

Allozyme polymorphisms within and among open-pollinated and adapted exotic populations of maize

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Summary. Twelve U.S. Corn Belt open-pollinated and five adapted exotic populations of maize (*Zea mays* L.) were assayed for allozyme (allele) variation at 13 enzyme marker loci. Extensive allozyme variability was observed in all populations studied. No locus was monomorphic over all populations. Each of the loci *Idh2*, *Got1*, *Mdh2*, *Pgd1*, and *Pgd2* expressed two allozymes over all populations, *Adh1*, *Acp1*, *Prx1*, and *Est1* each had three allozymes present, *Est4*, *Glu1*, and *Enp1* had five allozymes, and *Acp4* had six allozymes present. Significant deviations of genotypic frequencies were detected from Hardy-Weinberg equilibrium frequencies and 94% of average Fixation Index values indicated heterozygote deficiencies, which suggested that non-random mating and/or natural selection favoring homozygotes were possible factors affecting the maintenance or loss of genetic variability marked by these enzyme loci. Genetic distance and cluster analyses indicated that the observed genetic variability at the 13 enzyme loci was closely related to 'Dent' and 'Flint' types of maize.

Key words: *Zea mays* L. – Corn – Electrophoresis – Enzyme loci – Genetic variation – Germplasm resources

Introduction

The need for further understanding of the nature and amounts of genetic variation within and among populations of important crop plants and their wild relatives has been emphasized (e.g., Allard 1960; Day 1973; Frankel 1977; Marshall 1977; Brown 1978). In 1983, the

National Plant Genetic Resources Board of the United States Department of Agriculture reiterated the need to continue to characterize the amount and distribution of genetic variability in our plant germplasm resources. The importance of genetic variability to the improvement of crop plants is well known and issues concerned with genetic characterization, evaluation, and utilization of domestic and wild germplasm continue to be current topics. It also generally is recognized that the ultimate usefulness of our genetic resources in obtaining specific agronomic goals depends not only on the storage and successful maintenance of germplasm reservoirs, but also on appropriate and adequate characterization of genetic variability in the genome. Thus, a fundamental prerequisite to using genetic variability in plants involves an assessment of the genetic diversity that exists in our available germplasm.

Since 1971, studies have focused on the characterization of allozyme polymorphisms in experimental populations of maize (*Zea mays* L.) (Brown and Allard 1971; Stuber and Moll 1972; Stuber et al. 1980; Kahler 1983 a). These studies and electrophoretic assays of inbred lines (Goodman and Stuber 1980; Cardy et al. 1980; Stuber and Goodman 1983; Kahler 1984; Smith et al. 1985 a, b), hybrids (Smith 1984), Latin American (Stuber et al. 1977; Goodman and Stuber 1980) and Bolivian races (Goodman and Stuber 1983), and native collections from the southwestern United States (Doebley et al. 1983) have shown that there is extensive allozyme variation in maize germplasm as well as pronounced differences in numbers of allozymes per enzyme locus between U.S. Corn Belt germplasm and exotic races of maize.

Although open-pollinated populations of maize have provided much of the U.S. Corn Belt germplasm currently available to maize geneticists and breeders,

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Table 1. The number of individuals assayed per enzyme locus per each of 12 open-pollinated Corn Belt populations and five adapted exotic populations of maize

Population	Population code	Enzyme locus												Source of germplasm	
		<i>Adh1</i>	<i>Idh2</i>	<i>Got1</i>	<i>Mdh2</i>	<i>Acp1</i>	<i>Acp4</i>	<i>Ppx1</i>	<i>Est1</i>	<i>Est4</i>	<i>Glu1</i>	<i>Pgd1</i>	<i>Pgd2</i>		<i>Enp1</i>
Open-pollinated															
'Early Murdock'	EMU	83	82	83	83	83	83	82	74	81	80	55	55	51	J. Geadleman
'Falconer Flint'	FFL	117	113	117	117	113	114	117	117	108	109	86	86	82	A. Hallauer
'Golden Glow'	GGL	133	133	133	133	133	116	117	120	133	131	133	133	133	A. Hallauer
'Hays Golden'	HGO	172	172	172	172	172	167	170	141	171	171	171	171	172	C. O. Gardner
'Krug'	KRU	158	128	158	158	158	155	157	114	158	157	155	157	56	A. Hallauer
'Lancaster'	LAN	89	88	87	89	89	82	89	88	89	89	77	77	55	A. Hallauer
'Leaming'	LEA	112	168	112	162	161	132	112	106	112	161	168	168	168	A. Hallauer
'Longfellow Flint'	LFL	116	114	116	116	116	51	116	116	116	116	83	83	97	A. Hallauer
'Midland'	MID	167	195	167	185	194	167	166	162	167	193	194	194	195	A. Hallauer
'Minnesota 13'	M13	240	237	240	225	238	95	240	239	240	204	237	236	97	G. Geadleman
'Rainbow Flint'	RFL	241	241	241	241	239	230	239	237	233	236	241	241	239	A. Hallauer
'Reids Yellow Dent'	RYD	97	145	97	143	143	99	93	90	92	141	144	145	104	A. Hallauer
Adapted exotic															
'Caribbean Flint/Dent'	CFD	238	212	238	238	227	228	231	206	237	236	235	236	97	IPISA No. ^a
'Cateto Flint'	CFL	138	135	138	138	134	136	138	138	138	138	138	138	138	451690
'Coroico Flour'	COF	111	117	117	116	117	116	117	117	117	115	116	117	114	451691
'Cuzco Flour'	CUF	113	113	113	112	108	112	113	112	110	112	113	113	27	451692
'Mexican Dent'	MED	142	141	142	142	141	134	142	140	142	142	142	142	140	451693
															451694

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they have not been electrophoretically characterized for allozyme polymorphisms.

