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Intergradation among Latin American maize based on an analysis of chromosome knob frequencies*

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Summary. Published information on chromosome knobs found at 21 knob-forming positions and on abnormal 10 and B chromosomes in maize, *Zea mays* L., was used to place maize populations within a multidimensional space based on frequencies. From this space, similarities among populations were determined using a measure of gentic diversity based on a modified Cartesian distance. Populations were portrayed in 2 (or 3) dimensions based on these distances. The objective was to investigate patterns of "migration" that had occurred among indigenous populations of maize from Latin America. Widely dispersed collections classified as Tuxpeño had similar knob constitutions. Collections from Guatemala reflected continuous migration among adjacent areas with increased isolation (or association of knob types) with increased altitude of collection. Maize from southeastern Guatemala and their southeastern neighbours were similar. The high elevation collections from Guatemala and Mexico were surprisingly similar. The data reflected three distinct phenomena: long-term intergradation of maize germplasm among adjacent areas (as would result from pollen drift between closely cultivated areas or from seed exchange among neighbors), major, relatively recent shifts in gene flow (as had occurred with Tuxpeño's widespread distribution in Mexico), and precolonial dispersions (as between maize populations from the high elevations in Guatemala and Mexico).

Key words: *Zea mays* (L.) – Corn – Diversity – Migration – Chromosome knobs – Germplasm – Intergradation – Pollen drift

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Introduction

The initial classification of maize *Zea mays* L. collections and their interrelationships, as summarized by Brown and Goodman (1977), were based largely on the analyses of morphological characteristics. Chromosomal components are conservatively inherited, and the distribution of these components yields information on the history of maize (Kato 1976; McClintock 1959, 1960). Number of chromosome knobs (Mangelsdorf and Cameron 1942; Wellhausen et al. 1952) and distribution of chromosomal components were used to suggest patterns of migration for maize and interrelationships among collections (Kato 1976; Longley and Kato 1965; McClintock 1959, 1960, 1978; McClintock et al. 1981).

This paper characterizes the "migration" of maize germplasm that had occurred in Latin America. Migration among adjacent areas results in intergraded frequencies. A technique for interpreting such patterns of integrated frequencies will be developed. The analyses will be based on the frequency of chromosome knob types summarized by McClintock et al. (1981). Data available from the Guatemalan collections were selected for the principal analysis.

Measure of genetic diversity

Measures of genetic distance utilize allelic frequencies as the attribute data. Cavalli-Sforza and Edwards (1967) considered distances within a unit sphere representing allelic frequencies. Balakrishnan and Sanghvi (1968) and Kurczynski (1970) developed distances based on the concept of generalized distances. Rogers (1972) considered Cartesian distance within a space where positions are determined by allelic frequencies for a locus. Distances based on the identity, or nonidentity, of two random alleles for a locus, suggested by Sokal and Sneath (1963), were developed by Nei (1972, 1973). He defined a measure for

gene diversity and developed relationships for allelic identities among subpopulations. Sokal and Menozzi (1982) used spatial autocorrelations to relate HLA frequencies with area.

The modified Rogers' distance (Wright 1978) was selected for this paper. It represents a measure of genetic diversity involving multiple loci, a concept of primary interest in hybrid breeding programs. Further, it is measured within a well defined multidimensional space with corresponding adaptability to statistical and mathematical concepts including the analysis of migrational patterns.

