Genetic Analysis of the Morphological Differences Between Maize and Teosinte

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ABSTRACT

Molecular marker loci were used to investigate the inheritance of morphological traits that distinguish maize (*Zea mays* ssp. *mays*) from a closely related wild relative, teosinte (*Z. mays* ssp. *mexicana*). Regression and interval mapping analyses gave largely congruent results concerning the numbers of loci controlling the morphological traits and the magnitudes of their effects; however, interval mapping tended to give larger estimates for the magnitudes of the effects of the morphological trait loci. This tendency was exaggerated for traits that were non-normally distributed. Variation for most inflorescence traits is controlled by one or two regions of the genome with large effects plus several other regions with relatively small effects. As such, the data are congruent with a mode of inheritance for most traits involving one or two major loci plus several minor loci. Regions of the genome with large effects on one trait consistently had smaller effects on several other traits, possibly as a result of pleiotropy. Most of the variation for the dramatic differences in inflorescence morphology between maize and teosinte is explained by five restricted regions of the genome. One of these regions encompasses a previously described gene, *tb1* (teosinte branched), and the effects of this region on inflorescence architecture are similar to the known effects of *tb1*. Implications of this work for the genetic basis of morphological evolution in plants are discussed.

UNDERSTANDING the genetic basis of morphological change is a fundamental concern of both geneticists and evolutionary biologists. Two parameters of primary interest are the number of genes controlling a trait and the relative magnitudes of their effects. Gene number is important because selection could bring a single locus to fixation rapidly within a population, while the joint fixation of many loci would take much longer. However, as noted by MITCHELL-OLDS and RUTLEDGE (1986), the relative magnitudes of the effects are of greater importance because a trait controlled by n polygenes will respond very differently to selection than one controlled by n-1 polygenes plus a major locus.

Interest in the genetic basis of morphological change is heightened by recent observations that plant populations can undergo periods of rapid morphological evolution (HELENURM and GANDERS 1985; GOTTLIEB, WARWICK and FORD 1985; LOWREY and CRAWFORD 1985). Some authors have argued that such major shifts in morphology generally involve the cumulative effects of many loci each with a relatively small effect on the phenotype (CHARLESWORTH, LANDE and SLATKIN 1982; LANDE 1983). Support for this view comes from both theoretical (KIRKPATRICK 1982; LANDE 1983) and empirical studies (VAL 1977; TEMPLETON 1977; LANDE 1981). Authors supporting this view frequently argue that deleterious pleiotropic effects associated with major mutations severely reduce the likelihood of fixation in natural populations (CHARLESWORTH, LANDE and SLATKIN 1982; LANDE 1983).

Recently, some authors have proposed that major shifts in the morphology of plant species can be initiated by mutations with large effects on the phenotype (HILU 1983; GOTTLIEB 1984). GOTTLIEB (1984) proposed that allelic substitutions at only one or two loci can cause major changes in the structure, shape, architectural orientation and presence/absence of plant organs. GOTTLIEB (1984) suggested that the open, plastic system of morphogenesis of plants enables them to adjust to dramatic alterations in morphology without extensive deleterious pleiotropic effects that are seen in animals. Nevertheless, both HILU (1983) and GOTTLIEB (1984) recognized that selection for modifier loci might be required to reduce negative pleiotropic effects or otherwise modify the expression of a major locus.

An often cited example in discussions of the genetic basis of morphological evolution is the origin of the female inflorescence or ear of maize (*Zea mays* L. ssp. *mays*) (SMITH 1981; GOTTLIEB 1984; COYNE and LANDE 1985). The maize ear differs dramatically in architecture from that of its nearest wild relative and presumed progenitor, teosinte (*Zea* spp.). Available biosystematic and fossil evidence suggests that maize is a recent (within the past 10,000 years) domesticated derivative of teosinte (ILTIS 1987; DOEBLEY 1990), and it has been proposed that the evolution of maize from teosinte required only a few thousand years or

TABLE 1

List of morphological traits analyzed

Trait	Description
CUPR (cuples per rank)	Number 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 on the primary lateral branch
LFLN (leaf length)	Length of the fourth leaf from the top of the plant
LIBN	Number of branches in primary lateral inflorescence
PLHT (plant height)	Measured after pollen shed ceased
PEDS (pedicellate spikelet)	Percentage of cupules lacking the pedicellate spikelet
PROL (prolificacy)	Number of ears on the lateral branch
RANK (rank)	Number of rows of cupules
STAM (staminate score)	Percentage of male spikelets in primary lateral inflorescence
TILL (tiller number)	Number of basal shoots (tillers)

less (ILTIS 1987). In this paper, we report the results of an analysis of segregation for both molecular marker loci (MMLs) and morphological traits in a maize-teosinte F_2 population. This approach has enabled us to describe the genetic basis of the morphological differences between maize and teosinte with much greater precision than previously possible. We present minimal estimates of the number of loci affecting morphological traits and estimates of the percentage of phenotypic variation explained by different chromosomal regions.

MATERIALS AND METHODS

Plant materials: Maize race Chapalote (Sin 2) was crossed as the female parent to Chalco teosinte *Z. mays* ssp. *mexicana* (*Doebley 643*). A single F_1 plant was grown and self-pollinated. F_2 seed were planted in a winter nursery on Molokai Island, Hawaii, on November 25, 1988. Of 374 seeds planted, 260 plants were established and used in this study. Race Chapalote was chosen as the maize parent because it is a relatively primitive form of maize as indicated by its small ears with few (10–12) rows of small kernels (WELLHAUSEN *et al.* 1952; *cf.* BENZ 1986). A primitive maize race was chosen because the goal was to analyze genetic differences important in the origin of maize from teosinte and not those that distinguish primitive from advanced maize races. Chalco teosinte was chosen as the teosinte parent because it shows a close genetic relationship to maize as measured by allozyme frequencies (DOEBLEY, GOODMAN and STUBER 1984).

