The Origin of Cornbelt Maize: The Isozyme Evidence[1]

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Historical records show that the Midwestern dent corns of the United States originated from hybridization of two landraces, Northern Flint and Southern Dent. We examined the origin of Southern and Midwestern Dents by means of isozyme electrophoresis. Isozyme genotypes were determined for 23 loci in 12 plants each of 32 accessions of Southern Dent. Previously published isozyme data for maize landraces of Mexico and North America and for U.S. Midwestern Dents were included for comparative purposes. The data show that Northern Flint and Southern Dent are among the isozymically most divergent maize landraces. Nei's genetic identities between populations of these two landraces are very low for conspecific populations (ca. 0.80). Southern Dent of the southeastern U.S. appears closely related to similar dent corns of southern Mexico, supporting a previously published hypothesis that U.S. Southern Dent is largely derived from the dent corns of southern Mexico. The Midwestern Dents, which resulted from crosses of Southern Dent and Northern Flint, are much more like Southern Dent than Northern Flint in their isozyme profile. Similarly, public inbreds show greater affinity to Southern Dent with the exception of sweet corn lines, which resemble Northern Flint in their isozyme allele frequencies. North American public inbreds do not contain appreciable isozymic variation beyond that found in Northern Flint and Southern Dent.

In the pre-Columbian era, maize (*Zea mays* L. ssp. *mays*) agriculture in North America had two focal points, one in the southwestern U.S. and another in the Northeast (Weatherwax 1954). Maize of the southwestern U.S. is diverse both morphologically (Anderson and Cutler 1942) and isozymically (Doebley et al. 1983) and probably resulted from several separate introductions into that region from Mexico (Hernández Xolocotzi 1985). The maize of the northeastern U.S. is more uniform in morphology (Brown and Anderson 1947) and isozymes (Doebley et al. 1986). The maize of this region is often divided into the Northeastern Flints and the Great Plains Flints and Flours on morphological and cytological bases (Brown and Anderson 1947). However, these two groups are very closely related, especially in their isozyme constitution (Doebley et al. 1986), and they will be treated jointly under the name Northern Flint throughout this paper. Evidence from morphology and archaeology (Galinat and Campbell 1967; Galinat and Gunnerson 1963), and isozymes (Doebley et al. 1986) is consistent with the hypothesis that Northern Flint was derived from maize of the southwestern U.S. or northwestern Mexico (but see also Brown and Anderson 1947). Northern Flint

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TABLE 1. LIST OF MAIZE GROUPS ANALYZED, COLLECTIONS IN EACH GROUP, AND THEIR PRINCIPAL COMPONENT SCORES IN FIG. 1.

Group or race	Collections[a]	PC1	PC2
A. Southern Dents			
Gourdseed	AMES: 213715, 217405, 414179, 414183 WLB: GS-1, GS-2	−0.58	−1.12
Hickory King	AMES: 311327 PHS: 84-26	−0.39	−1.18
Jellicorse	WLB: Jellicorse PHS: 84-35	−0.48	−1.26
Mexican June	AMES: 221889, 311243 WLB: Mexican June	−0.25	−0.81
Red Cob Chisholm	WLB: RCC	−0.70	−0.29
Shoepeg	AMES: 269743 FTCO: 76049, 76050 TAES: Shoepeg	−0.44	−1.58
Tennessee Red Cob	AMES: 311235	0.36	−0.31
Tuxpan	TAES: Yellow tuxpan WLB: Tuxpan	−0.33	−0.17
White Dent	AMES: 221885, 233001, 311232, 311241, 363306 FTCO: 9432, 9438, 82757 TAES: White dent, Surecropper	−0.24	−0.78
Yellow Dent	FTCO: 9436	−0.44	−1.59
B. Northern Flints			
Assiniboine	[b]	1.80	0.36
Blackfoot	[b]	2.01	−0.24
Cheyenne	[b]	2.63	−0.47
Gaspe and Canada Flint	[b]	1.88	−0.78
Longfellow and Smut Nose	[b]	2.15	−0.95
Rhode Island and King Phillip	[b]	2.53	0.67
Sioux	[b]	2.06	0.06
Winnebago	[b]	1.64	0.56
C. Northern or high elevation Mexico			
Apachito	[c]	−0.52	0.79
Azul	[c]	−0.41	1.50
Blandito de Sonora	[c]	−0.22	1.04
Celaya	[c]	−0.57	−0.06
Chalqueno	[c]	−0.50	1.36
Chapalote	[c]	−0.26	0.94
Conico	[c]	−0.28	1.71
Conico Norteno	[c]	−0.36	0.37
Cristalino de Chihuahua	[c]	−0.14	0.09
Gordo	[c]	−0.66	0.91
Palomero Toluqueno	[c]	−0.68	1.10
Tablilla de Ocho	[c]	−0.51	0.25
D. Southern or low elevation Mexico			
Bolita	[c]	−0.69	−0.31
Harinoso de Ocho	[c]	−1.42	−1.59
Harinoso de Ocho Occidentales	[c]	−0.51	−0.51
Jala	[c]	−0.73	−0.22
Nal-Tel	[c]	−0.28	1.91
Olotillo	[c]	−0.69	−0.21