Diversity space

Consider the rth of n populations, $1 \leqq r \leqq n$, and let the frequency identified for the jth allele at the ith locus be p_{rij} where $1 \leqq j \leqq t_i$, $1 \leqq i \leqq s$, for t_i alleles at the ith of s loci. Place the rth population into $\sum_i t_i$ dimensions based strictly on allelic frequencies. Because $\sum_j p_{rij} = 1$, the coordinates contain redundant information, but transformed axes can be selected so that all information is resolved into $(\sum_i t_i\text{-}s)$ dimensions, or $(t_i\text{-}1)$ per locus. The contribution of each locus to distance is in a sense standardized since $\sum_j p_{rij} = 1$. The distance between the rth and the r'th subpopulations is taken to be the modified Cartesian distance,

$$C(r, r') = [\sum_{ij} (p_{rij} - p_{r'ij})^2/2s]^{1/2},$$

so that $0 \leqq C(r, r') \leqq 1$. This distance was chosen in lieu of distances based on absolute differences in frequencies because it is more readily adapted to mathematical and statistical concepts. It reflects the square root for the average sum of squares of differences in allelic frequencies per locus between two subpopulations and thus is a relative measure of genetic diversity between them (Cress 1966).

C (r, r') will be zero for two populations with identical gene frequencies and one if homozygous for two different alleles at each locus. Let $(p_{1ij} - p_{2ij}) = b_{ij}\,(p_{1ij} - p_{3ij})$. Then, if population (2) resulted from intergradation between populations (1) and (3) with (2) containing b proportion of its ancestry from (3), then $b_{ij} = b$, and $C(1, 2) = b\,C(1, 3)$ or $C(2, 3) = (1 - b)\,C(1, 3)$. Thus, if a series of populations result from one-dimensional migration along a cline (no selection), then a one dimensional diversity space will account for distances among populations. A two-dimensional diversity space would be required to reflect a two-dimensional migration pattern.

Distance estimates

Frequencies, p_{rij}, represent statistics. On the average, errors of sampling contribute positively to distances. That is,

$$E\sum_{ij} (p_{rij} - p_{r'ij})^2/2s = D^2(r, r') + [\sum_{ij} V(p_{rij}) + \sum_{ij} V(p_{r'ij})]/2s$$
$$= D^2(r, r') + K_{rr'}$$

where the operator E signifies expected value and

$$D^2(r, r') = \sum_{ij} (\pi_{rij} - \pi_{r'ij})^2/2s,\ Ep_{rij} = \pi_{rij}.$$

Distances can be estimated,

$$\hat{D}(r, r') = [\sum_{ij} (p_{rij} - p_{r'ij})^2/2s - K_{rr'}]^{1/2}.$$

The hypothesis, $D(r, r') = 0$, is tested with the F ratio,

$\sum_{ij} (p_{rij} - p_{r'ij})^2/2s\,K_{rr'}$, with appropriate degrees of freedom. Composition of $K_{rr'}$ will depend upon population structure. If m_{ri} genes represent a random sample of genes for the ith locus from the rth population,

$$K_{rr'} = [\sum_{ij} p_{rij}(1 - p_{rij})/m_{ri} + \sum_{ij} p_{r'ij}(1 - p_{r'ij})/m_{r'i}]/2s.$$

The adjustment for sampling variability is important when subpopulations are similar and/or sampling is limited.

Reduction of dimensions

The $n(n-1)/2$, $C(r, r')$ distances among n populations uniquely determine an n by n matrix of coordinates, $\{y_{kr}\}$, $\sum_r y_{kr} = 0$, which places the rth population in the kth dimension, $1 \leqq k \leqq n$. Gower (1966, 1972) developed a principal coordinate analysis which permits the resolution of variability, $\sum_{k,r} y_{kr}^2 = \sum_{r<r'} C^2(r, r')/n$, into $(n-1)$ components. The principal components of variability, Σx_{1r}^2, Σx_{2r}^2, ..., together with coordinates for the principal axes, $\{x_{1r}\}$, ..., are available from the analysis. If distance estimates, $\hat{D}(r,r') \geqq 0$, are uniquely determine an n by n coordinate matrix, they can be used in the analysis.