Morphological analysis: A list of the morphological traits analyzed is given in Table 1. Most of these traits define the differences between the architectures of the primary lateral branches (and their inflorescences) of maize and teosinte. To measure these traits, the second primary lateral branch from the top of the plant (see Figure 1B) was collected from each of the 260 F_2 plants and used for the morphological analyses. The length of this branch was measured and the number of internodes in it counted. These values were used to compute the average length of the internodes on the primary lateral branch (LBIL; Table 1). The inflorescences that terminate the primary lateral branches (primary lateral inflorescences) are normally female and unbranched (ears) in maize (Figure 2A) *vs.* male and branched (tassels) in teosinte (Figures 1D and 2D). Thus, the percentage of male spikelets (STAM) in the primary lateral inflorescence was calculated, and the number of branches in the primary lateral inflorescence (LIBN) counted. Prolificacy (PROL) was measured as the total number of inflorescences on the primary lateral branch and its subsidiary branches.

Traits of the inflorescence were measured on the basal-most secondary lateral inflorescence. The number of cupules in a rank (CUPR) along the length of the inflorescence was recorded. CUPR would be six or seven for the inflorescence (ear) depicted in Figure 3A and 22 for the ear in Figure 3G. The extent of disarticulation (DISA) of the ear was subjectively scored on a one (nonshattering) to ten (fully shattering) scale. The degree of induration of the outer glume (GLUM) was subjectively scored on a one (soft) to ten (highly indurate) scale. The presence/absence of the pedicellate spikelet in each cupule (PEDS) can vary among cupules within a single ear. For example, in the ear shown in Figure 4A, the two basal-most cupules lack the pedicellate spikelet while the nine upper cupules contain both the sessile and pedicellate spikelets. Accordingly, PEDS was recorded as the percentage of cupules in the ear lacking a pedicellate spikelet. The number of RANKs of cupules is the number of cupules around the circumference of the ear. RANK is always two in teosinte (Figure 3, A–E) and four or more in maize (Figure 3, F and G). Rank can vary over the length of a single ear of a F_2 plant (Figure 4B) and among ears within a plant (Figure 4C). Accordingly, RANK was scored as the weighted sum of the ranks times the proportion of the ear possessing each rank, and rank was consistently measured on the basal-most secondary lateral inflorescence.

Maize generally exhibits vegetative gigantism and has fewer tillers as compared to more slender, highly tillered teosinte plants. To evaluate these differences, plant height (PLHT), the length of the fourth leaf from the top of the plant (LFLN), and the number of tillers (TILL) were measured.

MMLs: Each of the 260 F_2 plants was assayed for its genotype at 58 MMLs (Figure 5). DNAs were extracted as described by SAGHAI-MAROOF *et al.* (1984) with a slightly modified extraction buffer (100 mM Tris-HCl, 2% mixed alkytrimethyl-ammonium bromide, 700 mM NaCl, 20 mM EDTA, 1% 2-mercaptoethanol, 1% sodium bisulfite, pH 8.0). Approximately 15 μg of each DNA sample were digested with restriction endonucleases (*Eco*RI, *Eco*RV or *Hind*III) 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) and University of Missouri-Columbia (COE, HOISINGTON and NEUFFER 1990). Cloned inserts were separated from the plasmid in low melting point agarose electrophoretic gels, labeled with [^{32}P]dCTP (FEINBERG and VOGELSTEIN 1983), and hybridized to the nylon membranes (HELENTJARIS *et al.* 1985). Isozyme loci were assayed according to previously published procedures (WENDEL and WEEDEN 1989).

Statistical analysis: 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

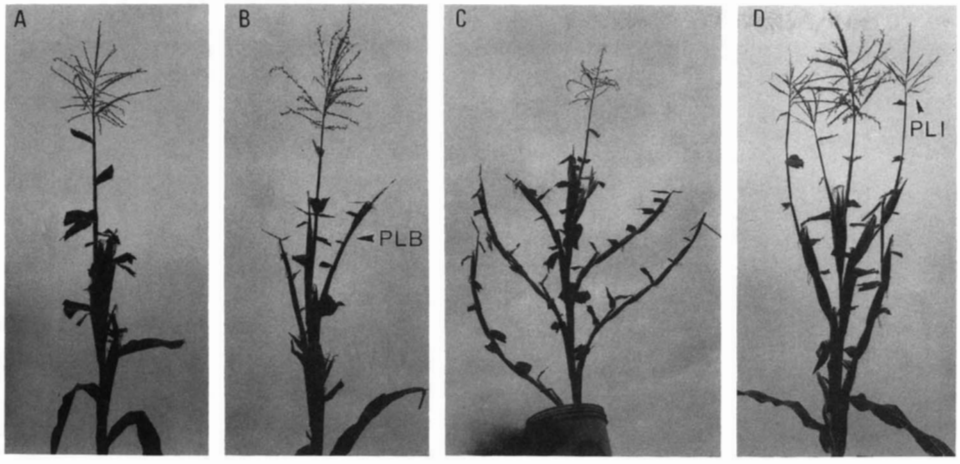

FIGURE 1.—Segregants from a maize-teosinte F_2 population showing the range in branching phenotypes. (A) Maize-like segregant with a short primary lateral branch; (B and C) maize-teosinte intermediate forms; (D) teosinte-like segregant with a long primary lateral branch. PLB primary lateral branch; PLI = primary lateral inflorescence.

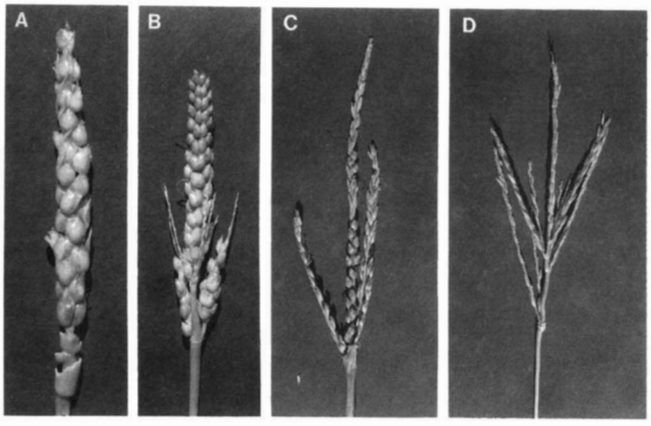

FIGURE 2.—Primary lateral inflorescences of segregants from a maize-teosinte F_2 population showing the range in branching and sex expression. (A) female, unbranched; (B) female, branched; (C) mixed-sex, branched; (D) male, branched.