This paper includes results of a survey of electrophoretically detectable variation within and among open-pollinated populations of maize. The primary objectives were to determine: 1) allozyme frequencies for 13 polymorphic enzyme marker loci within 12 open-pollinated populations and five adapted exotic sources; and 2) how the genetic variation marked by enzyme loci is distributed among the populations.

Materials and methods

The material included 12 familiar North American open-pollinated populations and five recently adapted exotic South American dent type populations derived separately, and in major proportion from Latin American racial complexes (Gerrish 1983; R.L. Wilson, personal communication). The populations and population codes, number of individuals assayed per enzyme locus per population, and the source of the germplasm are listed in Table 1. The number of seedlings assayed per population ranged from 83 in 'Early Murdock' (EMU) to 241 in 'Rainbow Flint' (RFL) and a total of 2,605 individuals were assayed.

A random sample of seedlings from each population was assayed by horizontal starch gel electrophoresis. One sample of inbred line B75 was included as a standard on each gel to aid gel reading. The electrophoretic methods have been reported for the 13 enzyme loci assayed and listed in Table 2 (Cardy et al. 1980; Kahler 1983 a). The method of denoting alleles (allozymes) and genotypes for each locus has been described in detail by Kahler (1983 b).

Data analyses were conducted using a FORTRAN program BIOSYS-1 written by Swofford and Selander (1981).

Results and discussion

Allozyme polymorphisms

The numbers of allozymes detected for the 13 enzyme loci assayed in the 12 North American open-pollinated populations and five adapted exotic Latin American populations are given in Table 3. A total of 43 allozymes were observed among the 13 loci and 17 populations assayed. This is approximately one third the total number of allozymes reported for these enzyme loci over all maize and teosinte (Stuber and Goodman 1983). The maximum number of allozymes detected at a single locus was six at locus *Acp4* in population 'Golden Glow' (GGL). The mean number of allozymes per locus per population ranged from 1.77 ± 0.26 in 'Longfellow Flint' (LFL) to 3.00 ± 0.34 in 'Coroico Flour' (COF). The percentage of polymorphic loci per population ranged from 53.85% in LFL to 100% in the five populations 'Hays Golden' (HGO), 'Leaming' (LEA), 'Minnesota 13' (M13), 'Rainbow Flint' (RFL), and 'Reids Yellow Dent' (RYD).

Allozyme frequencies presented in Table 4 were estimated from observed genotypic frequencies. Allo-

Table 2. Names and chromosomal locations of 13 polymorphic enzyme loci assayed in 12 open-pollinated populations and 5 adapted exotic populations of maize

Enzyme locus	Locus designation in original reference	Chromosomal location	References
Alcohol dehydrogenase 1 (<i>Adh1</i>)	<i>Adh1</i>	1L	Schwartz (1971)
Isocitrate dehydrogenase 2 (<i>Idh2</i>)	<i>Idh2</i>	6L	Goodman et al. (1980)
Glutamate oxaloacetate transaminase 1 (<i>Got1</i>)	<i>Got1</i>	3L	Scandalios et al. (1975) Goodman et al. (1980)
Malate dehydrogenase 2 (<i>Mdh2</i>)	<i>Mdh2</i>	6L	Yang et al. (1977) Goodman et al. (1980) Newton and Schwartz (1980) El-Metainy and Omar (1981) Goodman et al. (1980)
Acid phosphatase 1 (<i>Acp1</i>)	<i>Acp1</i>	9	Kahler (1983 b), Stuber (pers. comm.)
Acid phosphate 4 (<i>Acp4</i>)	<i>Acp4</i>	1L	Hamill (1968), Kahler and Whalen, unpub.
Peroxidase 1 (<i>Prx1</i>)	<i>Px1</i>	2L	Schwartz (1960) Birchler (1978)
Esterase 1 (<i>Est1</i>)	<i>E1</i>	7L	Harris (1966) Harris (1968)
Esterase 4 (<i>Est4</i>)	<i>E4</i>	3S	Stuber et al. (1977); Pryor (1978)
β -Glucosidase 1 (<i>Glu1</i>)	β <i>Glu1</i>	10L	Goodman et al. (1980)
6-Phosphogluconate dehydrogenase 1 (<i>Pgd1</i>)	<i>Pgd1</i>	6L	Goodman et al. (1980)
6-Phosphogluconate dehydrogenase 2 (<i>Pgd2</i>)	<i>Pgd2</i>	3L	Goodman et al. (1980)
Endopeptidase 1 (<i>Enp1</i>)	<i>Ep1</i>	6L	Melville and Scandalios (1972) Nielsen and Scandalios (1974)

zyme frequencies varied widely from population to population and some populations like LFL are unique in their allozyme frequencies. No population was devoid of allozyme variability for all 13 polymorphic enzyme loci and 5 of 17 (29%) populations were polymorphic at all loci. Generally, allozyme variation was extensive among the 17 populations, although the number of allozymes per locus for some loci like *Glu1* was substantially lower than the number found among inbred lines from the southwestern United States (13 allozymes), Bolivian races (16 allozymes), and all maize and teosinte (31 allozymes) assayed (Stuber and Goodman 1983).

