

Patterns of Isozyme Variation between Maize and Mexican Annual Teosinte¹

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Isozyme variation in 94 accessions of Mexican maize (Zea mays ssp. mays) and 37 collections of Mexican annual teosinte (Z. mays ssp. mexicana and var. parviglumis) are compared. Variety parviglumis (a predominantly wild plant) shows a closer genetic relationship to maize than does ssp. mexicana (a weedy teosinte often found in maize fields). The isozyme data suggest that maize and Z. mays var. parviglumis share a more recent common ancestor than either of these taxa share with other members of the genus Zea. In this sense, the isozyme data support the theory that maize is a domesticated form of teosinte. Isozyme data provide no evidence for independent origin of Mexican maize races from different taxa of teosinte. Isozyme analysis suggests that gene flow between maize and ssp. mexicana exists, but that it is highly restricted and more probably goes from weed into crop. Maize and var. parviglumis are isozymically too similar and too variable to allow patterns of gene flow between them (if any) to be discerned. The maize-teosinte complex does not fit a model applied to some other crops in that (1) weedy teosinte (ssp. mexicana) does not appear to be a hybrid of the wild form (var. parviglumis) and maize and (2) the weedy form does not act as a genetic bridge between wild form and crop.

Evolutionists studying crops and their wild relatives have focused much attention on (1) establishing which particular wild taxon gave rise to the cultivar and (2) the extent of genetic interchange between cultivated and wild forms once the domestication process is complete. The first question has been addressed for most important crop species; in approaching it, a broad range of morphological, genetic, and biochemical studies has been employed. The second question, however, has rarely been addressed experimentally although speculation on the topic abounds.

Recently, we have completed a survey of isozyme variation in Mexican maize (*Zea mays* L. ssp. *mays*) and the teosintes (*Zea* spp.) (Poaceae), the close wild relatives of maize (Doebley et al. 1984, 1985; Wilkes 1967). In these studies, we have examined patterns of isozyme variation in teosinte and in Mexican maize and have also addressed the question of the origin of maize. The isozyme data suggest that maize and a Mexican annual teosinte (*Z. mays* ssp. *parviglumis* Iltis and Doebley var. *parviglumis*) share a more recent common ancestor than either of these taxa share with other members of *Zea*. In this sense, the first author regards the isozyme data as supporting the theory that maize is a domesticated form of teosinte (cf. Smith et al. 1985). This work and other studies performed in the laboratory of the second and third authors (Doebley et al. 1983; Goodman and Stuber 1983a; Smith et al. 1984, 1985; Stuber and Goodman 1983) probably

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make maize and its wild relatives more thoroughly analyzed for isozymes than any other crop-progenitor complex. In the present paper, we look more closely at the relationship between maize and those teosintes most closely related to it, and assess the degree of reciprocal gene exchange between them.

TAXONOMIC AND EVOLUTIONARY BACKGROUND

The genus *Zea* is composed of section *Luxuriantes* including *Z. luxurians* (Durieu and Ascherson) Bird, *Z. diploperennis* Iltis, Doebley, and Guzman, and *Z. perennis* (Hitchc.) Reeves and Mangelsdorf; and section *Zea* including *Z. mays* ssp. *mays* (maize), *Z. mays* ssp. *mexicana* (Schrader) Iltis (central Mexican annual teosinte), and *Z. mays* ssp. *parviglumis*. The last subspecies is composed of var. *parviglumis* (southern and western Mexican annual teosinte) and var. *huehuetenangensis* Iltis and Doebley (western Guatemalan annual teosinte) (Iltis and Doebley 1980). The species of section *Luxuriantes* are clearly distinguished from maize by a number of morphological, biochemical, and genetic characteristics (Doebley 1983; Doebley et al. 1984; Timothy et al. 1979). Of the taxa of section *Zea*, only *Z. mays* var. *huehuetenangensis* is clearly differentiated from maize by several independent lines of evidence (Doebley et al. 1984; Kato 1976; Smith et al. 1985). The remaining wild taxa are the Mexican annual teosintes, *Z. mays* ssp. *mexicana* and var. *parviglumis*. Together with maize, these two taxa form a complex of genetically similar populations on which the present paper focuses.

Presently, the Mexican annual teosintes are known from Chihuahua in northern Mexico to Oaxaca in southern Mexico. Relationships among these populations are not clinal, but rather there is a sharp discontinuity along the Trans-Mexican Volcanic Belt. Populations north of this line (above 1,700 m) belong to ssp. *mexicana*; populations south of it (below 1,700 m) are in var. *parviglumis* (Fig. 1). This division is supported by morphological (Doebley 1983; Iltis and Doebley 1980), ecological (Doebley 1984), and isozyme (Doebley et al. 1984) evidence. Subspecies *mexicana* occurs mostly as a weed in maize fields or in other habitats disturbed by people. It commonly crosses with maize, and some F_1 hybrids are found in most populations. Variety *parviglumis* occurs most commonly as a part of the natural vegetation along streams, in arroyos, and in prairies, although usually within a few hundred meters of maize fields. Hybrids of var. *parviglumis* and maize are uncommon, and most populations of this teosinte lack them entirely.