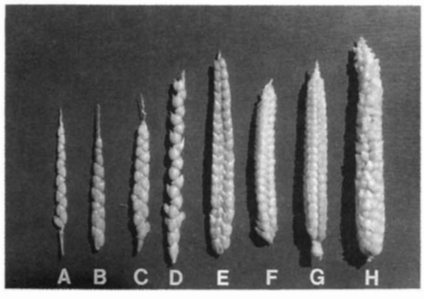

FIGURE 3.—Immature female inflorescences of segregants from a maize-teosinte F_2 population showing the range in spikelet arrangement and inflorescence size. (A) teosinte-like segregant with two ranks of cupulate fruitcases with clear abscission layers between them; (B, C, E) segregants with two ranks of cupulate fruitcases which are fused together; (D) segregant with two ranks of cupulate fruitcases which are slightly displaced from a strict distichous pattern; (F-G) segregants with four ranks of cupules that are fused to form a cob; (H) maize-like segregant with four ranks of cupules fused to form a cob.

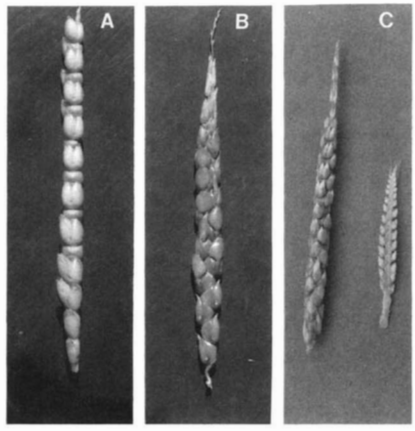

FIGURE 4.—Female inflorescences of segregants from a maize-teosinte F_2 population. (A) pedicellate spikelet absent in the two basal cupules, but present in the upper nine cupules; (B) basal portion of inflorescence two-ranked, upper portion partially three-ranked; (C) four-ranked primary lateral inflorescence and a two-ranked secondary lateral inflorescence from the same plant, demonstrating the effect of position on the number of ranks of cupules.

(multilocus R^2) simultaneously explained by all observed morphological trait loci (EDWARDS, STUBER and WENDEL 1987). These analyses were performed using the raw (untransformed) morphological data (DOEBLEY *et al.* 1990). 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; DOEBLEY *et al.* 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 morphological trait loci (MTLs) 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 2.37 based on Figure 4 of LANDER and BOTSTEIN (1989). MAPMAKER-QTL provides estimates of the percentage of the phenotypic variance explained (PVE) by a trait locus (or group of trait loci) that are equivalent to R^2 values from regression analyses. MAPMAKER-QTL was also used to compare the likelihoods of models involving two trait loci on a single chromosome to alternative models involving a single-trait locus. To correct non-normally distributed traits, transformations were selected to reduced skewness and kurtosis as follows: RANK was squared, and the cubic root of PEDS and the log of LBIL were taken.

To estimate the positions of the MTLs relative to flanking MMLs, we have employed both interval mapping (LANDER and BOTSTEIN 1989) and the flanking markers method (KNAPP, BRIDGES and BIRKES 1990). To test for digenic epistatic interactions, the mean trait expression for the nine possible two-locus genotypic classes were subjected to two-

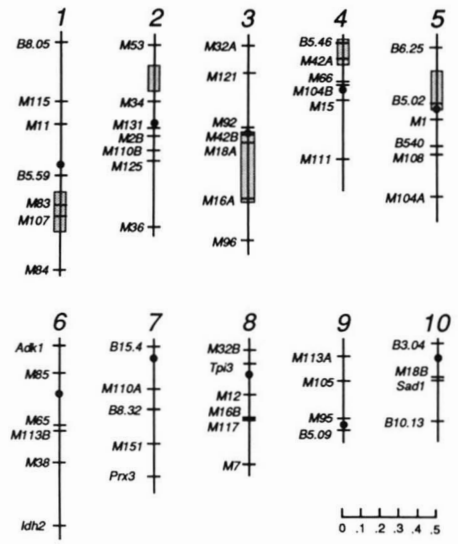

FIGURE 5.—Diagram of the ten teosinte-maize chromosomes showing the distribution of MMLs used in this study. Distances between the MMLs are shown as *r*, the recombination fraction (see scale). Stippled blocks highlight regions with major effects on the morphological differences between maize and teosinte inflorescence architecture (see Figure 7). Prefixes indicate source of cloned MMLs as either University of Missouri-Columbia (M = UMC) or Brookhaven National Laboatory (B = BNL). Five isozyme loci (*Adk1*, *Idh2*, *Prx3*, *Sad1* and *Tpi3*) are shown. Solid circles indicate the approximate positions of the centromeres (COE, HOISINGTON and NEUFFER 1990).

factor analysis of variance. A significant interaction term was interpreted as evidence for epistasis.

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: The 58 MMLs cover the majority of the genome (Figure 5) with a MML within a recombination fraction of 0.2 or less of all regions represented on the University of Missouri RFLP linkage map (COE, HOISINGTON and NEUFFER 1990). Two regions that may not be adequately covered are *8S* and *4S*. In general, distances between MMLs for our maize-teosinte map were smaller than those for the University of Missouri maize map with some regions showing distances only one-fifth as large (Table 2). We emphasize that the distances presented for the two maps in Table 2 are not strictly comparable because of differences in the F_2 population sizes and the presence of many more MMLs on the Missouri maize map. Nevertheless, a consistent trend for smaller map distances in the maize-teosinte map and the magnitude of the differences between the two maps suggests that there is less recombination in the maize-teosinte cross.

Twelve of the 58 MMLs showed distorted Mendelian segregation ratios (Table 3). Nine of the twelve distorted MMLs are found in one of two linkage groups: BNL5.02, BNL5.40, BNL6.25, UMC1 and UMC108 in chromosome *5* and UMC38, UMC65, UMC85 and UMC113B in chromosome *6* (Figure 5).

TABLE 2

Comparative distances for maize and maize-teosinte RFLP linkage maps

Loci[a]	Chromosome	Map distances[b]	
		Maize-maize	Maize-teosinte
UMC107-UMC83	*1*	27.5	6.6
UMC125-UMC2B	*2*	48.5	15.9
UMC2B-UMC131	*2*	19.5	3.9
UMC18-UMC92	*3*	22.9	6.5
UMC15-UMC66	*4*	43.8	8.6
UMC42A-BNL5.46	*4*	44.8	9.8
UMC108-UMC1	*5*	107.4	22.3
UMC38-UMC65	*6*	55.9	22.7
UMC151-UMC125B	*7*	60.9	23.9
UMC117-UMC12	*8*	41.0	15.2
BNL5.09-UMC95	*9*	43.8	5.7

[a] Only those regions in which there was a difference of at least 50% are listed.

