morphological traits and molecular marker loci

Trait	Nearest marker locus	Chr	Dir	Regression R^2	Interval mapping PVE	Interval mapping LOD
CUPR	*UMC157*	1	M	7.1	9.1	6.4
	UMC107	1	M	18.6	20.3	11.0
	UMC60	3	M	21.2	24.6	10.6
	UMC42A	4	M	12.9	12.2	6.0
	UMC110A	7	T	5.0	4.2	2.7
	UMC49B	10	M	3.7	4.1	2.6
DISA	*UMC157*	1	T	4.9	4.3	2.4
	UMC5A	2	M	5.4	4.9	2.7
	UMC60	3	T	31.2	41.7	18.6
	UMC127A	4	T	12.4	11.5	6.5
	UMC46	6	T	7.2	7.5	4.0
	UMC117	8	T	5.4	4.5	2.6
GLUM	*UMC23*	1	T	4.8	NS	NS
	UMC53	2	T	6.7	NS	NS
	UMC60	3	T	14.9	17.5	7.6
	UMC42A	4	T	49.2	62.4	40.6
	UMC110A	7	M	3.3	NS	NS
	UMC49B	10	T	3.6	NS	NS
LBIL	*UMC157*	1	T	10.2	15.4	9.2
	UMC107	1	T	17.4	24.6	10.3
	UMC60	3	T	14.7	45.3	11.7
	BNL14.28B	5	T	16.6	16.8	10.6
	UMC46	6	M	5.2	4.7	3.0
LIBN	*UMC157*	1	T	7.1	14.9	6.8
	UMC107	1	T	11.1	24.3	7.6
	UMC32	3	T	4.3	4.3	2.8
	BNL9.44	8	T	5.2	8.8	3.8
PEDS	*UMC37B*	1	T	14.4	25.1	9.6
	UMC107	1	T	10.6	12.9	6.0
	UMC6	2	T	6.6	8.0	2.9
	UMC60	3	T	16.1	19.3	8.0
	UMC49B	10	T	15.8	15.7	9.9
PROL	*UMC157*	1	T	19.4	24.5	12.9
	UMC60	3	T	10.4	15.5	6.3
	BNL14.28B	5	T	20.3	21.4	12.4
	UMC46	6	O	4.7	3.9	2.4
	UMC117	8	T	6.2	5.6	3.3
	UMC95	9	T	7.2	6.3	3.6
	UMC177B	10	T	7.7	6.4	2.8
RANK	*UMC157*	1	M	4.9	6.0	2.8
	UMC6	2	M	22.0	36.0	15.9
	PIO100080	3	M	7.8	6.2	3.8
	BNL14.28B	5	M	21.0	15.7	6.9
	UMC5B	7	T	6.2	7.4	3.4
	NPI253	9	M	5.1	5.0	3.1
STAM	*UMC104B*	1	T	24.3	22.5	15.9
	UMC5A	2	M	6.0	5.0	3.0
	PIO200042	3	T	16.9	21.3	6.0
	UMC60	3	T	10.5	9.6	5.1
	BNL14.28B	5	T	11.2	9.9	6.4

Chr = chromosome, and Dir = direction of the effect [*i.e.*, whether the maize (M) or teosinte (T) allele contributed positively to the effect or there was apparent overdominance (O)]. R^2 values are from regression analyses, and the percentage of phenotypic variance explained (PVE) and LOD scores are from interval mapping. NS indicates that no significant association was found.

TABLE 7

Percentage of phenotypic variance explained by all observed QTLs

Trait	Method of analysis: Multiple regression	Method of analysis: Interval mapping
CUPR	49.1	61.0
DISA	48.9	60.3
GLUM	61.9	74.5
LBIL	46.9	62.8
LIBN	29.0	41.8
PEDS	58.1	69.4
PROL	56.6	62.8
RANK	48.7	87.1
STAM	46.4	51.9

populations. In the R×P population, 20 of the 25 (80%) QTLs with R^2 values greater than 10% and 24 of the total 50 (48%) QTLs were located in one of these five regions. In the C×M population, these values are 13 of 20 (65%) QTLs with R^2 values greater than 10% and 28 of the total 48 (58%) QTLs. The five regions that encompass these QTLs represent about 20% of the genetic length of the genome.