Reciprocal introgression between Mexican annual teosinte and maize has been the subject of numerous papers since the beginning of this century (see Doebley 1984 for a review). From field observations alone, several authors have proposed extensive reciprocal introgression between Mexican annual teosinte and maize (Collins 1921; Wilkes 1970, 1977). Galinat (1973) outlined a genetic mechanism by which this gene exchange could take place: "Apparently, the Mexican teosintes and their maize partners have undergone a coevolution that permits a *constant gene flow between them* [emphasis ours] while maintaining their distinctive female spikes through block inheritance of controlling genes." The supposition that teosintes are substantially introgressed by maize has frequently been cited in reviews on introgression (Barrett 1983; Heiser 1973; Ladizinsky 1985). However, some have argued against extensive introgression between maize and Mexican annual teosinte on the basis of cytology (Kato 1976, 1984) and field observations (Doebley 1984).

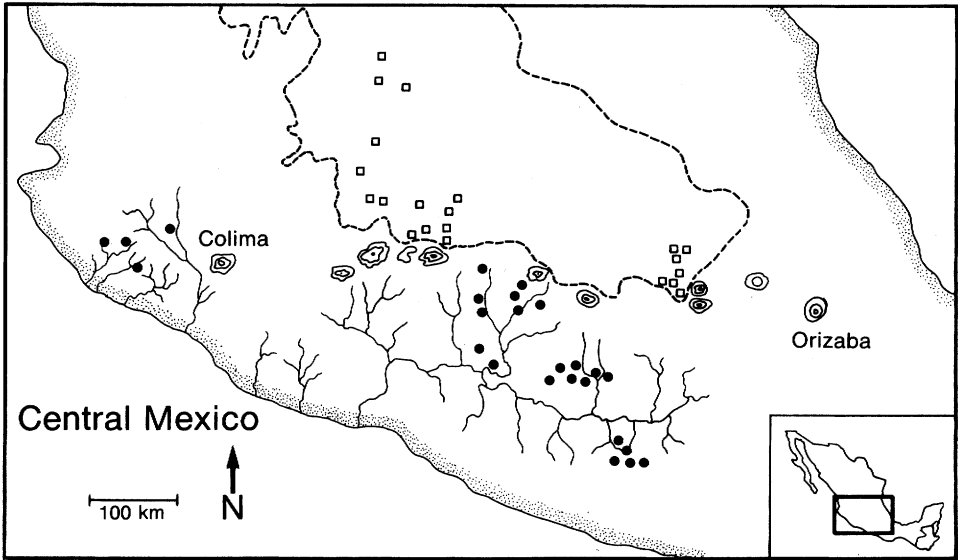


Fig. 1. Map showing distribution of Mexican annual teosinte in central Mexico. Populations of *Zea mays* var. *parviglumis* (●) occupy the river valleys (below 1,700 m) of southern and western Mexico. Populations of *Z. mays* ssp. *mexicana* (□) occupy the Mesa Central (above 1,700 m) of central Mexico. A string of volcanic mountains from Colima in the west to Orizaba in the east (the Trans-Mexican Volcanic Belt) divides the regions in which these taxa occur. Dashed line shows the approximate boundary of the Mesa Central and its extension into the Valley of Mexico.

MATERIALS AND METHODS

The isozyme data used here for comparison of maize and teosinte have been previously reported (Doebley et al. 1984, 1985). Ninety-four collections of maize (12 plants each and 37 collections of Mexican annual teosinte (9 to 25 plants each) were examined (Appendix 1). The 21 enzyme loci assayed and their chromosomal locations are listed in Table 1. The electrophoretic techniques and genetic analyses have been described elsewhere (Cardy et al. 1980; Goodman and

TABLE 1. LOCI STUDIED AND THEIR CHROMOSOMAL LOCATIONS.^a

Locus	Chromosome ^b	Locus	Chromosome
<i>Acp1</i>	9	<i>Mdh1</i>	8
<i>Adh1</i>	1L	<i>Mdh2</i>	6L
<i>Cat3</i>	?	<i>Mdh3</i>	3L
<i>Enp1</i>	6L	<i>Mdh4</i>	1L
<i>E8</i>	3S	<i>Mdh5</i>	5S
<i>Glu1</i>	10	<i>Mmm</i>	1L
<i>Got1</i>	3L	<i>Pgd1</i>	6L
<i>Got2</i>	5L	<i>Pgd2</i>	3L
<i>Got3</i>	5S	<i>Pgm1</i>	1L
<i>Idh2</i>	6L	<i>Pgm2</i>	5S
		<i>Phi1</i>	1L

^a From Goodman and Stuber 1983b.