TABLE 1. CONTINUED.

Group or race	Collections[a]	PC1	PC2
Reventador	c	−0.71	−0.86
Tabloncillo	c	−0.70	−0.24
Tehua	c	−0.89	−1.35
Tepecintle	c	−0.71	−0.93
Tuxpeno	c	−0.83	−1.35
Zapalote Chico	c	−0.87	0.24
Zapalote Grande	c	−1.02	−0.70
E. Southwestern U.S.			
Eastern Keres	d	0.71	0.56
Havasupai	d	0.95	0.73
Hopi	d	0.41	1.65
Papago	d	−0.39	0.16
Tewa	d	0.13	0.23
Tiwa	d	0.44	0.18
Western Keres	d	0.23	1.76
E. Teosinte			
Zea mays ssp. *mexicana*	e	−0.50	2.49
Zea mays var. *parviglumis*	e	−0.05	0.51

[a] Sources of kernels for Southern Dent are denoted as AMES = USDA Plant Introduction Station, Ames, Iowa; FTCO = National Seed Storage Laboratory, Ft. Collins, CO; TAES = Texas Agricultural Experiment Station, College Station, TX; WLB = W. L. Brown, Pioneer Hi-Bred International, Johnston, IA; PHS = Paul H. Sisco, Department of Crop Science, North Carolina State University, Raleigh, NC.

[b] Collections listed in Doebley et al. (1986).

[c] Collections listed in Doebley et al. (1985).

[d] Collections listed in Doebley et al. (1983).

[e] Collections listed in Doebley et al. (1984).

appears to have gone through an evolutionary bottleneck that produced a reduction in its genetic variation as compared to Mexican maize landraces (Doebley et al. 1986).

Other forms of maize were introduced into the southeastern U.S., probably from Mexico, during the 1600s (Brown and Anderson 1948). The Spanish have been credited with these introductions (Galinat 1985), and morphological and cytological evidence suggests that these new forms merged to produce what is now known as Southern Dent. Southern Dent appears to have been largely derived from similar dent corns of southern Mexico with some influence from Caribbean Flints (Brown and Anderson 1948).