DISCUSSION

Linkage map: Comparison of the degree of recombination between adjacent MMLs revealed restriction to recombination in the C×M population relative to the R×P population (Table 2). One possible explanation for this phenomenon is the relative genetic distances among the parents. Based on genetic distances calculated from allozyme frequencies, maize is more closely related to ssp. *parviglumis* than it is to ssp. *mexicana* (DOEBLEY, GOODMAN and STUBER 1984). Thus, the C×M population for which ssp. *mexicana* was the teosinte parent represents a wider cross than the R×P population for which ssp. *parviglumis* was the teosinte parent. In a wider cross, one might expect a greater degree of DNA sequence and structural differentiation (small inversions or deletions) between homologous chromosomes that could affect the amount of recombination (STEPHENS 1950; RICK 1963, 1969). Alternatively, the differences in the amount of recombination in the two populations may result from differences between our two maize parents or environmental conditions in which the F_1 plants were grown.

As in our previous analysis (DOEBLEY and STEC 1991), we observed some deviations from the expected Mendelian segregation ratio (1:2:1) for several regions of the genome (Table 3). For the R×P population, MMLs on chromosome *4* showed the greatest degree of segregation distortion. The reason for this result has a clear explanation. The short arm of chromosome *4* possesses a dominant gametophytic incom-

patibility locus (*GA1*) (KERMICLE and ALLEN 1990). Heterozygous plants (*Ga1/ga1*) do not normally accept pollen carrying the *ga1* allele. After we observed the strong segregation distortion for MMLs on this chromosome, we crossed our maize and teosinte parents to a *GA1* tester. Our ssp. *parviglumis*, ssp. *mexicana* and Chapalote parents all carried *Ga1*, while race Reventador maize carried *ga1* (J. Doebley, personal observation). Thus, we observed normal segregation for MMLs on chromosome *4* in the Chapalote by ssp. *mexicana* population, but distorted segregation for the Reventador by ssp. *parviglumis* population in which the F_1 was *Ga1/ga1*. Chromosome *4* carries other incompatibility loci that may also have contributed to the observed segregation distortion (KERMICLE and ALLEN 1990).

Comparison of quantitative trait inheritance in the two populations: Some differences in the inheritance of the traits in the two populations were anticipated for a variety of reasons. First, the two maize parents differ in their degree of similarity to teosinte. Race Chapalote appears more primitive (teosinte-like) than race Reventador by several criteria. It has smaller ears with fewer kernels along its length (lower CUPR) and fewer rows of kernels (lower RANK). It also produces a larger number of ears along the lateral branch (higher PROL) (Table 4). Second, the two teosinte parents represent two subspecies with different time-to-flowering responses. FREELING, BERTRAND-GARCIA and Sinha (1992) showed that genes affecting morphogenesis can behave differently in different time-to-flowering backgrounds. Third, the two F_2 populations were grown in different years and at different locations. PATTERSON *et al.* (1991) demonstrated that environment can have a strong effect on the detection of a QTL. Despite these and other potential sources of variation, the pattern of inheritance in the two populations is quite similar for some traits although very different for others.

The traits that we have analyzed can be divided into two groups. First, DISA, GLUM, LBIL, PEDS, RANK, and STAM measure the principal architectural (structural) differences between maize and teosinte. Maize and teosinte tend to show little variation for these traits, and these traits are stably expressed across environments. Second, CUPR and PROL measure differences in resource allocation, *i.e.*, whether the plant produces many small ears or a single large ear. These are components of yield for which there is considerable variation in maize and teosinte, especially as compared to highly stable traits such as GLUM, PEDS and RANK. The phenotype for CUPR and PROL can be strongly affected when the plants are grown under different environmental conditions.

Below, we discuss the inheritance of the individual traits in the two populations. As will be seen, those traits that define the principal architectural differences between maize and teosinte generally have similar patterns of inheritance in the two populations, while traits related to yield are controlled by largely different suites of QTLs in the two populations. These results might reflect the fact that architectural traits are more stably expressed across different environments, making the detection of QTLs for such traits more reproducible. Interestingly, architectural traits such as LBIL, PEDS, RANK and STAM have nonnormal distributions, while yield components CUPR and PROL have nearly normal distributions (Figure 2).

Cupules per rank: The patterns of inheritance for CUPR are not very similar in the two F_2 populations. Although both populations possess reasonably large QTLs for CUPR on chromosome arms *1S* and *1L*, they differ for all other QTLs. These dissimilarities are not entirely unexpected since CUPR is a component of yield that may not be stably expressed across environments. Moreover, yield components have likely been under continual human selection such that different QTLs for yield were selected in different lineages of maize. In this regard, it is interesting to note that the value for CUPR (6.0–9.0) in the earliest archaeological maize (MANGELSDORF, MACNEISH and GALINAT 1967) is similar to that of teosinte (Table 4). This suggests that selection for higher numbers of cupules per row was not an early event in the evolution of maize, increasing the likelihood that this trait evolved independently in different maize lineages.