[b] Map distances are in cM (Haldane estimates). Data for maize-maize from COE, HOISINGTON and NEUFFER (1990) and that for maize-teosinte from this paper.

TABLE 3

Loci showing segregation distortion

Locus[a]	Chromosome	Genotypes[b]		
		MM	*MT*	*TT*
BNL5.02**	*5*	33	125	91
BNL5.40**	*5*	38	131	90
BNL5.59*	*1*	49	147	64
BNL6.25**	*5*	48	115	89
*Prx3**	*7*	59	148	50
UMC1**	*5*	34	130	94
UMC38**	*6*	43	143	72
UMC65*	*6*	46	133	74
UMC85*	*6*	46	136	77
UMC108**	*5*	40	134	84
UMC113B*	*6*	45	128	74
UMC121*	*3*	42	133	64

[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.

Morphological traits: The dramatic morphological differences between maize and teosinte are readily apparent among segregants in F_2 populations derived from maize-teosinte hybrids. Figure 1 shows variation in branching phenotypes found among F_2 plants. Maize-like segregants possess short primary lateral branches tipped by female inflorescences (Figures 1A and 2A), and teosinte-like segregants possess long, primary lateral branches tipped by male inflorescences or tassels (Figures 1D and 2D). Some segregants bear intermediate length lateral branches (Figure 1, B and C) that are usually tipped with mixed-sex inflorescences (Figure 2C). In our F_2 population, both parental phenotypes for STAM (percentage of male spikelets in the primary lateral inflorescence) were recovered at relatively high frequencies (Table 4). Similarly, the

TABLE 4

Variation for the selected morphological traits

Trait	Mean			Percent of F_2	
	Maize parent	Teosinte parent	F_2	Maize-like	Teosinte-like
CUPR	29.3	6.5	14.1	1.2	1.2
DISA	1	10	6.0	4.8	11.4
GLUM	1	10	6.6	2.0	9.7
LIBN	0	6.1	3.8	27.9	23.3
PEDS	0%	100%	9%	42.0	0.8
RANK	5.6	2.0	3.3	11.4	12.2
STAM	0%	100%	49%	17.4	25.7

parental phenotypes for LIBN, unbranched (Figure 2A) *vs.* branched primary lateral inflorescences (Figure 2D), were recovered at high frequencies (Table 4).

Three traits, RANK, PEDS and CUPR, govern the number of spikelets in the inflorescence. Parental phenotypes for RANK were commonly recovered in the maize-teosinte F_2 population (Table 4). However, the inflorescences of most plants possessed mixed ranks, for example 2-ranked basally and 3-ranked terminally (Figure 4B). PEDS (the percentage of cupules lacking the pedicellate spikelet) was dramatically skewed in the population with the teosinte phenotype being nearly absent and the maize phenotype quite common (Table 4). Parental phenotypes for CUPR (the number of cupules in a single rank along the length of the inflorescence) were recovered only at low frequencies.

GLUM was scored as the degree of induration of the lower glume. The parental phenotypes for this trait were recovered in low to moderate frequencies (Table 4). Parental phenotypes for disarticulation of the inflorescence (DISA) were recovered at low to moderate frequencies (Table 4). Most individuals possessed fragile inflorescences that would fracture under moderate force, whereas the teosinte phenotype fractures at maturity without the application of any force and the maize phenotype does not fracture.

Numbers of MTLs: Table 5 lists the 64 independent significant associations between the MMLs and the morphological traits as determined by both regression and interval mapping analyses. For each trait, there were one to eight independent associations. Of the 64 significant associations, 58 were detected by both regression and interval mapping. Regression detected three associations not detected by interval mapping, and interval mapping detected three associations not found by regression. The six associations not detected by both methods generally had small effects and/or only marginally significant *P* values or LOD scores. Moreover, in some cases where only one method detected a significant association, the other method showed an effect just below the critical value for significance. The three significant associations detected by interval mapping but not by regression all involve a single trait (PEDS), which has more severe kurtosis and skewness than other traits.

When LOD scores were graphed along the length of a chromosome, we observed six cases in which two distinct peaks were separated by well-defined valleys (*i.e.*, a drop in the LOD score of 2.0 or more). For these cases, the likelihood of models involving one *vs.* two MTLs were compared as described by LANDER and BOTSTEIN (1989). The two-MTL model was rejected in four cases; however, for CUPR in chromosome *1* and STAM in chromosome *3*, the data are best explained by the model involving two MTLs (Table 5). The two MTLs for CUPR are 40 recombination units apart, while those for STAM are 43 recombination units apart.

Teosinte and maize are the products of strong disruptive selection: teosinte for survival as a wild plant, and maize for high yield and easy harvestability under domestication. This creates an expectation that maize alleles at MMLs should be consistently associated with a maize-like phenotype and teosinte alleles with a teosinte-like phenotype. The direction of the effects of the MTLs generally conform to this *a priori* expectation for traits that distinguish the inflorescence architectures of maize and teosinte [Table 5, see also DOEBLEY *et al.* (1990)]. This expectation is also met for TILL and LFLN, which reflect differences in vegetative architecture. This expectation does not hold for plant height (PLHT) for which three factors from maize and four factors from teosinte were positively associated with taller plants.

Magnitudes of the effects: R^2 values from the regression analyses range from 3.8 to 42.4% (Table 5). The comparable statistic from interval mapping, PVE (percent of phenotypic variance explained) ranges from 4.5 to 77.5%. In most cases, the values from interval mapping and regression are roughly equivalent; however, where appreciable differences exist, the estimates from interval mapping always exceed those from regression. These discrepancies most often involve traits that are strongly skewed or kurtotic such as LBIL, PEDS and RANK. For example, regression indicates that a MTL in chromosome *2* accounts for 42.4% of the variance in RANK, while interval mapping attributes 77.5% of variance to this MTL (Table 5).