^b L = Long arm; S = Short arm.

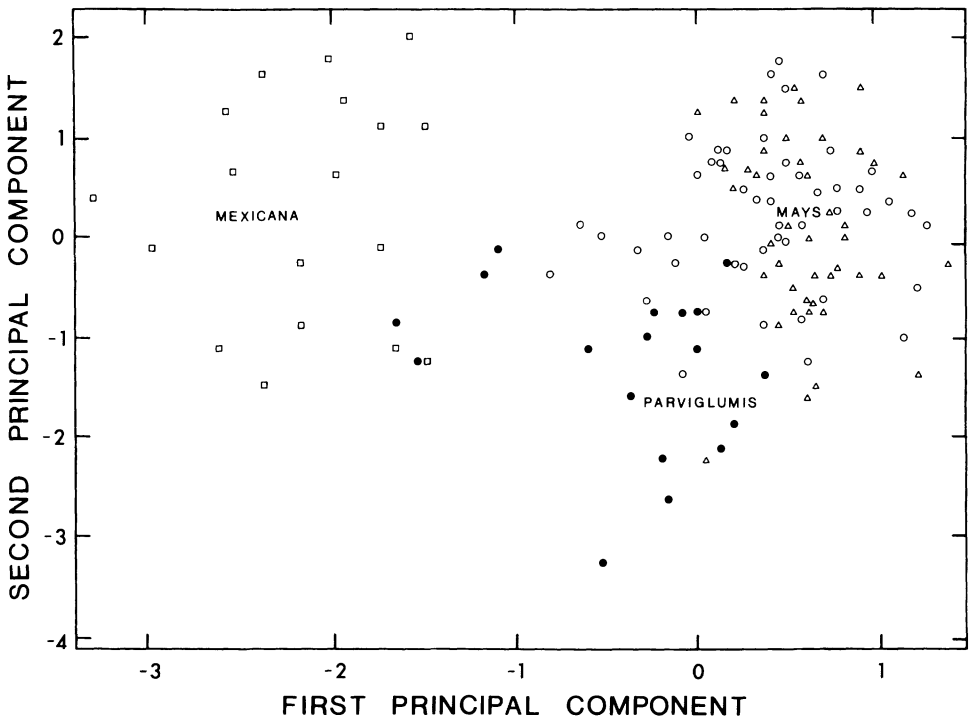


Fig. 2. Graph of the first two axes from a principal component analysis of 136 collections of maize and Mexican annual teosinte. The first component contains 22.1% of total variation; the second component, 8.4%. \square = *Zea mays* ssp. *mexicana*, \bullet = *Z. mays* var. *parviglumis*, \circ = *Z. mays* ssp. *mays* (northern, high-altitude complex), and \triangle = ssp. *mays* (southern, low-altitude complex).

Stuber 1983b; Stuber and Goodman 1983). The maize collections studied represent racial variation in this cultigen in Mexico available from germplasm banks (Centro Internacional de Mejoramiento de Maíz y Trigo, and the Instituto Nacional de Investigaciones Agrícolas of Mexico) and were chosen in a manner to maximize altitudinal and geographic variation (Doebley et al. 1985). The collections of Mexican annual teosinte are derived from all regions of Mexico from which seeds of this plant are available (Doebley et al. 1984). Full locality data for the collections can be found in our original publications.

RESULTS AND DISCUSSION

Figure 2 is a graph of the first two components from a principal component analysis based on the variance-covariance matrix of allele frequencies for all 131 populations of maize and Mexican annual teosinte. Principal component scores of the individual collections are listed in Appendix 1. As shown in our previous studies with a smaller sample of maize, *Z. mays* ssp. *mexicana* is isozymically fully distinct from maize. *Zea mays* var. *parviglumis* has a much closer isozymic relationship to maize, and populations of these taxa overlap along both axes of Fig. 2. Given that var. *parviglumis* and maize are isozymically more similar to one another than either is to any other member of *Zea*, it is reasonable to suggest that maize and var. *parviglumis* share a more recent common ancestor with one

TABLE 2. SIGNIFICANT SPEARMAN'S CORRELATION COEFFICIENTS BETWEEN ALLELE FREQUENCIES AND ALTITUDE FOR 37 POPULATIONS OF MEXICAN ANNUAL TEOSINTE.