Northern Flint from the New England region and Southern Dent spread among the farmers of the eastern U.S., and their ranges overlapped. The development of today's Cornbelt or Midwestern Dents began about 200 yr ago when these two varieties were accidentally crossed in the mid-Atlantic states (Wallace and Brown 1956). Out of these early chance hybridizations and later deliberate crosses, farmers and seedsmen selected improved varieties that outyielded and soon replaced the two parental races (Baker 1984; Wallace and Brown 1956). These open-pollinated Midwestern Dents were the standard on the farm for most of the 19th and part of the 20th century. In the early part of this century, Shull (1909) demonstrated that inbred lines derived from open-pollinated populations could be crossed to produce hybrids with superior vigor and yield. D. F. Jones made this system practical by introducing the double-cross method (Wallace and Brown 1956), and later H. A. Wallace and others translated these ideas into action by producing the first commercial hybrids (Baker 1984; Mangelsdorf 1974). The parent materials employed to create the inbreds for hybrid corn production were the open-pollinated populations derived from the Northern Flint-Southern Dent admixtures. Over the past 60 yr, corn breeders have continued to select and recombine this material to produce the modern Cornbelt hybrids. Today, most Cornbelt hybrids have as one parent a line derived in part from the open-pollinated variety Lancaster Surecropper, and as the other parent, a line derived largely from the open-pollinated variety Reids Yellow Dent. Lancaster and Reids are presumed to represent the vestiges of the historically important Northern Flint-Southern Dent combination, Lancaster representing predominantly the Flint contribution, and Reids the Dent contribution (Anderson and Brown 1952; Baker 1984). As a result of breeding gains and improved cultivation practices, today's hybrids outyield the first commercial hybrid corn three to one (Duvick 1984).

In this paper, we examine the isozyme evidence for the origins of the Southern and Midwestern (or Cornbelt) Dents. Further, we consider the extent to which Northern Flint and Southern Dent germplasms are represented in Midwestern Dents.

MATERIALS AND METHODS

Twelve plants each from 32 accessions of Southern Dent (Table 1) were assayed for their genotypes at 23 isozyme loci representing 13 enzyme systems. Electrophoretic methods (Cardy et al. 1983; Stuber and Goodman 1983a) and genetics of the loci examined (Goodman and Stuber 1983; Goodman et al. 1980; Stuber and Goodman 1983b, 1984; Stuber et al. 1977) have been summarized elsewhere. Loci examined are listed in Table 2.

For comparative purposes, previously published isozyme data for Mexican maize races (Doebley et al. 1985), Northern Flint (Doebley et al. 1986), Southwestern U.S. maize (Doebley et al. 1983), Midwestern Dents (Smith 1986), North American public inbreds (Smith et al. 1985; Stuber and Goodman 1983a), and teosinte (Doebley et al. 1984) are included (Table 1).

RESULTS AND DISCUSSION

Origin of Southern Dent

Figure 1 is the graph of the first two components from a principal component analysis of the groups listed in Table 1. For this analysis, the variance-covariance matrix of allele frequencies was employed. The first axis accounts for 33.1% of the total variation and the second axis for 11.2%. Figure 1 shows two major groups. On the right, Northern Flint (◆) is isolated from all other maize and teosinte, which appear together on the left. This exceptional genetic divergence of Northern Flint has been previously discussed (Doebley et al. 1986). Within the larger cluster, maize from the southwestern U.S. (□) and northern (■) and southern Mexico (○), and Southern Dent of the southeastern U.S. (●) are reasonably well separated. The coordinates of these groups correspond reasonably well to their geographic distribution, suggesting that geographic and genetic distances are correlated. In Fig. 1, Southern Dent appears close to the southern Mexican races.

TABLE 2. MEAN ALLELE FREQUENCIES IN SOUTHERN DENT (SD) AND NORTHERN FLINT (NF) MAIZE.