Figure 6 graphically depicts the range in magnitude of the R^2 values for 10 of the 12 traits. RANK shows a single major association ($R^2 = 0.42$) in chromosome *2* and six much smaller effects on other chromosomes. LBIL and GLUM show similar trends with the major association accounting for 42% and 31% of variance, respectively. In contrast, LIBN shows five roughly equal significant associations, none of which explains more than 15% of the variance. Most other traits show patterns intermediate between these two ex-

TABLE 5

Associations between morphological traits and marker loci

Trait	MML	Chr	Dir	Regression R^2	Interval mapping PVE	Interval mapping LOD
CUPR	UMC15-**UMC11**	*1*	M	19.7	24.0	9.3
	UMC107-UMC84	*1*	M	20.1	20.2	11.1
	BNL5.02	*5*	M	3.8	NS	NS
	UMC85-**UMC65**	*6*	O	8.3	13.3	3.8
	BNL8.32	*7*	M	6.0	7.0	3.5
	UMC95-BNL5.09	*9*	M	6.0	5.4	3.0
DISA	UMC83-UMC107	*1*	T	26.0	25.8	13.9
	UMC53-UMC34	*2*	T	12.1	20.4	5.6
	BNL5.46-**UMC42A**	*4*	T	8.6	6.8	2.9
	BNL6.25-**BNL5.02**	*5*	T	16.8	16.8	7.2
GLUM	**UMC107**-UMC84	*1*	T	8.1	6.0	2.7
	UMC34-UMC131	*2*	T	15.4	32.6	8.9
	UMC16A-UMC96	*3*	T	7.5	6.4	2.9
	BNL5.46-**UMC42A**	*4*	T	42.0	44.2	27.7
	BNL5.02	*5*	T	5.6	5.4	3.0
LBIL	UMC107	*1*	T	30.8	29.8	15.4
	UMC16A-UMC96	*3*	T	9.0	24.3	4.6
	BNL5.46-UMC42A	*4*	T	8.1	7.4	3.5
	BNL5.02-UMC1	*5*	T	6.6	6.5	3.2
	UMC85-UMC65	*6*	M	8.8	16.5	4.7
LFLN	**UMC11**-BNL5.59	*1*	M	16.1	20.1	7.3
	UMC131	*2*	M	17.0	18.4	10.5
	UMC42A-UMC16A	*3*	M	4.9	13.1	3.4
	UMC42A	*4*	O	6.3	6.3	3.7
	BNL5.02	*5*	M	7.2	6.4	3.6
	UMC65	*6*	O	5.1	12.5	3.2
	BNL15.40	*7*	M	5.4	5.3	3.0
	UMC12-**UMC16B**	*8*	M	6.1	6.2	3.0
LIBN	UMC42B-**UMC16A**	*3*	T	14.6	42.5	8.4
	BNL6.25	*5*	M	7.4	NS	NS
	UMC65	*6*	M	10.7	14.6	4.6
	Tpi3-**UMC12**	*8*	T	12.8	13.6	6.0
	UMC95-BNL5.09	*9*	T	12.5	10.9	5.8
PEDS	UMC11-UMC83	*1*	T	24.0	28.6	8.0
	UMC2B-UMC110B	*2*	T	4.5	7.3	3.5
	UMC92-UMC16A	*3*	T	13.4	46.1	11.7
	BNL5.46-UMC42A	*4*	T	5.4	4.9	2.4
	BNL5.02	*5*	T	NS	4.9	2.5
	UMC85-UMC65	*6*	M	NS	18.5	3.7
	BNL8.32-UMC151	*7*	T	NS	8.5	4.1
PLHT	**UMC11**-BNL5.59	*1*	M	34.8	42.6	17.4
	UMC2B-UMC125	*2*	M	5.9	5.1	2.7
	UMC42A	*3*	T	4.2	NS	NS
	UMC96	*3*	M	4.5	4.9	2.4
	Tpi3-UMC12	*8*	T	8.0	11.4	4.6
	UMC105-**UMC95**	*9*	T	17.0	19.8	8.1
	Sad1-**BNL10**.13	*10*	T	8.4	10.6	4.4
PROL	**UMC115**-UMC11	*1*	T	19.7	18.8	9.4
	UMC42A	*4*	O	5.4	5.5	2.9
	BNL5.02-UMC1	*5*	M	5.8	5.9	2.9
	BNL8.32-UMC151	*7*	T	10.2	9.4	5.1
RANK	UMC53-**UMC34**	*2*	M	42.4	77.5	32.1
	UMC18A-UMC16A	*3*	M	7.9	17.2	3.7
	BNL5.46	*4*	M	6.7	7.0	4.0
	BNL6.25-**BNL5.02**	*5*	M	11.1	8.6	4.6
	UMC12-UMC16B	*8*	M	6.1	5.1	2.6
	UMC105-**UMC95**	*9*	M	9.6	8.9	4.2
	UMC10.13	*10*	O	4.0	4.5	2.4
STAM	**UMC83**-UMC107	*1*	T	25.6	27.1	15.8
	UMC121-UMC92	*3*	T	14.1	16.3	5.0
	UMC18A-UMC16A	*3*	T	9.4	21.5	5.4
	UMC85-**UMC65**	*6*	M	7.8	14.5	4.2
	UMC12-UMC16B	*8*	T	8.3	7.5	3.6
TILL	UMC83-UMC84	*1*	T	24.1	35.9	14.8

MML = molecular marker loci, 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. In cases where a trait was significantly associated with two adjacent MMLs, both are listed and the MML with the larger associated effect appears in **bold**. If the trait showed roughly equal associations with both MMLs, then neither is in **bold**.

tremes. LFLN shows two moderately large associations (R^2 = 0.17) and six smaller associations. DISA and PEDS both show four significant associations that grade continuously from large to small effects.

In addition to the percent of variance explained by single regions of the genome, we also calculated multilocus estimates of the percentage of phenotypic variance explained for each trait by all observed MTLs (Table 6). Some of these values are surprisingly high. RANK and GLUM, for which single factors explain 42% of the phenotypic variance, have multilocus R^2 values exceeding 0.60. As with the estimates for single regions of the genome, multilocus estimates obtained from interval mapping tend to exceed those from regression analysis. The discrepancies between the two methods of analysis are large for traits that are non-normally distributed (*e.g.*, PEDS) and small for traits that are normally distributed (*e.g.*, LFLN).