Locus-allele	\bar{r}	<i>P</i>
<i>Got1-5.8</i>	0.792	<0.01
<i>Got1-4</i>	-0.748	<0.01
<i>Acp1-2</i>	0.673	<0.01
<i>Enp1-14</i>	0.644	<0.01
<i>Glu1-3</i>	-0.609	<0.01
<i>Glu1-8</i>	0.597	<0.01
<i>Phil-4</i>	-0.594	<0.01
<i>Phil-3</i>	0.578	<0.01
<i>Acp1-4</i>	-0.572	<0.01
<i>Pgm1-9</i>	-0.568	<0.01
<i>Pgm1-16</i>	0.466	<0.01
<i>Glu1-7</i>	0.456	<0.01
<i>Glu1-n</i>	-0.437	<0.01
<i>Enp1-4</i>	-0.432	<0.01
<i>Mdh3-16</i>	-0.419	<0.01
<i>Enp1-6</i>	-0.417	<0.05
<i>Mdh4-14</i>	-0.403	<0.05
<i>Pgm1-16.5</i>	0.387	<0.05
<i>Mdh3-18</i>	0.375	<0.05
<i>Pgd1-2</i>	-0.373	<0.05
<i>Mdh2-3.5</i>	0.373	<0.05
<i>Mdh1-4</i>	0.368	<0.05
<i>Glu1-7.2</i>	-0.365	<0.05
<i>Got1-1</i>	-0.365	<0.05
<i>Pgd1-3.8</i>	0.350	<0.05

another than they do with other members of *Zea*. Further, one may propose that the common ancestor of var. *parviglumis* and maize was a teosinte. Maize is an obligate cultigen unable to survive without sowing and harvesting by people. Teosinte is a wild plant that grows naturally as a part of the flora of Mexico. As Beadle (1980) has argued, it is much more probable that the cultigen arose from the wild plant than the reverse.

In our analysis of Mexican maize, we noted that maize of Mexico could be loosely segregated into a northern, high-altitude complex and a southern, low-altitude one (Doebley et al. 1985). On Fig. 2, the northern (○) and southern (△) groups are identified (see Appendix 1). Some populations of the northern complex tend to show a greater degree of overlap with var. *parviglumis* (Fig. 2). These same populations are also closer to ssp. *mexicana* along the first component. The greater proximity of these maize populations to ssp. *mexicana* could result from introgression of these populations by ssp. *mexicana*. Thus, it seems possible that ssp. *mexicana* (a weedy teosinte found mostly in or near maize fields) could be contributing to genetic diversity in maize (see below). Similarly, Fig. 2 demonstrates that the weedy ssp. *mexicana* is not a genetic bridge between the wild var. *parviglumis* and maize. This stands in contrast to models positing gene flow from wild through weedy to cultivated taxa (de Wet et al. 1971). Similarly, it provides an example of a weedy crop relative that is not a hybrid between wild and cul-

TABLE 3. FREQUENCIES OF ALLELES THAT SHOW PARALLEL DISTRIBUTIONS IN MAIZE AND ANNUAL TEOSINTE BETWEEN NORTHERN HIGH ALTITUDES AND SOUTHERN LOW ALTITUDES OF MEXICO.

Locus-allele	Frequency			
	Teosinte		Maize	
	<i>parviglumis</i> (southern)	<i>mexicana</i> (northern)	Southern	Northern
<i>Enp1-14</i>	0.00	0.30	0.00	0.01
<i>Glu1-8</i>	0.00	0.30	0.00	0.01
<i>Glu1-11</i>	0.00	0.01	0.00	0.01
<i>Pgd1-1.8</i>	0.00	0.01	0.00	0.01
<i>Pgd2-8</i>	0.00	0.03	0.00	0.01
<i>Pgm2-7.2</i>	0.00	0.02	0.00	0.01

tivated types. De Wet (1975) suggested that "weedy races of cereals commonly originate as derivatives of hybrids between wild and cultivated races."

Various authors have proposed that maize has undergone multiple independent domestications (Bird 1980; Kato 1984; Mangelsdorf 1974; McClintock 1959; Randolph 1959). Mangelsdorf and Galinat (1964) suggested that two or more types of maize were domesticated in Mexico. As shown in Fig. 2, maize of all regions of Mexico forms a single group; this group has its closest relationship to *Z. mays* var. *parviglumis*. This suggests that if maize were domesticated several times, then only var. *parviglumis* was involved and the other teosintes were not.

In our previous analysis of isozyme variation in Mexican maize, we reported the frequencies of 22 alleles to be significantly correlated to altitude. Table 2 provides the same statistics for Mexican annual teosinte. Twenty-five alleles show a significant correlation to altitude. Of these 25, only four also showed a significant correlation in Mexican maize. Three of the four (*Acp1-2*, *Glu1-8*, and *Phi1-4*) show the same type of correlation (positive or negative) in both maize and teosinte. *Glu1-n* shows a negative correlation to altitude in teosinte, but a positive correlation in maize. There is good reason to suspect that the *Glu1* null alleles found in these populations are not identical (Doebley et al. 1985; C. W. Stuber, unpubl.), hence such comparisons may be invalid. *Acp1-2* is found in maize and teosinte from most regions of Mexico but occurs at substantially higher frequencies in northern and high-elevation populations as compared to southern or low-elevation ones (65% vs. 15% in teosinte; 51% vs. 33% in maize). This pattern could result from introgression of *Acp1-2* between ssp. *mexicana* and high-elevation maize or from selection for the allele (or other genes linked to it) at high altitudes. *Glu1-8* is a rare allele (<1%) in maize and is found only in a few high-elevation populations. In ssp. *mexicana*, this allele is common (30–50%). Again, the reason for a similar correlation to altitude in maize and teosinte for this allele could be either introgression or convergence. If introgression is the causal agent, then gene flow most likely went from weed into crop. This supposition stems from the fact that *Glu1-8* occurs at a high frequency in ssp. *mexicana*, but at a much lower frequency in maize sympatric to it. It is difficult to imagine an allele at <1% in a maize being transferred to ssp. *mexicana* and then rising to a frequency of 30–50%. Rather, the reverse introgression provides a more parsimonious explanation of