Heterozygosity within populations

Observed heterozygote frequencies for each of the 13 enzyme loci and 17 populations are presented in Table 5. Heterozygosity values ranged from 0.00 in 23 of 221 (10%) locus-population estimates to 0.70 at locus *Est1* in the 'Mexican Dent' (MED) population. Mean heterozygosity over all loci in each population ranged from 0.15 ± 0.05 in LFL to 0.42 ± 0.05 in M13.

Chi-square values of "goodness of fit" to Hardy-Weinberg expectations are presented in Table 6. Approximately 27% (54 of 196) of the chi-square values were significant with $P \leq 0.05$. Significant deviations were obtained for at least one locus in every population except EMU, and they occurred more frequently than would be expected by chance alone.

Wright's (1969) genotypic fixation index

$$F = 1 - \frac{\text{Observed frequency of heterozygotes}}{\text{Expected frequency of heterozygotes}}$$

was calculated to quantify excesses or deficiencies of heterozygotes in each population. F is negative when observed frequencies exceed expected frequencies of heterozygotes. Heterozygotes tended to be deficient ($F \geq 0.05$) in 102 of 195 cases (Table 7). All populations had at least one locus that indicated deficiency in heterozygosity. Eight populations HGO, 'Krug' (KRU), LEA, M13, RYD, 'Caribbean Flint/Dent' (CFD), COF, and MED had at least nine of 13 loci that indicated significant deficiency of heterozygotes. Ten of 11 loci assayed in MED indicated heterozygote deficiency and five of the ten loci had F values ≥ 0.05 . The overall mean F for each population indicated deficiency of heterozygotes in 16 of the 17 populations assayed.

The observed significant deviations from Hardy-Weinberg equilibrium frequencies and the relatively high number of positive F values suggest that non-random mating and/or natural selection favoring homozygotes are common features of these open-pollinated and adapted exotic populations of maize.

Genetic distance and cluster analysis

Genetic distance values presented in Table 8 were calculated using the methods of Nei (1972). The distance values ranged from 0.02 for population pair

Table 3. Number of allozymes detected at 13 polymorphic enzyme loci in 12 open-pollinated populations and 5 adapted exotic populations of maize^a

Population	Enzyme locus													Mean no. of alleles per locus	% of polymorphic loci
	<i>Adh1</i>	<i>Idh2</i>	<i>Got1</i>	<i>Mdh2</i>	<i>Acp1</i>	<i>Acp4</i>	<i>Prx1</i>	<i>Est1</i>	<i>Est4</i>	<i>Glu1</i>	<i>Pgd1</i>	<i>Pgd2</i>	<i>Enpl</i>		
Open-pollinated															
'Early Murdock'	2	2	2	2	3	4	3	3	4	3	2	2	1	2.54 ± 0.24	92.31
'Falconer Flint'	2	2	2	2	3	4	3	3	5	4	2	1	2	2.69 ± 0.31	92.31
'Golden Glow'	2	2	1	2	3	6	3	3	4	3	2	2	2	2.69 ± 0.35	92.31
'Hays Golden'	2	2	2	2	3	4	3	3	4	3	2	2	2	2.62 ± 0.21	100.00
'Krug'	2	2	2	2	3	5	3	3	5	3	2	2	1	2.69 ± 0.33	92.31
'Lancaster'	2	2	1	2	3	4	3	3	3	3	2	1	1	2.31 ± 0.26	76.92
'Leaming'	2	2	2	2	3	4	2	3	4	3	2	2	2	2.54 ± 0.22	100.00
'Longfellow Flint'	1	2	2	1	3	4	1	2	1	1	1	2	2	1.77 ± 0.26	53.85
'Midland'	2	2	1	2	3	5	3	3	5	3	2	2	1	2.62 ± 0.35	84.62
'Minnesota 13'	2	2	2	2	3	5	3	3	5	4	2	2	2	2.85 ± 0.32	100.00
'Rainbow Flint'	2	2	2	2	3	5	3	3	4	5	2	2	3	2.92 ± 0.31	100.00
'Reids Yellow Dent'	2	2	2	2	3	5	3	3	5	3	2	2	2	2.77 ± 0.30	100.00
Total number ^b	2	2	2	2	3	6	3	3	5	5	2	2	3		
Adapted exotic															
'Caribbean Flint/Dent'	1	2	2	2	3	5	3	3	5	3	2	1	4	2.77 ± 0.36	84.62
'Cateto Flint'	1	2	2	2	3	4	2	3	5	3	1	1	3	2.46 ± 0.33	76.92
'Coroico Flour'	3	2	2	2	3	5	3	3	4	4	2	1	5	3.00 ± 0.34	92.31
'Cuzco Flour'	1	2	2	2	3	4	2	3	5	3	2	1	2	2.46 ± 0.31	84.62
'Mexican Dent'	1	2	2	2	3	4	3	3	4	2	2	1	3	2.46 ± 0.27	84.62
Total Number ^b	3	2	2	2	3	5	3	3	5	4	2	1	5		
Inbred Lines ^c	3	3	2	5	4	6	4	3	7	7	2	2	4		
Hybrids ^d	2	2	2	3	5	6	4	3	7	5	2	2	2		