	Frequency			Frequency	
Locus-allele	SD	NF	Locus-allele	SD	NF
Acp1-2	0.249	0.030	*Mdh1-0.1*	0.000	0.006
*2**	0.000	0.005	*1*	0.250	0.012
3	0.313	0.204	*6*	0.748	0.839
3.5	0.000	0.007	*8.5*	0.000	0.003
4	0.433	0.644	*9.2*	0.001	0.000
5.5	0.005	0.110	*10.5*	0.002	0.140
Adh1-4	0.931	0.464	*Mdh2-3*	0.417	0.091
6	0.069	0.537	*3.5*	0.135	0.008
Cat3-n	0.000	0.127	*5.6*	0.017	0.000
6	0.000	0.021	*6*	0.429	0.901
7	0.003	0.000	*Mdh3-n*	0.009	0.000
9	0.870	0.555	*16*	0.869	0.990
11	0.004	0.000	*18*	0.122	0.010
12	0.123	0.298	*Mdh4-10.5*	0.001	0.000
Enp1-n	0.013	0.000	*12*	0.990	1.000
1	0.000	0.050	*14.5*	0.009	0.000
4	0.084	0.004	*Mdh5-12*	0.884	0.965
6	0.713	0.421	*15*	0.116	0.030
8	0.141	0.000	*Me1-R*	0.999	1.000
10	0.049	0.526	*S*	0.001	0.000
Est8-4	0.809	1.000	*Mmm-M*	1.000	1.000
5	0.140	0.000	*Pgd1-n*	0.024	0.000
5.8	0.013	0.000	*2*	0.347	0.055
6	0.038	0.000	*3.8*	0.628	0.943
Glu1-n	0.224	0.279	*7*	0.001	0.000
1	0.040	0.000	*9*	0.000	0.003
2	0.163	0.020	*Pgd2-2.8*	0.026	0.009
3	0.002	0.022	*5*	0.974	0.991
3.2	0.000	0.003	*Pgm1-8*	0.001	0.000
5	0.004	0.000	*9*	0.848	0.990
6	0.127	0.229	*16*	0.140	0.010
7	0.435	0.421	*16.5*	0.008	0.000
10	0.005	0.027	*Pgm2-0.45*	0.001	0.000
Got1-1.2	0.000	0.038	*1*	0.000	0.002
4	0.962	0.870	*2*	0.000	0.018
5.8	0.001	0.000	*3*	0.111	0.341
6	0.042	0.092	*4*	0.882	0.605
Got2-2	0.061	0.337	*6*	0.001	0.000
4	0.940	0.663	*8*	0.005	0.034
Got3-4	1.000	1.000	*Phi1-2*	0.052	0.083
Idh1-2	0.004	0.000	*3*	0.005	0.005
4	0.952	1.000	*4*	0.679	0.899
6	0.044	0.000	*5*	0.264	0.013
Idh2-4	0.664	0.136			
6	0.336	0.864			