The objective of this paper is to determine whether estimated distance (genetic diversity) between populations reflects a two-dimensional migration scheme. Both the proportion of the variability that is explained in two dimensions and the spatial relationships among collections are important. The percent of Σy_{kr}^2 explained by two principal coordinate axes will be obtained from the two largest eigen values in Gower's analysis (1966). However, we are not interested necessarily in how populations relate to these principal axes, rather, in how they relate to a joint two-dimensional migration model. Least square estimates for coordinates in two dimensions will be identified so that distances based on these coordinates yield minimum variability from the corresponding $\hat{D}(r, r')$, Hanson (1983),and populations will be mapped using these coordinates. The resulting genetic diversity map can be compared to the map for area of collection.

Analyses of chromosome knob frequencies

Data selection

McClintock et al. (1981) summarized the knob types (absent, small, intermediate, or large) found at 21 knob forming positions together with the presence (or absence) of abnormal 10 chromosome and B chromosomes found in maize collections from North and South America. There are (88–23) potential dimensions, where $88 = 4(21) + 2(2)$.

Johannessen (1982) concluded that ancient varieties are still being planted in Guatemala with little admixture with new varieties. There was a feeling among the farmers that the "spirit of maize" would be offended if moved to a new area. Seed stock is maintained and passed as a gift to sons. The collections of maize from Guatemala are from indigenous farmers and should show minimum disruption from modern maize introductions. Further, sampling involved small political subdivisions. Therefore, the Guatemalan data were selected to investigate migration patterns in maize. This information will be collated with information from other collections from Latin America.

Collections were placed into areas based on political subdivision and altitude of collection given by Mc-

Clintock et al. (1981, pp 181–196). The Guatemalan collections were grouped into nine areas (Table 1) and Mexican into ten (Table 2). The collections grouped are given in Appendix Tables 1 and 2. For some cases, collections within a political subdivision were placed in different areas when altitude of collection justified this placement. For example, Guatemalan collections from Alta Verapaz were assigned to groups 1a or 4 based on low and intermediate altitudes of collection, respectively, while collections from San Marcos were assigned to groups 3 or 8 based on low and high altitudes of collection, respectively. Data from all collections were used unless information available did not permit assignment of collection to an area. Information from 168 of the 177 available Guatemalan collections was used. Approximate areas of collection are identified in Fig. 1. The range and mean altitude for collections combined for a group are given in Tables 1 and 2. Collections from two Guatemalan areas (1a, b) had similar frequencies, and the data for these two groups were combined.

For each individual analyzed (McClintock et al. 1981), the knob types for the 21 knob-forming positions were usually identified; somewhat fewer classifications were made for abnormal 10 and B chromosomes. The number classified varied among collections. The average sample size for an area is given in Tables 1 and 2. Frequencies for knob and chromosome types were calculated from these pooled tabulations.

Table 1. Grouping of maize collections from Guatemala together with Department where collected, range and mean altitudes of collections, and number of collections grouped

Group	Department	Altitude (m)		Number	
		Range	Mean	Collections	m[a]
1a	A. Verapaz, Petén, Izabal, Zacapa	3– 610	170	20	88
1b	Chiquimula, El Progreso	280– 915	580	16	67
2	Jutiapa, S. Rosa	360–1410	960	21	71
3	Escuintla, Retalhuleu, S. Marcos, Suchitepéquez	90–1060	470	23	70
4	A. Verapaz, B. Verapaz	970–1460	1200	16	54
5	Chiquimula, Guatemala, Jalapa	825–1830	1300	14	61
6	Quiché, Huehutenango	1370–2350	1900	18	94
7	Chimaltenango, Guatemala, Sololá	2040–2580	2300	17	82
8	Quetzaltenango, S. Marcos, Totonicapán	2320–3050	2600	23	83

[a] Average no. classifications made per knob-forming position abnormal 10 chromosome, and B chromosomes. Numbers classified per knob-forming position were similar with fewer numbers available for abnormal 10 and B chromosome classifications

Table 2. Grouping of maize collections from Mexico together with State where collected, range and mean altitudes of collections, and number of collections grouped