^a A total 43 allozymes were observed among the 13 loci and 17 populations studied^b The total number of allozymes observed per locus over the open-pollinated populations and over the adapted exotic populations of this study^c The number of allozymes observed among inbred lines of corn belt maize (Smith et al. 1985 a,b); Kahler 1983)^d The number of allozymes observed among hybrids of corn belt maize (Smith 1984)

Table 4. Allozyme frequencies for 13 polymorphic enzyme loci in 12 open-pollinated and 5 adapted exotic populations of maize^a

Locus	Allozyme	Open-pollinated												Adapted exotic				
		EMU	FFL	GGL	HGO	KRU	LAN	LEA	LFL	MID	M13	RFL	RYD	CFD	CFL	COF	CUF	MED
<i>Adh1</i>	Null																	0.31
	1	0.16	0.32	0.12	0.17	0.18	0.25	0.44	1.00	0.19	0.23	0.48	0.21					0.12
	2	0.84	0.68	0.88	0.83	0.82	0.75	0.56		0.81	0.77	0.52	0.79	1.00	1.00	0.56	1.00	1.00
<i>Idh2</i>	1	0.40	0.39	0.35	0.42	0.41	0.41	0.31	0.72	0.40	0.38	0.64	0.55	0.34	0.47	0.04	0.23	0.61
	2	0.60	0.61	0.65	0.58	0.59	0.59	0.69	0.29	0.60	0.62	0.37	0.45	0.67	0.53	0.96	0.77	0.39
<i>Got1</i>	1	0.07	0.03		0.12	0.02		0.07	0.12		0.03	0.12	0.05	0.01	0.33	0.63	0.16	0.17
	2	0.93	0.97	1.00	0.88	0.98	1.00	0.93	0.88	1.00	0.97	0.88	0.95	0.99	0.67	0.37	0.84	0.83
<i>Mdh2</i>	1	0.57	0.27	0.63	0.63	0.70	0.76	0.45		0.64	0.58	0.11	0.54	0.59	0.49	0.68	0.71	0.70
	2	0.43	0.73	0.37	0.37	0.30	0.24	0.55	1.00	0.37	0.42	0.89	0.47	0.41	0.51	0.32	0.29	0.30
<i>Acp1</i>	1	0.61	0.61	0.60	0.54	0.64	0.85	0.61	0.70	0.39	0.58	0.64	0.41	0.26	0.62	0.15	0.21	0.37
	2	0.27	0.32	0.01	0.11	0.09	0.12	0.28	0.29	0.05	0.15	0.16	0.16	0.19	0.16	0.26	0.38	0.11
	3	0.12	0.07	0.39	0.36	0.28	0.03	0.11	0.01	0.57	0.27	0.21	0.43	0.56	0.22	0.59	0.41	0.52
<i>Acp4</i>	1	0.29	0.17	0.38	0.45	0.31	0.32	0.50	0.04	0.33	0.30	0.28	0.39	0.21	0.07	0.42	0.18	0.06
	2	0.40	0.73	0.24	0.46	0.49	0.63	0.30	0.79	0.47	0.23	0.39	0.49	0.70	0.52	0.19	0.40	0.17
	3		0.01	0.01	0.02	0.02		0.09	0.09	0.01	0.01	0.13	0.01	0.01		0.01		
	4			0.02														
	5	0.27	0.09	0.27	0.08	0.11	0.04	0.11	0.08	0.05	0.26	0.05	0.05	0.03	0.09	0.01	0.01	0.35
	6	0.04		0.07		0.05	0.01			0.14	0.21	0.15	0.07	0.06	0.32	0.38	0.41	0.42
<i>Prx1</i>	Null																	0.48
	1	0.16	0.01	0.10	0.05	0.05	0.24			0.02	0.02	0.15	0.14	0.00				0.03
	2	0.59	0.96	0.36	0.64	0.74	0.54	0.62	1.00	0.54	0.72	0.80	0.71	0.57	0.55	0.51	0.97	0.90
	3	0.25	0.03	0.54	0.31	0.21	0.22	0.38		0.44	0.26	0.05	0.15	0.43	0.45	0.01	0.04	0.07
<i>Est1</i>	1	0.21	0.10	0.11	0.36	0.35	0.57	0.26	0.16	0.32	0.26	0.11	0.49	0.11	0.35	0.01	0.03	0.22
	2	0.51	0.84	0.80	0.11	0.26	0.35	0.33	0.84	0.65	0.60	0.85	0.29	0.67	0.59	0.94	0.96	0.40
	3	0.28	0.06	0.09	0.53	0.39	0.09	0.42		0.03	0.14	0.04	0.21	0.23	0.06	0.06	0.01	0.38
<i>Est4</i>	1		0.01			0.00				0.05	0.02		0.05	0.23	0.01	0.02	0.04	0.17
	2	0.69	0.32	0.61	0.63	0.86	0.82	0.66		0.68	0.36	0.68	0.60	0.55	0.80	0.74	0.93	0.75
	3	0.20	0.44	0.16	0.08	0.08	0.01	0.02	1.00	0.01	0.10	0.13	0.17	0.13	0.04		0.01	
	4	0.03	0.21	0.02	0.10	0.02		0.19		0.21	0.15	0.14	0.13	0.01	0.08	0.22	0.02	0.04
	5	0.08	0.02	0.21	0.20	0.04	0.17	0.14		0.05	0.37	0.05	0.05	0.08	0.08	0.02	0.01	0.05
<i>Glu1</i>	1	0.74	0.77	0.35	0.88	0.77	0.68	0.66	1.00	0.90	0.41	0.80	0.80	0.73	0.87	0.21	0.46	0.82
	2	0.24	0.20	0.57	0.06	0.17	0.31	0.28		0.10	0.46	0.12	0.16	0.24	0.01	0.74	0.52	0.18
	3	0.03	0.03	0.08	0.05	0.06	0.01	0.06		0.01	0.09	0.02	0.04			0.04		
	4		0.01											0.03	0.12	0.01	0.02	
	7											0.01						
<i>Pgd1</i>	1	0.69	0.77	0.63	0.64	0.76	0.58	0.75	1.00	0.68	0.55	0.81	0.72	0.62	1.00	0.83	0.73	0.96
	2	0.31	0.23	0.37	0.36	0.24	0.42	0.25		0.32	0.45	0.19	0.28	0.38		0.17	0.27	0.04
<i>Pgd2</i>	1	0.97	1.00	0.99	0.99	0.97	1.00	0.99	0.99	0.98	0.96	0.98	0.98	1.00	1.00	1.00	1.00	1.00
	2	0.03		0.01	0.01	0.03		0.01	0.01	0.02	0.05	0.02	0.02					
<i>Enp1</i>	Null													0.47				
	1		0.04		0.01			0.03	0.26		0.21	0.34	0.04		0.01	0.01		
	2			0.01								0.02			0.01	0.03		0.69
	3	1.00	0.96	0.99	0.99	1.00	1.00	0.97	0.74	1.00	0.79	0.64	0.96	0.48	0.98	0.92	0.98	0.08
	4													0.01		0.01		
	5													0.04		0.03	0.02	0.24