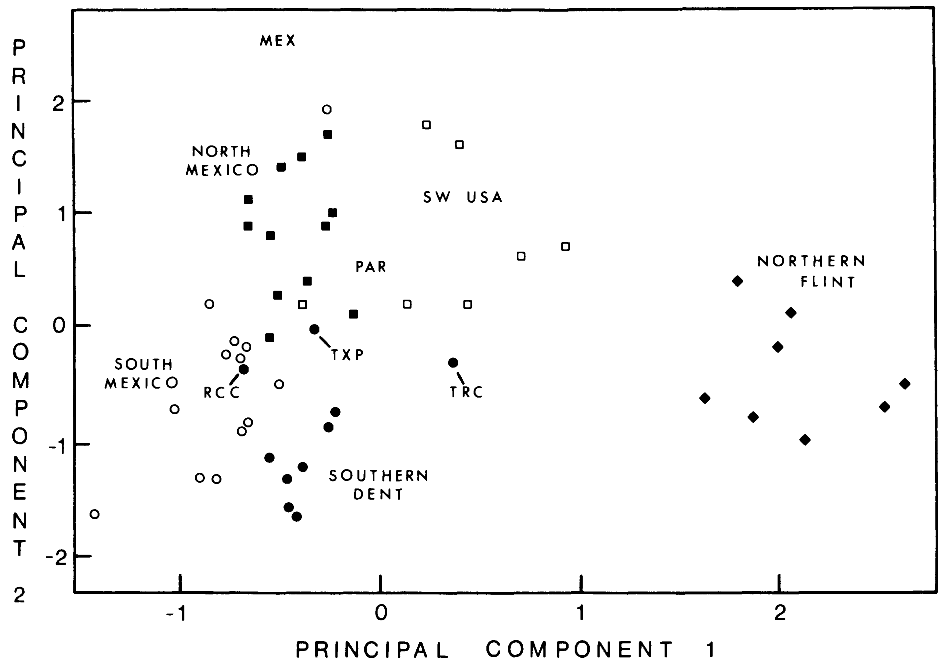

Fig. 1. Graph of the first two axes from a principal component analysis of the groups listed in Table 1, including Northern Flint (◆), Southern Dent (●), Northern Mexican (■), Southern Mexican (O), and Southwestern U.S. (□) maize, and teosintes—*Zea mays* ssp. *mexicana* (MEX) and ssp. *parviglumis* (PAR). RCC indicates Red Cob Chisholm, TRC—Tennessee Red Cob, and TXP—Tuxpan.

Thus, our data support the conclusion of Brown and Anderson (1948) that Southern Dent is largely derived from the dents of southern Mexico. Southern Dent is presumed to have been derived in part from southern Mexican maize during the recent past (1600s), when the Spanish brought maize from Mexico to the southern U.S. (Galinat 1985).

To some extent, Southern Dent separates from the southern Mexican races in a direction that approaches Northern Flint (Fig. 1). This implies introgression of modern Southern Dent by Northern Flint (see Brown and Anderson 1948). Several alleles typical of Northern Flint occur at low frequency in Southern Dent accessions, but are absent in maize from southern Mexico. These include *Adh1-6, Got2-2, Acp1-5.5,* and *Cat3-12.* Two of the Southern Dents (Tuxpan and Red Cob Chisholm) are not separated by isozyme analysis from Mexican races (Fig. 1). Tuxpan is a recent derivative of the Mexican race Tuxpeno. Another Southern Dent, Tennessee Red Cob, also has an aberrant position in Fig. 1 and appears nearer to Northern Flint. Tennessee Red Cob possesses many alleles typical of Northern Flint, including *Acp1-5.5, Adh1-6, Cat3-12,* and *Pgm2-3.* This may be the result of introgression from Northern Flint.

In Fig. 1, Southern Dent and Northern Flint are clearly well separated. The degree of divergence between these two landraces can also be assessed by Nei's (1972) genetic identity (I). Typically, I between two conspecific populations ranges between 0.90 and 1.00 (Crawford 1983). However, I's between Northern Flint and Southern Dent populations are much smaller, generally around 0.80. For

TABLE 3. EXPECTED HETEROZYGOSITY (H_s), PERCENT POLYMORPHIC LOCI PER POPULATION (PLP), AND ALLELES PER LOCUS IN MEXICAN AND NORTH AMERICAN MAIZE.

	H_s	PLP	Alleles/locus
Mexican	0.212	49.0	7.09
Southern Dent	0.223	64.7	3.30
Northern Flint	0.150	41.8	2.78

comparison, one may consider that I's among the races of maize from Mexico ranged from 0.87 to 0.99 with an average of 0.95.

Genetic constitution of Midwestern Dents

The relative degree to which Northern Flint and Southern Dent contributed to Midwestern Dent populations can be assessed with isozyme data. To address this question, all Midwestern Dents were projected onto the line connecting the Northern Flint and Southern Dent centroids through the hypervolume in which each axis is defined by the frequency of an allele. This was done by summing the weighted allele frequencies for each population, the weights being the direction cosines for the angles between each allelic axis and the axis from the Northern Flint to Southern Dent centroids. The equation used is $\mathbf{y} = \mathbf{X}(\mathbf{x}_d - \mathbf{x}_f)[(\mathbf{x}_d - \mathbf{x}_f)'(\mathbf{x}_d - \mathbf{x}_f)]^{-0.5}$, where $\mathbf{X}$ is the data matrix of 77 populations by 88 alleles, $\mathbf{x}_d$ is the vector of mean allele frequencies for Southern Dent, and $\mathbf{x}_f$ is the vector of mean allele frequencies for Northern Flint; $\mathbf{y}$ is a vector of coordinates along the Flint-Dent axis at which each population occurs, except for an arbitrary constant. This method, similar to that of Bray and Curtis (1957), is reasonable unless the presumed intermediate populations contain significant allelic variation not found in the populations used to define the axis. As is documented in the next section, this is not the case for the data set analyzed herein.