Disarticulation: Disarticulation of the ear (DISA) showed one of the most dissimilar patterns of inheritance in the two populations. The two populations share only one potential QTL on chromosome *4* in common. Since this level of difference was not anticipated, we considered several explanations for this result. First, the QTLs controlling ear disarticulation are different in our two teosinte parents. If this is the case, then it may be possible to recover non-disarticulating ears from an F_2 population of our two teosinte parents. Second, the loss of ear disarticulation may have been selected independently in different lineages during the early evolution of maize. Third, we failed to detect the same set of QTLs for artifactual reasons (*e.g.*, differences in the environments in which the F_2 populations were grown) as discussed above.

We have some preliminary evidence that the third explanation partially explains the differences in the inheritance of DISA in the two populations. Preliminary analysis of an isogenic line derived from the R×P population indicates that there is a QTL for DISA on chromosome arm *1L* (J. DOEBLEY and A. STEC, unpublished), although it was not detected in the R×P F_2 population. Thus, both populations appear to possess a QTL for DISA on *1L*.

Glume induration: The evolution of soft glumes is arguably the most important event in the domestication of maize. The hard glume of teosinte, along with the cupule, completely encase the kernel, making the teosinte kernel inaccessible for easy use by humans (BEADLE 1972). Thus, change to the softer glume and exposed kernels of maize was a crucial step that would have dramatically enhanced the utility of teosinte as a crop. Soft glumes are a feature of the earliest archaeological maize (MANGELSDORF, MACNEISH and GALINAT 1967), suggesting that this change took place early in the domestication process. For these reasons, we anticipated a similar pattern of inheritance in the two populations. This expectation was met. In both populations, glume induration was controlled by a major QTL on chromosome *4* and minor QTLs on chromosomes *1*, *2* and *3*.

Lateral branch architecture: The importance of changes in the architecture of the lateral branch in maize evolution has been highlighted by ILTIS (1983). We studied three traits, LBIL, LIBN, and STAM, that measured variation in lateral branch architecture. LBIL and STAM are strongly correlated with one another in both F_2 populations (Table 5), and they probably represent different adult manifestations of a common developmental program. The inheritance of lateral branch internode length (LBIL) is controlled by QTLs on chromosome arms *1L*, *3L* and *5* in both populations (Table 6; Figure 3). The inheritance of the sex of the primary lateral inflorescence (STAM) is controlled by QTLs on chromosome arms *1L*, *3L*, and *3S* in the both populations. As expected, QTLs affecting STAM are located in several of the same regions as those affecting LBIL (Table 6).

DOEBLEY and STEC (1991) suggested that the QTL on chromosome arm *1L* for STAM and LBIL could be the known maize locus, *TB1* (*teosinte branched*). *tb1* causes maize to resemble teosinte, having long lateral branches tipped by tassels. Recently, P. SPRINGER and J. BENNETZEN (*Maize Genetics Newsletter*, 1992, **66:** 116) have shown that *TB1* is 4.5 cM proximal to *ADH1*. This location is within three map units of *UMC107* and thus very close to our QTL for STAM and LBIL. These mapping data and our detection of this QTL in both F_2 populations strengthen the hypothesized role of *TB1* in the evolution of maize.

The inheritance of the number of branches in the inflorescence terminating the primary lateral branch (LIBN) is strikingly different in the two populations. While this may indicate that different suites of QTLs are segregating in the two populations, it is noteworthy that none of the QTLs for LIBN in either population have a particularly large effect (Figure 3). As mentioned above, QTLs of small effect were the least likely to be detected in both populations. This may indicate that LIBN is subjected to considerable environmental effects.

Single vs. paired spikelets: The presence of single *vs.* paired spikelets in the female inflorescence is one of the fundamental architectural differences between maize and teosinte. MANGELSDORF, MACNEISH and GALINAT (1967) reported that paired spikelets were already established in the earliest archaeological maize, suggesting that this trait arose early in maize evolution. For these reasons, we anticipated a similar pattern of inheritance in our two populations. This expectation was met with PEDS being controlled by major QTLs on chromosomes *1* and *3* in both populations.

Prolificacy: During the domestication of maize, humans selected for a reduction in the number of ears on the lateral branches (PROL) and coincidentally for the concentration of resources in a single large ear borne at the apex of the lateral branch. There is some variance for PROL among contemporary Latin American landraces of maize, suggesting the reduction to a single ear was not fully established during the early evolution of maize. The inheritance of PROL was different in the two populations. The two populations share a single QTL on chromosome arm *1S*. This QTL has a large effect ($R^2 = 20\%$) in both populations and may represent an early step in maize evolution.