^a Allozyme frequencies that do not sum to 1.00 for each locus are due to roundoff errors

KRU-HGO to 0.55 for population pair COF-LFL. This result supports the observation that allozyme frequencies are heterogeneous among populations.

The genetic cluster method of Farris (1972) was used to construct the genetic distance dendrogram presented in Fig. 1. The results indicate that the genetic variability marked by the 13 enzyme loci assayed represents at least two subgroups of maize. Subgroup I is represented by EMU, GGL, M13, LEA, 'Lancaster' (LAN), HGO, KRU, RYD, and 'Midland' (MID), which

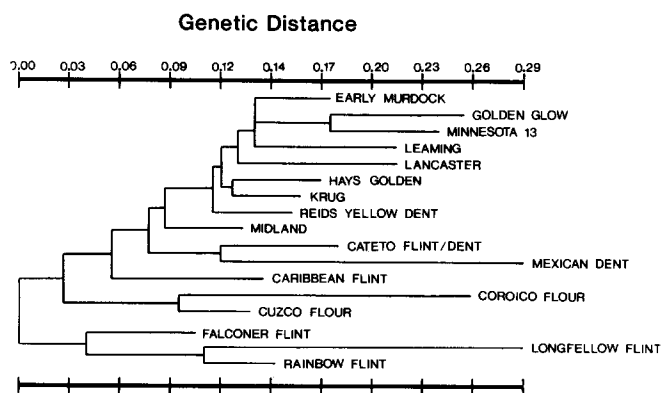
are primarily dent types. Subgroup II includes CFD, MED, CFL, FFL, LFL, and RFL, which are primarily flint types. Populations COF and 'Cuzco Flour' (CUF) seem to be genetically more similar to the flint types than to the dent types.

Conclusions

The results of the electrophoretic assays showed that extensive allozyme polymorphism was the predominant

Table 5. Observed heterozygote frequencies at each of 13 polymorphic enzyme loci and mean heterozygosity ($\pm$ SE) over loci in each of 17 maize populations