Group	State	Altitude (m)		Number	
		Range	Mean	Collections	m[a]
1	Nay., Sin., Son.	3– 560	320	26	317
2a	Col., Gro., Mich.	7– 500	200	23	214
2b	Chis., Oax.	30– 600	140	30	319
3	Tam., N.L., S.L.P.	30– 530	250	16	164
4	Camp., Q.R., Tab., Ver., Yuc.	30– 366	80	43	413
5	Chih., Coah., Dgo.	350–2100	1400	37	359
6	Gto., Jal., Nay., S.L.P., Zac.	720–2350	1500	34	365
7a	Pue., Mor.	885–1190	1000	14	135
7b	Chis., Gro., Mich., Oax.	730–2300	1400	30	283
8	Mex., Qro., Tla.	2280–2655	2500	14	225

[a] Average no. classifications made per knob-forming position, abnormal 10 chromosome, and B chromosomes. Numbers classified per knob-forming position were similar with fewer numbers available for abnormal 10 chromosome and B chromosome classifications

Appendix

Table 1. Guatemalan maize collections which were grouped to represent an area

Area	Collection no.
G1a	100, 103, 105, 209, 210, 262, 316, 329, 333, 344, 448, 456, 459, 473, 544, 573, 793, 806, 809, 821
G1b	90, 92, 107, 108, 109, 110, 111, 114, 115, 207, 220, 253, 296, 326, 338 349
G2	88, 129, 130, 131, 133, 134, 135, 151, 231, 239, 242, 257, 260, 280, 281, 298, 581, 594, 649, 760, 765
G3	60, 68, 69, 72, 74, 77, 79, 81, 85, 87, 120, 155, 158, 174, 178, 179, 314, 320, 321, 351, 552, 738, 746
G4	22, 27, 143, 145, 148, 279, 600, 603, 651, 674, 678, 704, 710, 769, 778, 820
G5	106, 116, 123, 127, 225, 226, 229, 269, 313, 322, 331, 367, 477, 635
G6	4, 8, 31, 37, 160, 161, 164, 426, 529, 744, 835, 852, 875, 902, 924, 934, 937, 944
G7	382, 393, 455, 539, 576, 577, 583, 590, 591, 607, 619, 627, 637, 647, 705, 717, 720
G8	20, 375, 386, 413, 423, 427, 458, 461, 465, 480, 491, 492, 497, 500, 508, 513, 522, 596, 642, 742, 895, 908, 909

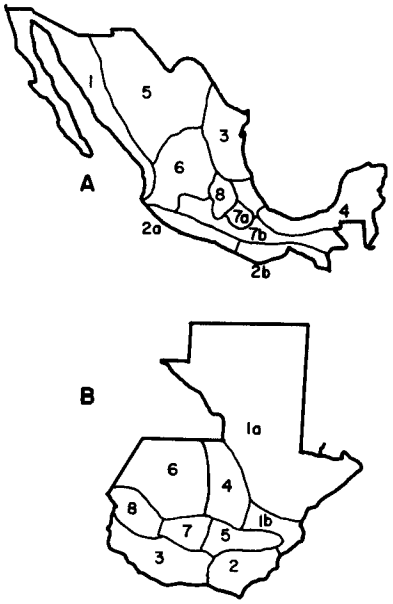

Fig. 1. Approximate areas corresponding to grouping of maize collections obtained from Mexico (*A*) and Guatemala (*B*)

Migration patterns

The Guatemalan groups (G1, G2, and G3) represent collections from lower altitudes with increasing altitudes for the G4, G5, G6, G7, and G8 collections, respectively (Table 1). Two principal coordinates account for 94.9% of the variability in coordinates corresponding to the 28 distance estimates (Table 3). The graphic representation (Fig. 2) reflects both an east-west migration and an association with altitude. The positions of collections within the diversity space reflect that expected for two-dimensional intergradation between adjacent areas with increasing isolation with higher altitudes.