the joint occurrence of this allele in the two taxa. The last of the three alleles showing parallel correlation to altitude is *Phi1-4*, the most common allele at *Phi1*. In *ssp. mexicana*, this allele is replaced by *Phi1-3* about 30% of the time. In high-elevation maize, *Phi1-4* is replaced by *Phi1-2* about 7% of the time. Thus, *Phi1-4* shows the same correlation to altitude in maize and teosinte, but possibly for different reasons.

Overall, the relationship of allele frequencies with altitude in maize and Mexican annual teosinte shows few parallels. Of the 43 alleles that show significant correlations to altitude in maize or Mexican annual teosinte, only three show the same correlation in both taxa. In part, these three parallels may represent cases where common alleles in *ssp. mexicana* have been transferred to sympatric maize populations. Thus, the data provide no good evidence that isozyme alleles have been selected over altitudinal clines. If such selection does occur, the various alleles should show the same correlation to altitude in maize and teosinte.

Several other alleles, although not significantly correlated to altitude, show a parallel relationship in maize and teosinte to altitude (Table 3). In each case, the allele is absent in *var. parviglumis* and the southern maize complex, but occurs in both *ssp. mexicana* and the northern maize complex. In all cases, these alleles had their highest frequency in *ssp. mexicana*, although in some cases the frequencies in *ssp. mexicana* and northern maize were quite close. Introgression could be responsible for the occurrence of these alleles in both *ssp. mexicana* and maize sympatric to it. As discussed above for *Glu1-8*, introgression is more parsimoniously explained if one hypothesizes gene movement from the taxon with the higher allele frequency to the one with the lower frequency. In this case, gene movement would most likely be from teosinte to maize, although the direction of introgression cannot be assured. The loci involved (Table 3) are located on four different chromosomes (3, 5, 6, 10). This suggests that introgression may be occurring at several locations in the genome. For two of these alleles, the relationship between geography-taxonomy and allele frequency is graphically displayed (Fig. 3, 4).

If one accepts that the alleles listed in Table 3 have been transferred from *ssp. mexicana* into maize, then maize accessions with teosinte introgression can be identified using these alleles (Table 4). For the most part, these accessions represent high altitude races. Some of the races share with *ssp. mexicana* several morphological traits including dark red, densely pilose leaf sheaths and a weak root system. Common isozyme and morphological characteristics of northern Mexican maize and *ssp. mexicana* could be explained in part through introgression of maize by *ssp. mexicana*. Convergence, especially for morphological characteristics, cannot be ruled out.

We have found no alleles with distributions suggestive of introgression between maize and *var. parviglumis*. Practically, such alleles would be difficult to find as these taxa are so similar overall in their isozyme constitution. Similarly, there are no alleles that show a high frequency in northern Mexican maize, a lower frequency in the sympatric *ssp. mexicana*, and absence in southern Mexico. This pattern, if it existed, would suggest introgression from maize into *ssp. mexicana*.

CONCLUDING REMARKS

An analysis of the pattern of variation for 21 isozyme loci between Mexican maize and Mexican annual teosinte provides some evidence for low levels of