Population	Enzyme locus													Mean heterozygosity over loci
	<i>Adh1</i>	<i>Idh2</i>	<i>Got1</i>	<i>Mdh2</i>	<i>Acp1</i>	<i>Acp4</i>	<i>Prx1</i>	<i>Est1</i>	<i>Est4</i>	<i>Glu1</i>	<i>Pgd1</i>	<i>Pgd2</i>	<i>Enp1</i>	
Open-pollinated														
'Early Murdock'	0.26	0.45	0.13	0.49	0.57	0.59	0.55	0.50	0.43	0.39	0.40	0.06	0.00	0.37 $\pm$ 0.06
'Falconer Flint'	0.39	0.52	0.07	0.37	0.46	0.26	0.08	0.29	0.48	0.38	0.36	0.00	0.02	0.28 $\pm$ 0.05
'Golden Glow'	0.22	0.50	0.00	0.43	0.53	0.42	0.57	0.36	0.51	0.55	0.52	0.01	0.01	0.36 $\pm$ 0.06
'Hays Golden'	0.28	0.46	0.21	0.42	0.61	0.36	0.43	0.54	0.44	0.19	0.42	0.01	0.01	0.34 $\pm$ 0.05
'Krug'	0.30	0.51	0.03	0.39	0.46	0.44	0.34	0.56	0.22	0.37	0.32	0.04	0.00	0.31 $\pm$ 0.05
'Lancaster'	0.40	0.61	0.00	0.28	0.28	0.45	0.37	0.47	0.30	0.63	0.69	0.00	0.00	0.34 $\pm$ 0.06
'Leaming'	0.45	0.47	0.12	0.42	0.60	0.47	0.37	0.62	0.38	0.45	0.42	0.02	0.02	0.37 $\pm$ 0.05
'Longfellow Flint'	0.00	0.34	0.22	0.00	0.42	0.18	0.00	0.31	0.00	0.00	0.00	0.01	0.41	0.15 $\pm$ 0.05
'Midland'	0.33	0.48	0.00	0.43	0.53	0.51	0.45	0.48	0.43	0.18	0.48	0.03	0.00	0.33 $\pm$ 0.06
'Minnesota' 13'	0.36	0.50	0.05	0.49	0.60	0.56	0.38	0.55	0.63	0.60	0.44	0.11	0.17	0.42 $\pm$ 0.05
'Rainbow Flint'	0.53	0.45	0.24	0.19	0.56	0.37	0.23	0.22	0.29	0.35	0.35	0.03	0.45	0.33 $\pm$ 0.05
'Reids Yellow Dent'	0.36	0.45	0.09	0.44	0.56	0.44	0.35	0.58	0.40	0.35	0.43	0.01	0.04	0.35 $\pm$ 0.05
Adapted exotic														
'Caribbean Flint/Dent'	0.00	0.39	0.02	0.45	0.61	0.32	0.38	0.45	0.58	0.41	0.43	0.00	0.03	0.31 $\pm$ 0.06
'Cateto Flint'	0.00	0.50	0.46	0.45	0.54	0.51	0.43	0.49	0.25	0.21	0.00	0.00	0.02	0.30 $\pm$ 0.06
'Coroico Flour'	0.26	0.08	0.46	0.43	0.50	0.58	0.00	0.12	0.31	0.44	0.22	0.00	0.12	0.27 $\pm$ 0.05
'Cuzco Flour'	0.00	0.28	0.30	0.38	0.67	0.54	0.07	0.08	0.07	0.54	0.36	0.00	0.04	0.26 $\pm$ 0.06
'Mexican Dent'	0.00	0.47	0.27	0.41	0.57	0.42	0.13	0.70	0.41	0.29	0.06	0.00	0.41	0.32 $\pm$ 0.06

**Fig. 1.** A dendrogram of genetic distances among 12 open-pollinated and five adapted exotic populations of maize

feature of the 12 open-pollinated populations and five adapted exotic populations of maize. The number of allozymes per locus generally was about one third the number possible based on assays of all maize and teosinte. However, the number of allozymes observed per locus in these genetically broad based populations was more comparable to the number of allozymes observed in extensive assays of inbred lines and hybrids of U.S. Corn Belt maize. This is not unexpected because most of the inbred lines and hybrids grown in

the United States were derived from the open-pollinated populations.

It was expected, however, that the adapted exotic populations would be more comparable to Latin American and Bolivian races of maize. For example, only four allozymes were observed for locus *Glu1* in the adapted exotic populations, whereas 13 and 16 allozymes were observed in the collections of maize from the southwestern United States and Bolivian races, respectively. Apparently, either particular allozymes available in the Latin American races were not originally included in the synthesis of these populations or natural selection eliminated many of the allozymes during the short period of adaptation to the corn belt. The methods used in the synthesis and adaptation of the exotic sources probably contributed to the differences observed (Gerrish 1983).

We conclude that open-pollinated populations are effective means of maintaining genetic variability, marked by enzyme loci, currently available in adapted germplasm. Although our data for exotic populations are limited, the results also suggest that exotic germplasm probably should not be maintained in open-pollinated populations in the Corn Belt. Rather, exotic germplasm should be grown in areas of origin to preserve the maximum genetic variation possible for future use by maize geneticists and breeders in the U.S. Corn Belt and other areas of the world.

Table 6. Chi-square values (probabilities are in parentheses) for goodness of fit to Hardy-Weinberg expectations in 12 open-pollinated and 5 adapted exotic populations of maize