Figure 2 is a plot of the Dent-Flint axis described above. This axis accounts for 31.2% of the variance in the full dimensional space, a proportion similar to the first component of Fig. 1. Below the axis, the positions of the individual Northern Flint, Midwestern Dent, and Southern Dent accessions are shown. Above the axis, the mean values for the various groups including North American inbreds are indicated. The most salient feature of this graph is that the bulk of the Midwestern materials are located much closer to the mean for Southern Dent populations than that for Northern Flint populations. The mean for the Midwestern Dents is more than four times as distant from the Northern Flint mean as from the Southern Dent mean. This indicates that the Midwestern Dents are composed predominantly of Southern Dent germplasm. One of the Midwestern Dents, Lancaster, is presumed to be largely a Northern Flint. Our data include two Lancaster accessions. In Fig. 2, one of these (PI 280061) does appear more Northern-Flint-like than other midwestern material, however, the other Lancaster accession (PI 213697) is typical of Midwestern Dents. Inbred lines derived from the Midwestern Dents show a much closer relationship to Southern Dent, with the exception of sweet corn lines, which appear substantially more Northern-Flint-like. As expected, the Southern inbred lines have the greatest similarity to Southern Dent. Curiously, the widely used lines (as defined by Stuber and Goodman 1983a) are

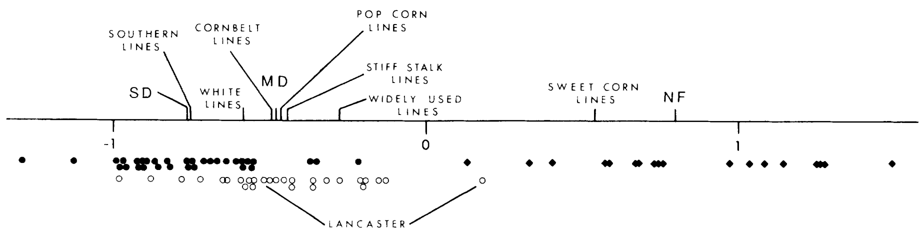

Fig. 2. Axis between Northern Flint and Southern Dent centroids for isozyme allele frequencies. Positions of individual Northern Flint (♦), Southern Dent (●), and Midwestern Dent (○) accessions are shown below the axis. The mean values for Northern Flint, Southern Dent, Midwestern Dent, and various groups of public inbreds are shown directly on the axis.

somewhat more Northern-Flint-like in their isozyme character than other public inbreds. It is also of interest that the mean for Cornbelt inbreds (as defined by Smith et al. 1985) is very close to the mean for Midwestern Dents (Fig. 2). This suggests that the overall allele frequencies of these inbreds do not differ appreciably from the open-pollinated Midwestern Dents, from which they were derived, in respect to their relative proportions of Northern Flint and Southern Dent germplasm.

Figure 3 graphically depicts allele frequency variation for eight alleles among Northern Flint, Midwestern Dent, North American inbreds, and Southern Dent. The alleles shown are those that best differentiate Northern Flint and Southern Dent. The Midwestern Dents and North American inbreds show the expected intermediacy for several of these alleles. However, for some alleles (*Acp1-2, Cat3-9, Got2-2,* and *Pgd1-2*), the Midwestern Dents and inbreds are clearly closer to Southern Dent in allele frequency than to Northern Flint. The trends for individual alleles (Fig. 3) confirm the trend seen for the overall genetic distance (Fig. 2), and indicate that Midwestern Dents and inbreds contain a greater share of Southern Dent germplasm than Northern Flint germplasm.

Genetic variation in U.S. maize landraces

Northern Flint and Southern Dent represent quite distinct germplasm as shown by morphological and cytological studies (Brown and Anderson 1947, 1948), and the isozyme data presented herein and elsewhere. Of the 88 alleles we found in Northern Flint and Southern Dent (Table 2), 35 are restricted to one or the other of these landraces. Most of the alleles that are restricted to either Northern Flint or Southern Dent are uncommon (<5%), but several—including *Cat3-n, Enp1-8,* and *Est8-5*—have frequencies greater than 0.10. Fifty-three alleles occur in both Northern Flint and Southern Dent, but most of these differ appreciably in frequency between the two landraces as shown in Fig. 3 (see also Table 2).