Chromosomal locations of MTLs: Table 5 lists the nearest MML or flanking MMLs for each independent significant association between a MML and a trait. For the great majority of the associations, interval mapping and regression concurred on the MML nearest to the MTL or the interval in which the MTL is located. Moreover, estimates of the most probable location for major MTLs obtained from the flanking marker (KNAPP, BRIDGES and BIRKES 1990) and interval mapping (LANDER and BOTSTEIN 1989) methods are generally within a recombination fraction of 0.03 of one another. The only serious discrepancy between these two mapping methods concerns the placement of MTLs controlling PEDS. A MTL for PEDS was placed in the interval BNL5.59-UMC83 in chromosome *1* by flanking marker analysis, while the interval mapping location for this MTL is in the interval UMC11-BNL5.59. The difference in recombination fraction between these two locations is 0.19.

Eight of the twelve traits (CUPR, DISA, GLUM, LBIL, LIBN, PEDS, RANK and STAM) define the differences in inflorescence architecture between

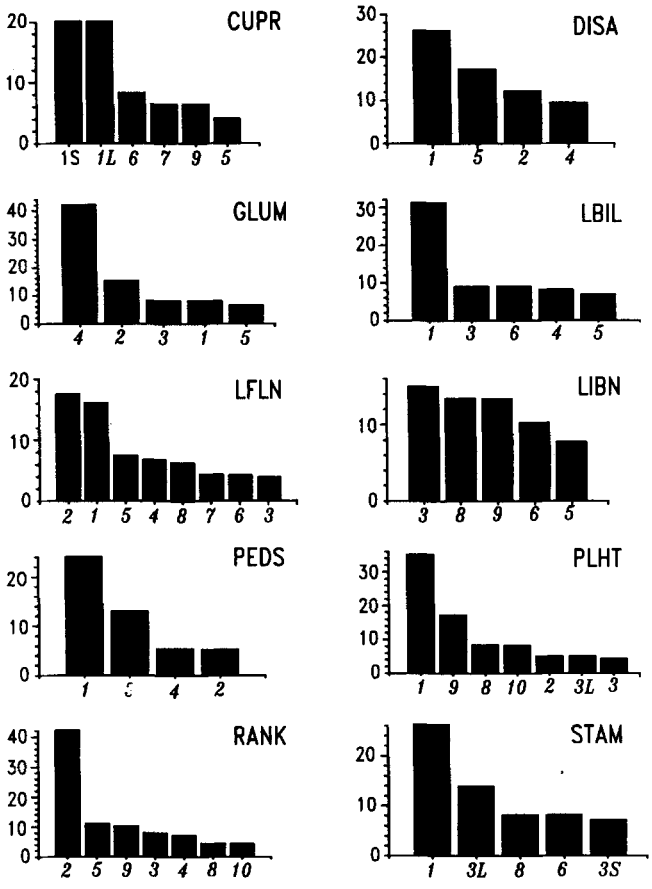

FIGURE 6.—Column graphs showing the number and magnitudes of significant associations between MMLs and the morphological traits. The heights of the columns represent the R^2 values from the regression analysis expressed as a percentage. The numbers below each column are the chromosome or chromosome arm on which the effect was seen. A key to the acronyms for the traits can be found in Table 1.

maize and teosinte. The chromosomal regions with the largest effects on these eight traits have a rather narrow distribution, being found only in chromosomes *1L*, *2S*, *3L* and *4S* (DOEBLEY *et al.* 1990). For five of these traits (CUPR, DISA, LBIL, PEDS and STAM), the largest R^2 values are observed on *1L* near UMC107 (Figures 5 and 7; Table 5). The three remaining traits, RANK, LIBN and GLUM, have their largest significant association in chromosomes *2S*, *3L* and *4S*, respectively. Chromosomal regions that have a large effect on one inflorescence trait tend to have smaller effects on other inflorescence traits (Figure 7). For example, the region near UMC42A on *4S* has a major effect on GLUM and smaller effects on DISA, LBIL, PEDS and RANK (Figure 7; Table 5).

In addition to those regions on *1L*, *2S*, *3L* and *4S* just described, *5S* showed significant associations with seven traits affecting inflorescence architecture. Six of these effects map close to BNL5.02 (Figure 7). Although the effects of the MTLs in this region are generally small (most accounting for less that 10% of phenotypic variance), the large number of significant associations mapping near BNL5.02 suggests that this region has considerable impact on inflorescence architecture.

TABLE 6

Percentage of phenotypic variance explained by all observed MTLs

Trait	Method of analysis: Multiple regression	Method of analysis: Interval mapping
CUPR	45.0	52.2
DISA	52.2	60.3
GLUM	61.1	72.2
LBIL	52.7	63.1
LFLN	50.5	57.4
LIBN	41.7	53.5
PLHT	61.3	67.1
PEDS	39.2	95.3
PROL	34.3	34.4
RANK	61.0	85.4
STAM	55.0	58.7

Epistasis: If all trait-MML combinations are considered, there would be nearly 20,000 tests for digenic epistasis that could be performed. To reduce this to a more manageable number, tests of epistasis were performed only for combinations in which the R^2 values for the main effects of the trait-MML associations exceeded 0.10. In all, 19 tests of epistasis were performed, only one of which was significant (P = 0.0001). This case involved PEDS (Table 7). The data indicate that the teosinte allele for a MTL near UMC107 has little effect on the PEDS phenotype unless the plant also possesses at least one copy of the teosinte allele for a MTL near UMC92. These data help explain the low level of recovery of the teosinte phenotype for PEDS in the population (Table 4).

DISCUSSION

Maize-teosinte linkage map: EMERSON and BEADLE (1932) found that levels of crossover in hybrids of maize and several different types of teosinte were equivalent to those in maize itself, indicating similarity of the maize and teosinte genomes. Contrastingly, recombination between MMLs in our maize-teosinte F_2 population often appeared less than that found between the same MMLs in a maize-maize F_2 population (COE, HOISINGTON and NEUFFER 1990). In some cases, this may be artifactual because there are additional intervening MMLs in the maize-maize population; however, this does not appear to explain all the differences. Differences in recombination rates may indicate restriction to recombination in maize-teosinte hybrids because of structural differences between the genomes of our teosinte and maize parents or a factor (or factors) that regulates recombination throughout the genome (BONIERBALE, PLAISTED and TANKSLEY 1988). Detailed analyses will be required to discriminate among these possibilities.