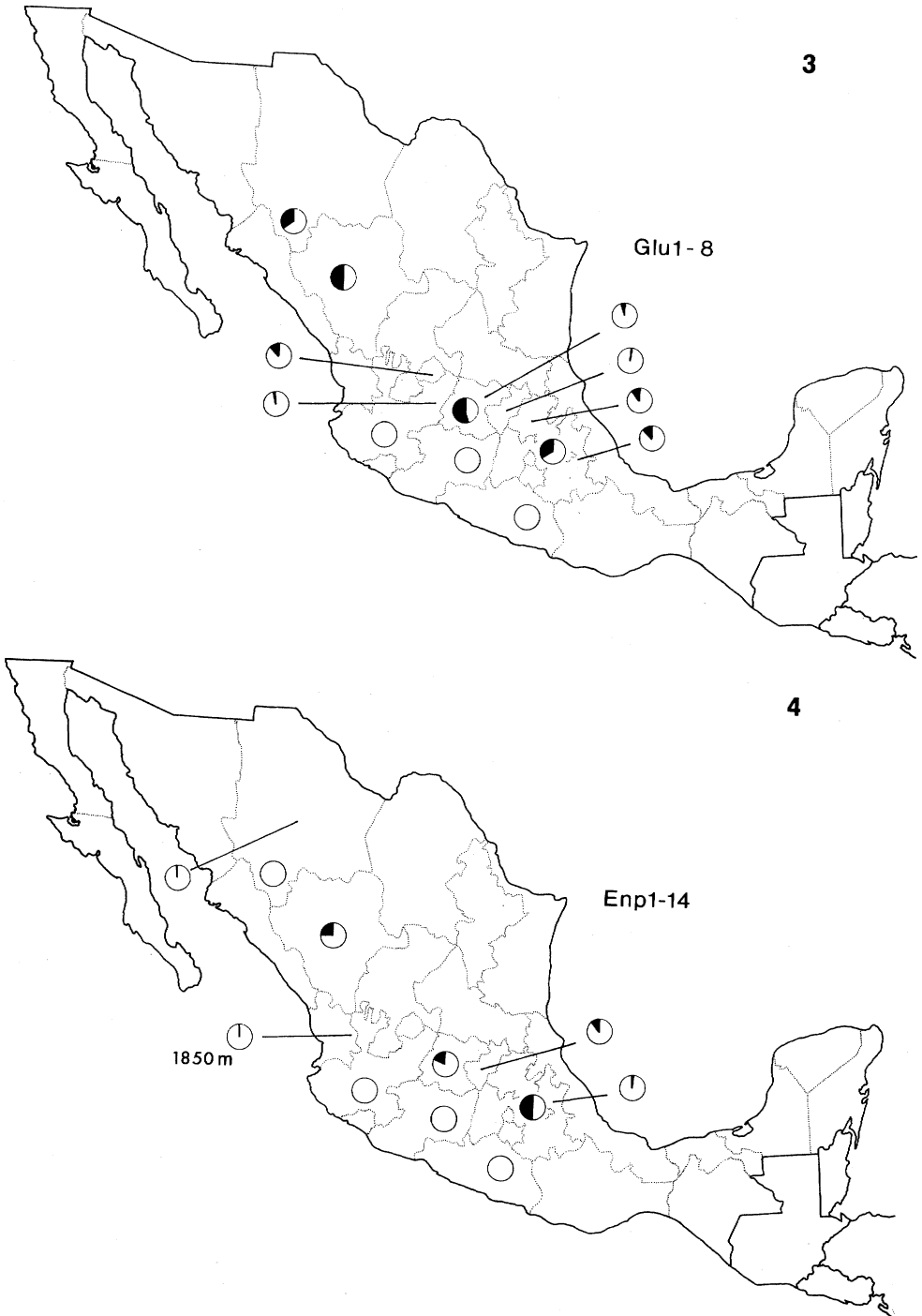


Fig. 3, 4. Frequency of isozyme alleles in Mexico for maize (circles off the continent) and teosinte (circles on the continent). Percentage of the circle that is darkened equals the frequency of the allele. Fig. 3. *Glu1-8*. Fig. 4. *Enp1-14*.

TABLE 4. MEXICAN MAIZE RACES POSSESSING ISOZYME ALLELES POSSIBLY DERIVED FROM TEOSINTE (*Z. MAYS* SSP. *MEXICANA*).

Race	Collection	Locus-allele	Frequency
Apachito	CHH138	<i>Enp1-14</i>	0.13
Apachito	CHH177	<i>Enp1-14</i>	0.42
Arrocillo Amarillo	PUE91	<i>Pgd1-1.8</i>	0.17
Celaya	GTO84	<i>Glu1-8</i>	0.13
Chalqueño	HGO7	<i>Pgd1-1.8</i>	0.13
Chalqueño	MEX48	<i>Pgd1-1.8</i>	0.29
Chalqueño	MEX48	<i>Pgd2-8</i>	0.13
Cónico	PUE32	<i>Glu1-8</i>	0.33
Cónico	PUE32	<i>Pgm2-7.2</i>	0.25
Cónico	PUE109	<i>Enp1-14</i>	0.21
Cónico Norteño	QRO2	<i>Glu1-8</i>	0.04
Cónico Norteño	QRO2	<i>Enp1-14</i>	0.13
Gordo	CHH131	<i>Enp1-14</i>	0.08
Harinoso de Ocho-Occidentales	JAL71	<i>Glu1-8</i>	0.04
Maíz Dulce	JAL78	<i>Glu1-11</i>	0.42
Palomero Toluqueño	MEX6	<i>Pgd1-1.8</i>	0.04
Tablilla de Ocho	JAL301	<i>Pgd1-1.8</i>	0.13
Tablilla de Ocho	ZAC187	<i>Pgd1-1.8</i>	0.04