The North American inbreds should possess the same array of isozyme alleles as Northern Flint and Southern Dent. For the most part, this is true, but 13 of the 80 alleles reported in North American inbreds (Stuber and Goodman 1983a) were not found in Northern Flint or Southern Dent. These 13 alleles are all rare (<1%) and include five nulls (*Adh1-n, Est8-n, Mdh1-n, Mdh2-n, Mdh5-n*) and one recessive (*mmm-m*) which could be obscured in the heterozygous condition in the Northern Flint and Southern Dent populations. Spontaneous mutations

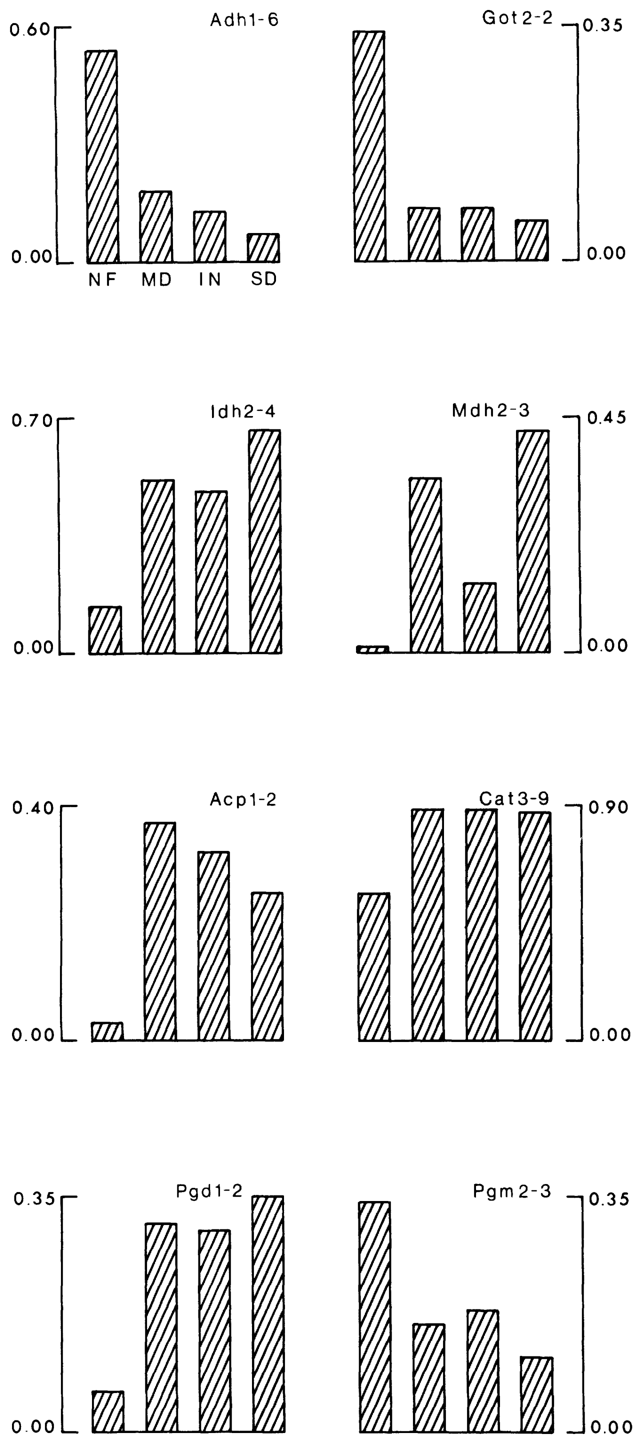

Fig. 3. Histograms showing changes in allele frequencies between Northern Flint (NF), Midwestern Dent (MD), North American inbred lines (IN), and Southern Dent (SD).

occurring after the divergence of these inbreds from Northern Flint-Southern Dent could also explain the restriction of these alleles to the inbreds. Overall, the North American inbreds to not appear to contain much allelic variation beyond that found in Northern Flint and Southern Dent. Moreover, the 80 alleles recorded in North American inbreds represent only one-half the 163 isozyme alleles reported in Mexican landraces.