Appendix

Table 2. Mexican maize collections which were gouped to represent an area

Area	Collection no.
M1	NAY: 15, 25, 34, 35, 36, 39; SIN: 1, 2, 6, 7; SON: 1, 4, 5, 20, 21, 23, 26, 27, 29, 30, 31, 32, 44, 49, 51, 55
M2a	COL: 8, 17, 23; GRO: 17, 36, 39, 100, 121, 134, 150, 153, 166, 168, 174, 177, 210, 212; MICH: 105, 162, 166, 170, 176, 178
M2b	CHI: 22, 24, 104, 110, 112, 113, 222, 223, 224, 234, 236, 237; OAX: 6, 7, 11, 20, 35, 48, 50, 51, 52, 54, 57, 66, 70, 148, 171, 174, 175, 179
M3	NL: 4, 12, 23; SLP: 95 128; TAM: 1, 2, 4, 8, 13, 28, 32, 39, 41, 44, 45
M4	CAMP: 5, 18, 29, 37, 39, 41C, 54, 99, 101, 102, 103; QR: 1; TAB: 1, 2; VER: 39, 44, 78, 101, 123, 128, 132, 133, 149, 165, 179, 185, 191, 215, 218, 225; YUC: 7, 36, 37, 43, 70, 75, 102, 129, 130, 134, 146, 148, 151
M5	CHIH: 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 15, 17, 23, 28, 35, 46, 96, 103; COAH: 2, 3, 4, 5, 7, 12, 14, 19, 40, 64, ( ), 81; DGO: 2, 7, 9, 12, 18, 28
M6	GTO: 36, 100, 101, 102; JAL: 12, 24, 28, 35, 37, 38, 64, 99, 161, 163, 211, 239, 263; NAY: 2, 4, 6, 7, 59, 72; SLP: 5, 12, 17, 78, 150;ZAC: 2, 4, 5, 6, 10, 26
M7a	MOR: 1, 3, 13, 14, 15, 17, 18; PUE: 196, 200, 219, 223, 229, 260, 262
M7b	CHIS: 6, 7, 11, 139, 144, 196, 197, 235, 238, NC; GRO: 3, 4, 6, 8, 9, 77, 221; MICH: 78, 79, 150, 157, 186, 191, 200; OAX: 28, 40, 63, 100, 116, 180
M8	MEX: 5, 6, 7, 7A, 36, 142, 207, 208, 210, 211; QRO: 20, 48; TLA: 1, 3

The relationships among groups of collections from Mexico (Fig. 3) are not as clear cut as that found among the Guatemalan collections. Collections from the Yucatan peninsula (M4) differed from the rest. For the remaining nine areas two principal coordinates accounted for 82.3% of Σy_{kr}^2. The coordinates for M4 in three dimensions were determined so that distances involving M4 have minimum variability from the corresponding $\hat{D}(r, r')$. Group M2b represents low-altitude collections

Table 3. Distance estimates between maize populations from Guatemala grouped by area of collection[a]

Area	Area						
	G2	G3	G4	G5	G6	G7	G8
G1	0.055	0.101	0.051	0.063	0.233	0.305	0.396
G2		0.097	0.091	0.113	0.271	0.336	0.433
G3			0.144	0.150	0.292	0.368	0.456
G4				0.044	0.198	0.267	0.355
G5					0.198	0.257	0.348
G6						0.109	0.183
G7							0.150

[a] All estimated distances differ significantly from zero

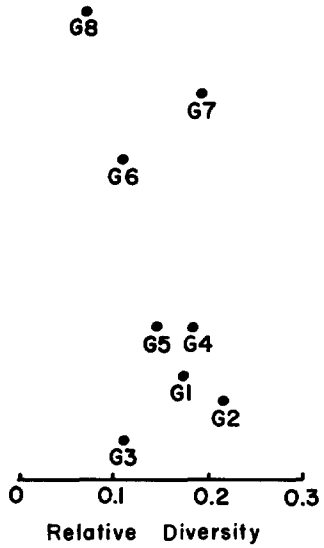

Fig. 2. Two-dimensional mapping of genetic diversity for maize collections from Guatemala so that distances calculated from these coordinates yield minimum variability from corresponding estimated distances