introgression between teosinte (ssp. *mexicana*) and its sympatric maize. The evidence is in the form of alleles that are found in ssp. *mexicana* and maize sympatric to this subspecies, but absent from maize and teosinte elsewhere in Mexico. There are few such alleles and they occur at low frequency, suggesting introgression (if it occurs) is highly restricted. It is suggested that this introgression most likely goes from ssp. *mexicana* to maize. The data also demonstrate that ssp. *mexicana* is quite distinct genetically from maize of the same region. Thus, the idea of Galinat (1973) that there is a "constant gene flow between maize and teosinte" must be greatly modified. The data support the less common view that ssp. *mexicana* is little affected by gene transfer from maize (Doebley 1984; Kato 1984). The data also demonstrate that all maize races of Mexico are isoenzymatically closer to var. *parviglumis* than to other teosintes, suggesting that the latter teosintes were not directly involved in the ancestry of maize. The isozyme data cannot rule out the possibility that maize was domesticated more than once. However, given that any transformation of teosinte into maize must have involved a series of improbable mutations (Galinat 1983; Iltis 1983), it seems more reasonable to hypothesize that this transformation occurred only once. The variation that exists in maize could have arisen after domestication by drift, selection, mutation, and subsequent introgression from teosinte.

The relationships between the wild and weedy teosintes and maize are also elucidated by the isozyme data. This crop-weed complex, while showing a morphological-ethological continuum suggestive of evolution from wild (var. *parviglumis*) to weed (ssp. *mexicana*) to crop (ssp. *mays*), does not fit the model applied to the evolution of other domesticates (de Wet 1975; de Wet et al. 1971; Harlan 1975). Specifically, (1) the weedy form (ssp. *mexicana*) does not act as a genetic bridge between the wild (var. *parviglumis*) and cultivated types; and (2) the weedy form is not a hybrid between the crop and the wild type.

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Appendix 1.

List of collections analyzed and the scores for each collection on principal components 1 and 2 of Fig. 2.

Taxon ^a	Collection ^b	PC1	PC2	Taxon ^a	Collection ^b	PC1	PC2
PAR-B	Beadle s.n.	-1.17	-0.35	MAZ-S	CHS 29	0.99	-0.38
PAR-B	Iltis 308	0.19	-1.82	MAZ-S	CHS 31	0.62	-1.53
PAR-B	K-67-15	-0.61	-1.09	MAZ-S	CHS 38	0.59	0.64
PAR-B	Iltis 81	0.18	-0.28	MAZ-S	CHS 53	0.38	-0.09
PAR-B	K-67-13	-0.02	-1.07	MAZ-S	CHS 56	0.21	1.36
PAR-B	K-67-17	-0.02	-0.78	MAZ-S	CHS 76	0.36	-0.35
PAR-B	K-67-20	-0.07	-0.77	MAZ-S	CHS 81	0.58	-0.66
PAR-B	K-67-22	-0.27	-0.95	MAZ-S	CHS 86	1.36	-0.23
PAR-B	K-69-14	-1.62	-0.93	MAZ-S	CHS 91	0.42	-0.86
PAR-B	K-77-13	-0.37	-1.66	MAZ-S	CHS 104	0.88	0.88
PAR-B	Beadle s.n.	-1.08	-0.15	MAZ-S	CHS 112	0.55	0.68
PAR-B	W-71-2	-0.26	-0.75	MAZ-S	CHS 159	1.14	0.58
PAR-B	Cobia s.n.	-0.20	-2.31	MAZ-S	CHS 204	0.43	-0.31
PAR-J	Guzman s.n.	-0.15	-2.57	MAZ-S	CHS 224	0.63	-0.43
PAR-J	Guzman 32	-1.51	-1.28	MAZ-S	CHS 225	0.70	-0.69
PAR-J	Iltis 1480	-0.51	-3.19	MAZ-S	CHS 234	0.73	-0.40
PAR-J	Puga 11065	0.13	-2.16	MAZ-S	CHS 30A	0.35	0.93
PAR-J	Iltis 28888	0.34	-1.41	MAZ-S	CHS 52B	0.86	1.44
MEX-C	Iltis 276	-1.47	-1.25	MAZ-N	DGO 110	1.15	0.24
MEX-C	Prior s.n.	-1.98	1.72	MAZ-N	DGO 123	1.12	-0.96
MEX-C	Puga 11066	-3.28	0.34	MAZ-S	GRO 3	0.97	0.78
MEX-C	Guzman 110	-2.14	-0.22	MAZ-N	GTO 22	0.75	0.54
MEX-C	Doebley 625	-2.36	-1.48	MAZ-N	GTO 29	-0.12	-0.29
MEX-C	K-69-2	-1.71	-0.13	MAZ-N	GTO 36	1.22	-0.53
MEX-C	K-69-3	-2.60	-1.07	MAZ-N	GTO 84	0.31	0.35
MEX-C	K-69-5	-1.97	0.68	MAZ-N	GTO 88	0.61	-1.29
MEX-C	K-69-7	-2.16	-0.84	MAZ-S	GUA 45	0.60	-0.78
MEX-C	K-69-9	-1.62	-1.11	MAZ-N	HGO 7	0.03	0.04
MEX-N	Beadle s.n.	-2.53	0.62	MAZ-S	JAL 42	0.74	-0.43
MEX-N	K-1-78	-2.95	-0.14	MAZ-S	JAL 43	0.58	1.39
MEX-M	Doebley 479	-2.57	1.24	MAZ-S	JAL 44	0.80	0.02
MEX-M	Doebley 481	-1.74	1.10	MAZ-S	JAL 54	0.31	0.61
MEX-M	Doebley 482	-1.55	2.01	MAZ-S	JAL 69	0.21	0.51
MEX-M	Iltis 178	-2.35	1.64	MAZ-S	JAL 71	0.48	0.11
MEX-M	Iltis 769	-1.33	2.05	MAZ-N	JAL 78	0.19	-0.29
MEX-M	Iltis 401	-1.93	1.36	MAZ-S	JAL 100	0.59	0.02
MEX-M	K-68-2	-1.49	1.12	MAZ-S	JAL 102	0.67	0.94
MAZ-N	DHT 70-2	0.14	0.76	MAZ-N	JAL 301	0.22	-0.25
MAZ-N	AGS 7	-0.17	-0.01	MAZ-N	MEX 5	-0.27	-0.58
MAZ-N	CHH 131	0.39	1.61	MAZ-N	MEX 6	0.41	0.42
MAZ-N	CHH 138	0.33	0.63	MAZ-N	MEX 7	-0.31	-0.07
MAZ-N	CHH 160	0.46	1.49	MAZ-N	MEX 48	0.47	0.03
MAZ-N	CHH 177	0.07	0.78	MAZ-N	MEX 58	-0.80	-0.40
MAZ-N	CHH 182	0.13	0.83	MAZ-N	MEX 72	0.40	0.68
MAZ-N	CHH 207	0.49	0.73	MAZ-S	MOR 17	0.53	1.51
MAZ-N	CHH 214	0.69	1.56	MAZ-S	NAY 6	0.97	0.70