Population	Enzyme locus												
	<i>Adh1</i>	<i>Idh2</i>	<i>Got1</i>	<i>Mdh2</i>	<i>Acp1</i>	<i>Acp4</i>	<i>Prx1</i>	<i>Est1</i>	<i>Est4</i>	<i>Glu1</i>	<i>Pgd1</i>	<i>Pgd2</i>	<i>Enp1</i>
Open-pollinated													
'Early Murdock'	0.001 (0.999)	0.328 (0.849)	0.378 (0.828)	0.001 (0.999)	2.367 (0.796)	14.271 (0.113)	3.337 (0.648)	7.157 (0.209)	5.716 (0.768)	0.175 (0.999)	0.292 (0.864)	0.029 (0.986)	
'Falconer Flint'	1.063 (0.588)	0.898 (0.638)	0.128 (0.938)	0.581 (0.748)	3.407 (0.638)	108.760** (0.000)	0.166 (0.997)	2.599 (0.762)	120.531** (0.000)	4.043 (0.853)	0.042 (0.979)		42.129** 0.000
'Golden Glow'	0.000 (1.000)	1.439 (0.487)		1.001 (0.606)	1.828 (0.872)	87.727** (0.000)	0.994 (0.963)	1.323 (0.932)	8.503 (0.484)	2.359 (0.798)	1.506 (0.471)	0.000 1.000	0.000 1.000
'Hays Golden'	0.010 (0.995)	0.386 (0.824)	0.042 (0.979)	1.764 (0.414)	15.282** (0.009)	62.311** (0.000)	339.350** (0.000)	2.234 (0.816)	45.513** (0.000)	11.860* (0.037)	1.449 (0.485)	0.000 1.000	0.000 1.000
'Krug'	0.237 (0.888)	0.266 (0.875)	0.033 (0.984)	1.146 (0.564)	3.279 (0.657)	57.531** (0.000)	13.401** (0.020)	11.400* (0.044)	14.461 (0.342)	0.939 (0.967)	2.085 (0.352)	7.173** (0.028)	
'Lancaster'	0.591 (0.744)	6.116** (0.047)		5.130 (0.077)	0.971 (0.965)	3.479 (0.901)	26.736** (0.000)	5.560 (0.351)	166.912** (0.000)	18.361** (0.001)	12.599** (0.002)		82.081** (0.000)
'Leaming'	0.741 (0.690)	1.788 (0.409)	0.456 (0.796)	3.909 (0.142)	4.886 (0.430)	61.038** (0.000)	5.028 (0.081)	3.270 (0.658)	62.173** (0.000)	1.439 (0.920)	2.987 (0.225)		0.514 (0.773)
'Longfellow Flint'		3.122 (0.210)	0.317 (0.853)		7.429 (0.191)	112.253** (0.000)		1.947 (0.378)				32.131** (0.000)	
'Midland'	0.896 (0.639)	0.024 (0.988)		1.226 (0.542)	0.455 (0.994)	45.389** (0.000)	4.495 (0.480)	2.702 (0.746)	55.101** (0.000)	1.421 (0.922)	2.417 (0.299)	12.404** (0.002)	
'Minnesota 13'	0.000 (1.000)	0.601 (0.740)	3.649 (0.161)	0.002 (0.999)	4.501 (0.480)	28.236** (0.008)	2.519 (0.774)	1.176 (0.947)	25.445** (0.030)	501.905** (0.000)	3.197 (0.202)	0.624 (0.732)	22.531** (0.000)
'Rainbow Flint'	1.191 (0.551)	0.304 (0.859)	4.251 (0.119)	0.199 (0.905)	8.319 (0.139)	231.227** (0.000)	51.210** (0.000)	9.915 (0.078)	140.509** (0.000)	320.341** (0.000)	3.867 (0.145)	0.060 (0.971)	8.133 (0.149)
'Reids Yellow Dent'	0.585 (0.746)	1.005 (0.605)	0.203 (0.903)	1.993 (0.369)	6.605 (0.252)	24.214* (0.043)	14.575* (0.012)	2.035 (0.844)	77.413** (0.000)	4.098 (0.535)	113.482** (0.705)		27.600** (0.000)
Adapted exotic													
'Caribbean Flint/Dent'		3.818 (0.148)	0.021 (0.989)	1.017 (0.601)	1.723 (0.886)	187.307** (0.000)	13.975** (0.007)	4.799 (0.441)	173.104** (0.000)	4.663 (0.458)	1.497 (0.473)		165.398** (0.000)
'Cateto Flint'		0.006 (0.997)	0.368 (0.832)	1.518 (0.468)	2.929 (0.711)	32.688** (0.000)	2.641 (0.267)	2.440 (0.786)	75.349** (0.000)	1.020 (0.961)			134.680** (0.000)
'Coroico Flour'	121.527** (0.000)	0.166 (0.920)	0.016 (0.992)	0.017 (0.991)	2.781 (0.734)	9.231 (0.816)	368.850** (0.000)	0.439 (0.979)	34.457** (0.000)	6.986 (0.538)	5.632 (0.060)		335.881** (0.000)
'Cuzco Flour'		4.792 (0.091)	1.624 (0.444)	0.591 (0.744)	1.547 (0.908)	17.207 (0.046)	0.132 (0.936)	0.173 (0.999)	352.741** (0.000)	4.789 (0.442)	0.798 (0.671)		0.000 (1.000)
'Mexican Dent'		0.056 (0.973)	0.371 (0.831)	0.024 (0.988)	0.030 (0.303)	50.067** (0.000)	25.266** (0.000)	4.954 (0.421)	2.686 (0.975)	0.080 (0.961)	3.598 (0.165)		15.281** (0.009)

* Significant at the 0.05 probability level

** Significant at the 0.01 probability level

Table 7. Genotypic fixation index (F) for 13 enzyme loci assayed in 12 open-pollinated and 5 adapted exotic populations of maize ^a