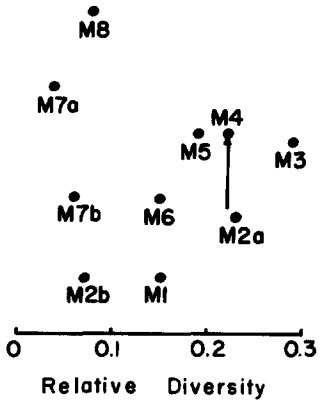

Fig. 3. Two-dimensional mapping of genetic diversity for nine groups of maize collections from Mexico so that distances calculated from these coordinates yield minimum variability from corresponding estimated distances. Group *M4* required a third dimension for presentation

from southwest Mexico. They do not fall into a pattern expected for two dimensional migration between contiguous areas but are similar to the Sonoran and Sinaloan collections (note also McClintock 1978; McClintock et al. 1981). If one disregards this group, then there is a general pattern of diversity which reflects migration between adjacent areas with increased isolation with increased altitude of collection. Group M8 represents the high altitude collections from Mexico. Collections from the States of Morelos and Puebla (M7a) with an average altitude of 1,000 m appear to be the primary intermediate to these high altitude collections.

Collections from southeastern Guatemala and countries immediately to the southeast were quite similar (Table 4). These comparisons included collections made at higher elevations (1,100 m to 3,000 m) in Honduras (H2). There appears to be a general intergradation of maize germplasm extending into this area.

Some distinct differences exist between the Guatemalan collections and their Mexican neighbors (Table 5). The collections from northwestern Guatemala

Table 4. Distance estimates between groups of maize collections from Southeastern Guatemala, El Salvador, Honduras, and Nicaragua[a]

Collection	Collection				Altitude (m)[b]
	H1	H2	S	N	
G1	0.089	0.148	0.110	0.099	350
G2	0.099	0.136	0.100	0.088	960
G5	0.082	0.183	0.131	0.116	1300
H1		0.126	0.113	0.081	500
H2			0.104	0.073	1700
N			0.048[a]		470
Altitude (m)[b]	500	1700	450	470	

[a] All distances differ significantly from zero except for 0.048. Collections identified as being Guatemalan (G), Honduran (H), Salvadoran (S), and Nicaraguan (N)
[b] Average altitude of collection

Table 5. Distance estimates between groups of maize collections from Northwestern Guatemala and their Mexican neighbors[a]

Mexican	Guatemalan					Average
	G1	G3	G4	G6	G8	
M2b	0.148	0.222	0.122	0.201	0.344	0.207
M4	0.225	0.273	0.213	0.140	0.268	0.224
M7a	0.346	0.419	0.312	0.175	0.189	0.288
M7b	0.223	0.298	0.200	0.152	0.268	0.228
M8	0.400	0.461	0.363	0.202	0.174	0.320
Average	0.268	0.335	0.242	0.174	0.249	

[a] All distances differ significantly from zero

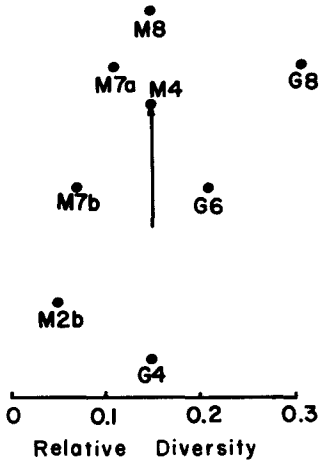

Fig. 4. Two-dimensional mapping of genetic diversity for Guatemalan (*G*) and Mexican (*M*) maize collections so that distances estimated from these coordinates yield minimum variability from corresponding estimated distances. Group *M4* required a third dimension for presentation