Inflorescence phyllotaxy: Inflorescence phyllotaxy, the arrangement of organs along the axis of the inflorescence, is a fundamental architectural trait distinguishing maize and teosinte. It is also a component of yield (kernel row number) that has been under continual human selection. The earliest archaeological maize showed four ranks of cupules around the circumference of the ear (MANGELSDORF, MACNEISH and GALINAT 1967), revealing that the switch from two- to four-ranked phyllotaxy was an early event in maize evolution. Over the millennia that followed, higher levels of ranking gradually evolved. The Chapalote parent plant that we used had five ranks of cupules, while the Reventador parent plant had six ranks. Consequently, we anticipated seeing some similarities and some differences in the inheritance of inflorescence phyllotaxy in our two populations.

The inheritance of RANK was similar with both F_2 populations possessing QTLs on chromosomes *2*, *3* and *5*. In the C×M population, the QTL on *2S* has the largest effect, and, in the R×P population, it is one of two major QTLs with R^2-values near 20%. We have investigated the inheritance of RANK further by studying segregation for two- *vs.* four-ranked ears in 131 F_3 families derived from the R×P population (J. DOEBLEY and A. STEC, unpublished). This work has shown that the QTL on *2S* primarily controls the difference between two-ranked (distichous) and four-ranked (decussate) phyllotaxy. Perhaps, this QTL

largely controlled the initial switch from two to four ranks of cupules, while the other QTLs affecting RANK represent either modifier loci or loci involved in the evolution of the higher ranks (five and six) exhibited by the maize parents we used.

QTL distribution: DOEBLEY and STEC (1991) defined five regions on chromosomes *1L*, *2S*, *3L*, *4* and *5S* in the C×M population that encompass most of the QTLs controlling the key differences between maize and teosinte. These same regions controlled most of the variation in the R×P population as well (Figure 1). These five regions possess a high proportion (65–80%) of QTLs with R^2 values greater than 10% despite the fact that they represent about 20% of the genome. The concentration of effects in these five regions of the genome can be explained by single QTLs with pleiotropic effects on several traits, by multiple linked QTLs affecting the individual traits, or, mostly likely, by a mixture of linkage and pleiotropy. If subsequent analyses demonstrate that these regions possess major QTLs with pleiotropic effects on several traits, then these data would lend support to models that selection during evolution acts principally on a relatively small subset of the loci with potential effects on a trait (PATTERSON *et al.* 1991) and that genes of large effect are often important in plant evolution (GOTTLIEB 1984).

In addition to these five regions, there are other regions of the genome that affect several traits in one or both populations. Chromosome arm *1S* is most notable, having a large effect on CUPR and PROL in both populations (Figure 1; Table 6). This region is clearly important in distinguishing maize and teosinte; however, since CUPR and PROL are components of yield rather than fundamental structural differences between maize and teosinte, we suggest that *1S* does not encompass loci involved in the evolution of the key structural differences between maize and teosinte. The QTLs on other chromosomes have mostly small effects, and there are no QTLs of large effect identified in both populations that occur outside the five regions discussed above.

Maize as a model for morphological evolution in plants: Our analysis of this second F_2 population provides additional evidence that the principal differences between maize and teosinte are controlled by five restricted regions of the genome. Moreover, we find no evidence that any of the structural differences between maize and teosinte are polygenic in the sense that they involve many loci with small effects. Rather our data suggest that single traits may be controlled by a small number of QTLs with unequal effects. For example, the evolution of soft glumes might have involved a single major locus plus several modifiers. In this sense, our results lend some support for BEADLE's (1939, 1980) view that a small number of gene changes established the fundamental structural differences between maize and teosinte.

While the model that loci with large effects played a central role in the evolution of maize is still hypothetical, it is interesting to consider whether this mode of evolution is restricted to crop species or might be a more general feature of plant evolution. The early evolution of a crop may be envisioned as a shift from a highly competitive (wild) niche to a new, essentially unoccupied niche (the cultivated field) with much reduced competition. WRIGHT (1982) proposed that species that invade unoccupied niches experience reduced competition, and therefore they are capable of "using" mutations with drastic effects even if these mutations are accompanied by unfavorable pleiotropic effects. Moreover, WRIGHT (1982) suggested that the occupation of new ecological niches "*may require* [emphasis ours] allelic substitutions with major effects" (p. 441). If WRIGHT is right, then the evolution of maize, rather than being a special case, may represent a common mode of evolution, *viz.* the invasion of a new niche. Similarly, the establishment of a new trait under reduced competition might commonly involve few loci of large effect as proposed by WRIGHT. QTLs of large effect appear to be a common feature in the evolution of several crops (PATTERSON *et al.* 1991; FATOKUN *et al.* 1992). The application of QTL mapping to natural progenitor-derivative species pairs will reveal whether this is also a common feature of the evolution of new traits under natural selection in plants.

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