Population	Enzyme locus													Mean F
	<i>Adh1</i>	<i>Idh2</i>	<i>Got1</i>	<i>Mdh2</i>	<i>Acp1</i>	<i>Acp4</i>	<i>Prx1</i>	<i>Est1</i>	<i>Est4</i>	<i>Glu1</i>	<i>Pgd1</i>	<i>Pgd2</i>	<i>Enp1</i>	
Open-pollinated														
'Early Murdock'	0.00	0.06	-0.06	-0.00	-0.04	0.13	0.03	0.19	0.09	0.03	0.07	-0.02	-	0.06
'Falconer Flint'	0.09	-0.09	-0.03	0.07	0.12	0.39	-0.03	-0.02	0.28	-0.02	-0.02	-	0.66	0.11
'Golden Glow'	0.00	-0.10	-	0.09	-0.07	0.41	0.00	-	0.09	-0.00	-0.11	-0.00	-0.00	0.05
'Hays Golden'	0.01	0.05	-0.01	0.10	-0.06	0.38	0.13	0.07	0.20	0.12	0.09	-0.00	-0.00	0.11
'Krug'	-0.04	-0.04	-0.01	0.08	0.10	0.30	0.18	0.15	0.14	0.02	0.11	0.20	-	0.11
'Lancaster'	-0.08	-0.26	-	0.24	-0.06	0.09	0.39	0.16	0.01	-0.44	-0.40	-	-	-0.03
'Leaming'	0.08	-0.10	0.06	0.15	-0.15	0.27	0.21	0.05	0.26	0.07	-0.13	0.39	0.66	0.09
'Longfellow Flint'	-	0.16	-0.05	-	0.02	0.51	-	-0.13	-	-	-	-0.00	-0.07	0.08
'Midland'	-0.07	0.01	-	0.08	-0.00	0.22	0.14	-0.00	0.13	0.06	-0.11	0.24	-	0.05
'Minnesota 13'	0.00	-0.05	0.12	-0.00	-0.05	0.26	0.08	0.01	0.10	0.02	0.12	-0.05	0.48	0.08
'Rainbow Flint'	-0.07	0.03	-0.13	-0.03	-0.06	0.49	0.32	0.14	0.43	-0.01	-0.13	-0.01	0.04	0.12
'Reids Yellow Dent'	-0.08	0.08	-0.04	0.12	0.10	0.27	0.22	0.08	0.32	-0.05	-0.07	0.80	0.48	0.12
Adapted exotic														
'Caribbean Flint/Dent'	-	0.13	-0.01	0.06	-0.03	0.31	0.24	0.10	0.07	0.01	0.08	-	0.93	0.17
'Cateto Flint'	-	-0.01	-0.05	0.10	-0.01	0.18	0.14	0.08	0.27	0.06	-	-	0.56	0.09
'Coroico Flour'	0.34	-0.04	0.01	0.01	0.11	0.11	1.00	-0.05	0.25	-0.10	0.22	-	0.26	0.18
'Cuzco Flour'	-	0.20	-0.12	0.07	-0.03	0.17	-0.03	-0.03	0.48	-0.03	0.08	-	-0.00	0.06
'Mexican Dent'	-	0.02	0.05	0.01	0.02	0.38	0.29	-0.08	0.01	0.02	0.15	-	0.13	0.08

^a Negative values of F indicate an excess of heterozygotes

Table 8. Matrix of average allelic distance values (Nei 1972) among populations of maize

Population	Open-pollinated populations													Adapted exotic populations				
	EMU	FFL	GGL	HGO	KRU	LAN	LEA	LFL	MID	M13	RFL	RYD	CFD	CFL	COF	CUF	MED	
EMU	0.06																	
GGL	0.05	0.13																
HGO	0.03	0.12	0.10															
KRU	0.02	0.10	0.08	0.02														
LAN	0.03	0.12	0.08	0.05	0.03													
LEA	0.03	0.09	0.08	0.04	0.04	0.06												
LFL	0.27	0.11	0.39	0.34	0.32	0.34	0.26											
MID	0.04	0.10	0.06	0.05	0.04	0.06	0.06	0.32										
M13	0.04	0.09	0.04	0.08	0.07	0.07	0.06	0.30	0.06									
RFL	0.09	0.06	0.16	0.15	0.12	0.15	0.10	0.12	0.11	0.11								
RYD	0.03	0.08	0.09	0.02	0.02	0.05	0.05	0.25	0.03	0.06	0.09							
CFD	0.08	0.12	0.09	0.10	0.09	0.12	0.12	0.36	0.06	0.10	0.16	0.08						
CFL	0.05	0.10	0.11	0.08	0.06	0.09	0.09	0.30	0.05	0.11	0.11	0.06	0.11					
COF	0.21	0.26	0.16	0.27	0.24	0.27	0.21	0.55	0.20	0.19	0.27	0.24	0.23	0.21				
CUF	0.08	0.12	0.09	0.14	0.10	0.13	0.13	0.41	0.08	0.09	0.15	0.11	0.10	0.10	0.10			
MED	0.16	0.24	0.23	0.17	0.14	0.22	0.21	0.45	0.17	0.18	0.20	0.15	0.15	0.14	0.31	0.17		

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