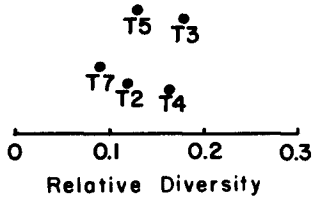

Fig. 5. Two-dimensional mapping of genetic diversity for maize collections classified as Tuxpeño grouped by areas of collection *M2, M3, M4, M5* and *M7* so that distances calculated from these coordinates yield minimum variability from corresponding estimated distances

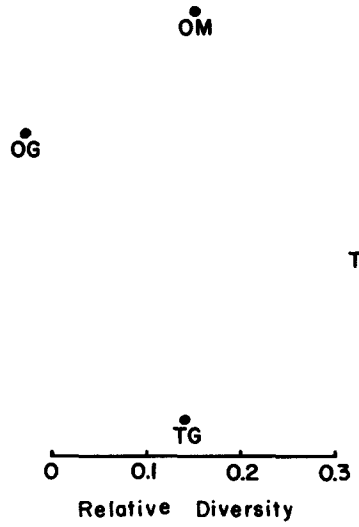

Fig. 6. Two-dimensional mapping of genetic diversity for maize collections classified as Olotón (*O*) and Tepecintle (*T*) in the Guatemalan (*G*) and Mexican (*M*) collections so that distances calculated from these coordinates yield minimum variability from estimated distances

(G3) differed from other Guatemalan collections (Fig. 2) and from Mexican collections including the adjacent area (M2b), and the G1 and M4 collections are more dissimilar than that expected for adjacent areas reflecting possible barriers to migration (Table 5). Of the remaining areas, seven (less M4) essentially plot in two dimensions (92.2% of $\Sigma^2 y_{kr}$ being explained by two principal axes). Collections from the plateau area G6 have the lowest average distance from the Mexican collections (Table 5). The highland collections, G8 and M8, are surprisingly similar with collections M7a and G6 appearing as intermediates (Fig. 4). Such similarities have been noted by others with the pattern extending into South America (Brown and Goodman 1977). Kato and Blumenschein (1967) noted a similar association involving a complex of small chromosome knobs.

Collections classified as Tuxpeño were obtained from widely dispersed areas (M2, M3, M4, M5, and M7) with two principal coordinates accounting for 77.4% of the coordinate variability. While the dispersion among the Tuxpeño collections is small, their interrelationships reflect associations with areas of collection (Figs. 3 and 5). Sample sizes were sufficiently large for Olotón and Tepecintle to make similar comparisons (Fig. 6) with two principal coordinates accounting for 89.6% of the coordinate variability. In contrast to the Tuxpeño collections, collections classified as Olotón and Tepecintle in Mexico had little relationship to the corresponding Guatemalan collections.

Discussion

Principal components can be extracted directly from the multidimensional space based on knob frequencies (Smith et al. 1982); however, numerous components were required to resolve the variability due to the multiplicity of the spatial arrangement. Conceivably, one could associate knob groups with such components. The $\hat{D}(r,r')$ measure estimates distance between two populations within this multidimensional space and represents a measure for genetic diversity between two populations. It represents information averaged for all loci and permit the representation of n groups in $(n-1)$ dimensions based on genetic diversity.

With continued migrations between adjacent areas, the $n(n-1)/2$, $\hat{D}(r, r')$ values should resolve into two dimensions. Two principal coordinates accounted for 77.4% and 82.2% of the variability in the coordinate matrix for the Tuxpeño and Mexican collections other than M4 (Figs. 3 and 5). The $D(r, r')$ estimates between areas are essentially determined by two dimensions for the Guatemalan and Guatemalan-Mexican (other than M4) groups (Figs. 2 and 4). A joint two-dimensional mapping was selected for presentation which reflected genetic diversity between populations.