During its evolution, Northern Flint appears to have undergone a reduction in within-populational variation (Doebley et al. 1986), perhaps as a result of inbreeding due to low effective population size or Founder Effect. This does not appear to be the case for Southern Dent, which has heterozygosity and percent polymorphic loci per population (PLP) equivalent to or greater than that found in Mexican maize (Table 3). Northern Flint and Southern Dent both contain far fewer alleles than Mexican maize, as expected. Combined, Northern Flint and Southern Dent possess 88 alleles (Table 2) compared to 163 for Mexico (Doebley et al. 1985). The data also suggest that Southern Dent contains somewhat greater isozymic variation than Northern Flint (Table 3).

CONCLUDING REMARKS

From historical records and classical botanical study (Brown and Anderson 1948), it is thought that Southern Dent originated largely from similar dent corns of southern Mexico with a minor contribution coming from Caribbean Flint. The isozyme data presented here support this interpretation. Historical records also indicate that Midwestern Dents arose from the hybridization of Northern Flint from New England and Southern Dent (Anderson and Brown 1952). The isozyme data are in agreement with this scenario, but further indicate that Midwestern Dents contain a greater share of Southern Dent germplasm as compared to Northern Flint germplasm. Inbred lines derived from the Midwestern Dents are also skewed toward a Southern-Dent-like isozyme constitution. One notable exception to this rule is the sweet corn inbred lines, which are clearly Northern-Flint-like in isozyme character. This is in agreement with historical records documenting that much of the U.S. sweet corn has Northern Flint in its parentage (Galinat 1971).

Previous morphological (Brown and Anderson 1947) and isozymic (Doebley et al. 1986) studies demonstrated that Northern Flint is extremely well-differentiated from other maize landraces. Two recent cytological studies demonstrated that Northern Flint has the smallest genome of all maize types, while Southern Dent has a genome among the largest in *Zea* (Laurie and Bennett 1985; Rayburn et al. 1985). In this paper, we demonstrate that Northern Flint and Southern Dent are among the isozymically most dissimilar maize landraces examined to date. Anderson and Brown (1952) reported that Northern Flint-Southern Dent crosses produce an extreme heterotic response, although they provide no data to support this claim. It would be of interest to experimentally evaluate the relative heterosis associated with this exceptional morphological, isozymic, and cytological divergence (cf. Moll et al. 1965).

The fact that Northern Flint and Southern Dent represent contrasting germplasm pools is expressed in their disparate allelic composition. Of the 88 isozyme alleles recorded in these two landraces, nearly 40% are restricted to one race or the other, including several alleles with frequencies greater than 0.10. On the other hand, inbred lines derived largely, if not exclusively, from Northern Flint-Southern Dent mixtures contain very few alleles not found in the parent landraces, and these alleles are all rare (< 1%). These data indicated that North American inbreds contain little isozyme allelic variation beyond that found in Northern Flint and Southern Dent. The relatively limited range of isozyme variation in North American inbreds is further demonstrated by the fact that these inbreds contain only half the isozyme alleles reported for Mexican maize.

It is clear from studies of isozymes (Doebley et al. 1985; Stuber and Goodman 1983a), genome size (Laurie and Bennett 1985; Rayburn et al. 1985), restriction site polymorphism (Helentjaris et al. 1985; Johns et al. 1983), and chromosome knobs (McClintock et al. 1981) that maize has a very active and variable genome. In many respects Northern Flint and Southern Dent represent the opposite ends of the spectrum of variation in maize. These two remarkable landraces should prove fertile ground for future studies of genetic variation in *Zea.*

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