Appendix 1. (continued).

Taxon ^a	Collection ^b	PC1	PC2	Taxon ^a	Collection ^b	PC1	PC2
MAZ-N	CHH 218	0.44	1.80	MAZ-S	NAY 12	0.91	0.24
MAZ-N	CHH 256	0.36	1.05	MAZ-S	NAY 15	1.23	0.17
MAZ-S	CHS 26	0.52	-0.45	MAZ-S	NAY 16	0.87	0.47
MAZ-S	NAY 24	1.06	0.32	MAZ-S	OAX 70	0.48	1.01
MAZ-S	NAY 29	0.67	0.52	MAZ-S	OAX G43	0.52	-0.71
MAZ-S	NAY 38	0.68	-0.65	MAZ-S	PUE 27	0.79	0.12
MAZ-S	NAY 39	0.75	0.20	MAZ-N	PUE 32	-0.53	-0.05
MAZ-S	NAY 41	0.72	0.85	MAZ-N	PUE 82	-0.63	0.18
MAZ-N	NAY 185	0.55	-0.70	MAZ-N	PUE 91	0.03	-0.71
MAZ-N	NAY 189	0.57	0.10	MAZ-N	PUE 109	-0.03	0.94
MAZ-N	NAY 191	0.48	0.17	MAZ-N	QRO 2	-0.09	-1.38
MAZ-N	NAY 203	0.26	0.45	MAZ-N	SIN 2	0.45	0.06
MAZ-S	OAX 9	0.59	-1.56	MAZ-N	SON 57	0.35	-0.07
MAZ-S	OAX 28	0.88	-0.39	MAZ-S	VER 39	0.74	0.23
MAZ-S	OAX 40	0.12	0.78	MAZ-S	VER 44	1.20	-1.38
MAZ-S	OAX 44	0.04	-2.28	MAZ-S	YUC 7	0.01	1.24
MAZ-S	OAX 48	0.57	0.75	MAZ-N	ZAC 4	-0.01	0.63
MAZ-S	OAX 50	0.35	1.25	MAZ-N	ZAC 12	0.34	-0.93
MAZ-S	OAX 51	0.37	1.35	MAZ-N	ZAC 187	0.17	0.81
MAZ-S	OAX 68	0.62	-0.60				

^aTaxa are abbreviated as follows: Zea mays var. parviglumis from the Balsas river drainage (PAR-B) and from the state of Jalisco (PAR-J); Z. mays subsp. mexicana from the Central Plateau (MEX-C), from the Nobogame Valley (MEX-N), and from the Valley of Mexico (i.e. Chalco teosinte) (MEX-M); Z. mays subsp. mays from northern or high-elevation localities (MAZ-N) and from southern or low-elevation localities (MAZ-S).

^bFor full locality data, readers are referred to Doebley et al. (1984, 1985).