Chromosome knobs are conservatively inherited. They arose as DNA modifications and became established in a population through the "founder effect" or through selective advantage. They are single-event changes in population structure. However, migration is a dominant factor modifying population structure. Through human intervention, seeds can be transported for considerable distances and become established as secondary epicenters for a knob type. The spread of a knob from a primary epicenter identifies migration ties; however, if a knob type is suggestive of a tie between two populations, then all knob types should contribute information to this relationship. An analytical procedure such as presented can help integrate this mass of confusing information.

Collections from Guatemala offered the best source of material to examine migration patterns in maize. A consistent pattern of changes in knob frequencies between adjacent areas was noted for the Guatemalan collections. Two dimensions accounted for 94.9% of the variability among coordinates. The results fit that which is expected from continued migration between adjacent areas but with increased isolation with increased altitude. The association of knob types with altitude has been reported (Mangelsdorf and Cameron 1942). Could certain knob types impart a selective advantage for higher altitudes and thus account for the association? The answer is not clear, but migration effects can completely overshadow selection effects (Hanson 1966). Successful migration of genotypes presumes movement into areas where adapted, and therefore, migration patterns should tend to reflect migration into similar altitudes.

Proximity also was important in determining closeness of relationships (Figs. 2–5). Tuxpeño from M2, M3, and M4 are low altitude collections while those from M5 and M7 are intermediate altitude collections (Table 2). Their differences reflect area of collection rather than altitude of collection (Figs. 3 and 5). There has been a general intergradation between collections in Honduras which transcended altitude (Table 4). The lower altitude collections G1, G2, and G3 from Guatemala reflect intergradation with G3, which is isolated by mountains, showing greatest isolation. The M7a area (1,000 m) reflects primary intergradation with area M8 (2,300 m) in Mexico (Fig. 2). Collections from G6 and M7a reflect possible migration between M8 and G8 (Fig. 4).

From the wealth of information available on the distribution of maize types (Brown and Goodman 1977; Mangelsdorf 1974; McClintock et al. 1981), the similarity between highland collections from Guatemala and Mexico is not surprising. What is interesting is the closeness of the relationship. The genetic diversity between G8 and M8 (0.174) was similar to that found between G8 and its neighbors G6 and G7 (Tables 3 and 5). Major exchange of germplasm must have occurred between the highlands of Guatemala and Mexico with subsequent isolation. Because man is the primary vector for seed dispersal of maize, major exchanges of maize seed could have occurred between these two highland areas under the sophisticated Indian cultures which once existed in these areas. Both altitude and latitude influences where successful migration and establishment occurs. The pattern of diversity (Table 5, Fig. 4) is suggestive of direct, rather than stepwise, exchanges between G8 and M8 or from G8 via some lower altitude (say M7a), to compensate for northern migration.

Widely-distributed collections were classified as Tuxpeño based on detailed morphological characterization (Wellhausen et al. 1952). They also had similar frequencies of knob types. Documentation based on morphological characteristics can lead to groups with similar knob types; however, major discrepancies were found between collections characterized at a different time and place (Fig. 6). This discrepancy probably reflects the need for more extensive evaluation. Further, collections were selected to represent area primarily (McClintock et al. 1981).

Migration per se does not ensure intergradation of germplasms. However, Hanson (1966) concluded that in the long run the identity of maize populations would not be maintained under many cultural conditions followed without pollen control. All of the data analyzed in this study reflected continued intergradation of maize genotypes between adjacent areas. Continued gene flow may have resulted from pollen drift between neighboring fields or from seed exchange. With long-termed continued gene flow, a uniform intergradation of knob types between adjacent areas would be expected as found among Guatemalan collections (Fig. 2). Single-knob "migrations" can be used to identify major disruptions in gene flow as had occurred with Tuxpeño or as had presumably occurred between the high altitude areas of Mexico and Guatemala. The totality of the knob data reflects maize as a dynamic population where major disruptions in gene flow had occurred but where continuity exists between adjacent areas.

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