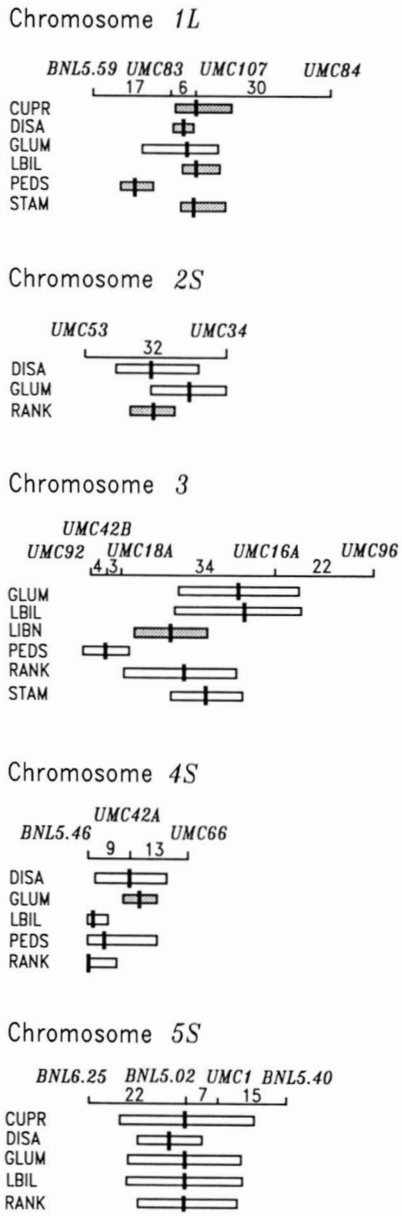

FIGURE 7.—Maps for five regions of the genome with major effects on the differences in inflorescence architecture between maize and teosinte (*cf.* Figure 5. Vertical black bars show the most probable position for the MTL; horizontal bars are the 95% confidence intervals for these positions. Stippled horizontal bars represent associations between traits and MMLs that have the largest R^2 values for that trait. Acronyms for the traits (Table 1) are listed on the left, and MML names are shown above the chromosome. Numbers on the chromosome are the recombination fractions between adjacent markers. MTL positions and confidence intervals were calculated by the flanking marker method (KNAPP, BRIDGES and Birkes 1990).

In recent studies employing MMLs with broad genomic coverage, segregation distortion has been shown to be a common phenomenon. WENDEL, EDWARDS and STUBER (1987) reported segregation distortion for seven of ten chromosomes in a cross between two maize inbreds. PATTERSON *et al.* (1988) reported segregation distortion for 21 distinct regions of the genome in a cross of tomato and a related wild species. BONIERBALE, PLAISTED and TANKSLEY (1988) reported segregation distortion for eight regions in a cross between potato and a related species. In our F_2 population, five independent regions of the genome exhibit distorted segregation ratios. Two of these regions (chromosomes *5* and *6*) show strong distortion with deviations from Mendelian expectations that are highly significant ($P < 0.0$l). The other three regions show much weaker, although significant ($P < 0.05$), distortion. The extent of segregation distort in our F_2 population is no greater and perhaps less than that found in other crosses of crops and their wild relatives.

TABLE 7

Mean expression of PEDS for nine genotypic classes at UMC107 and UMC92

	UMC107		
UMC92	*MM*	*MT*	*TT*
MM	0.03	0.02	0.04
MT	0.02	0.06	0.29
TT	0.06	0.14	0.44

M = maize allele; *T* = teosinte allele. Analysis of these data with two factor ANOVA gave a highly significant interaction term (F = 7.55; P = 0.0001). Values of the maize and teosinte parents for PEDS are 0.0 and 1.0, respectively.

MTL numbers and magnitudes: Through the use of marker loci, we have been able to make the most precise available estimates of the number of genes controlling the dramatic morphological differences between maize and teosinte. However, these estimates are biased because loci with small effects may not be detected and several linked loci with small effects can not be distinguished from a single locus with a large effect (DOEBLEY *et al.* 1990). Thus, our estimates should be considered minimal ones.

Our data indicate that the key traits distinguishing the inflorescences of maize and teosinte are each under multigenic control with minimally four to eight genes affecting each trait. However, a more important observation may be that the effects associated with different regions of the genome vary widely in magnitude. For most traits, one or two regions of the genome (possibly one or two major genes) control a far greater share of the phenotypic variance than other regions affecting the traits (Figure 6). This situation is most pronounced for RANK and GLUM for which single regions of the genome explain over 40% of the phenotypic variance. Although our data can not distinguish between single major loci and a group of linked loci each with small effects, it would seem difficult to argue that our results are consistent with polygenic inheritance in the sense of many genes each with small effects on the phenotype.

Epistasis: Previously, several authors have employed molecular markers to examine epistatic interactions between different regions of the genome in tomato (TANKSLEY, MEDINA-FILHO and RICK 1982;

PATTERSON *et al.* 1988, 1990) and in maize (EDWARDS, STUBER and WENDEL 1987). The tentative conclusion of these studies is that epistasis is not common. One of the 19 tests for digenic epistasis that we performed was significant. This single case of epistasis involved the presence of the pedicellate spikelet (PEDS). This trait was highly skewed with the maize phenotype recovered at high frequency and the teosinte phenotype nearly absent (Table 4). Epistasis appears to explain a significant proportion of the variance for PEDS. Thus, our data disagree with earlier evidence that PEDS is controlled by a single locus (LANGHAM 1940). This discrepancy may be the result of the different maize and teosinte parents used by LANGHAM and us.

Putative major loci: BEADLE (1972, 1980) reported that maize-like and teosinte-like segregants are recovered in maize-teosinte F_2 populations at a frequency of 1:500. BEADLE interpreted this result to mean that there are five independently inherited major genes that distinguish maize and teosinte and he clearly viewed the origin of maize as the result of a small number of mutations each with a major effect on the phenotype. Our results agree well with BEADLE's observations insofar as we have identified five independent regions of the genome that account for much of the phenotypic variance in inflorescence architecture (Figures 5 and 7). Moreover, our analyses have allowed us to identify the specific chromosomal regions in which these factors are located and to associate these regions with effects on specific traits.

A question that can not be answered definitively is whether the five regions of the genome that we have identified represent single major loci or tightly linked groups of loci each with small effects. Furthermore, although each of these regions has effects on several traits, it is not known whether this is the result of the pleiotropic effects of a single locus or independent loci for each of the traits. In the near future, these questions can be approached by fine-mapping the regions of the genome with major effects on one trait or apparent pleiotropic effects on several traits (PATTERSON *et al.* 1990). At present, arguments can be presented that at least some of these five regions encompass loci with major effects on one trait and minor effects on others. We now present these arguments.

Chromosome 1L (teosinte branched, tb1): The long arm of chromosome *1* near UMC107 shows major effects on five of the traits that define inflorescence architecture. Two of these traits, STAM and LBIL, are strongly correlated ($R = 0.75$), distinguishing short primary lateral branches tipped by female inflorescences from long primary lateral branches tipped by male inflorescences. There exists a gene in maize (teosinte-branched, *tb1*) that maps to this region of the genome and produces long primary lateral branches tipped by tassels. *tb1* arose as a spontaneous mutant in a maize population (C. BURNHAM, personal communication). *tb1* affects other traits including CUPR, GLUM and PEDS (J. DOEBLEY, personal observation) for which we also find effects mapping to the region near UMC107. We believe that it is a reasonable hypothesis that most of the effects on inflorescence architecture that map near UMC107 are the result of a single locus with a major effect on several traits. It is noteworthy that *tb1* causes tillering and that our only significant association between tiller number (TILL) and MMLs maps to this same region of the genome.

Chromosome 2S (two-ranked, tr?): LANGHAM (1940) defined *tr*, although he was not able to ascertain its genomic location. Our data provide strong evidence for a major factor controlling RANK on *2S* (Table 5; Figure 7). The region on *2S* affecting RANK also has smaller effects on GLUM and DISA. Because the switch from two-ranked to four-ranked could easily disrupt both the ability of the inflorescence to form abscission layers (disarticulate) and the formation of the outer glume, we believe that it is reasonable to hypothesize that there is a major locus on *2S* controlling RANK and that this locus has smaller pleiotropic effects on DISA and GLUM.

Chromosome 3L: In chromosome *3L* near UMC18A and UMC16A, we identified effects on six of the eight traits used to define inflorescence architecture. They include the largest observed effect on LIBN and smaller effects on GLUM LBIL, PEDS, RANK and STAM. The estimated positions of these putative MTLs are not as tightly clustered as those in the other major regions (Figure 7). This would appear to indicate several loosely linked MTLs; however, it may also be artifactual because of the large interval (34% recombination) between the two markers (UMC18A and UMC16A) flanking these effects. Several of the traits affected by this region of the genome (GLUM, LBIL, PEDS and STAM) are the same as those affected by the region near *tb1*. Three of the traits (LBIL, LIBN and STAM) affected by the region between UMC18A and UMC16A define the differences between long primary lateral branches tipped by branched male inflorescences *vs.* short lateral branches tipped by unbranched female inflorescences. It seems reasonable to hypothesize that there exists a locus in *3L* which affects these traits pleiotropically. There are no known genes in *3L* that can clearly be associated with the effects that we have observed.

Chromosome 4: The short arm of chromosome *4* has a major effect on GLUM and smaller effects on DISA, LBIL, PEDS and RANK (Figures 6 and 7). It is easy to envision how a major locus controlling glume and rachis induration may have pleiotropic effects that would enhance the expression of other traits. A softer

rachis may enhance expression of polystichy (RANK) and inhibit the formation of abscission layers (DISA). Thus, it seems possible that the effects mapping near BNL5.46 and UMC42A in *4S* could result, in part, from a major locus controlling induration that has pleiotropic effects on several other traits.

ROGERS (1950; see also MANGELSDORF 1947) demonstrated linkage between *su* (sugary) in *4S* and glume induration with several types of teosinte. Beadle (1972) suggested that the operative locus was *Tu1* (tunicate) in *4L*, a gene that principally affects glume length. This suggestion has been favorably received in the literature by some (GALINAT 1985; GOTTLIEB 1984). Our analyses call BEADLE's hypothesis into question and indicate that the factor detected by ROGERS is an undescribed gene(s) in *4S*.

Chromosome 5S: A region of *5S* near BNL5.02 affects five of the eight traits that define inflorescence architecture, although its effects on these traits are generally small (Table 5; Figure 7). The effects for four of these five traits mapped precisely to the marker locus (BNL5.02). It will be of interest to isolate this region in an isogenic background and to better characterize its effects on inflorescence morphology.

Implications for morphological evolution in plants: In this paper, we describe the genetic control of the morphological traits involved in the evolution (domestication) of maize. While the mode of evolution under domestication clearly does not apply to all or even many examples of evolution under natural selection, it may parallel cases of natural evolution involving strong selection for a new trait.

While our evidence from maize is compatible with a mode of inheritance for several inflorescence traits involving one or two major loci plus modifiers, this interpretation does not necessitate that genes with major effects resulted from single major mutations. A series of stepwise mutations at a single locus could create alleles with dramatically different effects, although as the result of incremental rather than revolutionary changes. Thus, our data do not enable us to infer whether maize evolution involved (1) an initial phase during which mutations with large effects dramatically altered inflorescence morphology followed by a refinement phase during which modifier loci were selected to stabilize the expression of the traits, or (2) an incremental process composed of a series of small steps.

Whether major shifts in plant morphology generally result from few or many genes is currently under debate (HILU 1983; GOTTLIEB 1984; COYNE and LANDE 1985). Authors on both sides of this debate have relied largely on theoretical or indirect evidence. Given the nature and extent of the available evidence, it would seem prudent to retain an open mind and encourage empirical studies that will provide more direct evidence on the genetic basis of morphological differences (SMITH 1981; BARTON and TURELLI 1989). If, as we believe, evolution is opportunistic, one would predict that major shifts in the morphological traits of plants could be controlled by the full range of genetic mechanisms from few genes with large effects to many genes with small effects. The relative importance in plant evolution of these contrasting modes of inheritance remains to be determined. The use of molecular markers provides the most powerful available means for determining the minimum number of genes governing morphological differences and the relative magnitudes of their effects (ZENG, HOULE and COCKERHAM 1990). Determining whether loci with major effects on morphology generally evolve by single major mutations or by a series of small stepwise mutations will be a more difficult task.

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