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Allozyme polymorphisms of maize populations from southwestern China

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Abstract Maize (*Zea mays* L.) is one of the most-important food crops in southwestern China. The diversity of maize populations from southwestern China has been evaluated on the basis of agronomic and morphological data, but not on marker data. Our objectives were to evaluate the allozyme polymorphism of these populations, and group the populations on the basis of allozyme data. We analyzed 27 maize populations from southwestern China and two populations [BS13(S)C2 and Lancaster] from the USA for genetic variation at 18 allozyme loci. We found a total of 69 alleles at 18 allozyme loci with an average of 3.8 alleles per locus. Compared with inbreds, hybrids, and populations from the U.S. Corn Belt, the 27 Chinese populations had a significantly higher (p<0.01) number of allozyme alleles per locus. Maize populations from southwestern China have accumulated abundant genetic diversity, and might be valuable germplasm for broadening the genetic base of U.S. Corn Belt breeding germplasm. The analyses of allele-frequency distributions and the expected heterozygosity also reflected the differences between the Chinese and the U.S. germplasm. The Chinese populations might be valuable germplasm for complementing U.S. Corn Belt breeding germplasm. The analysis of gene diversity showed that 77% of the allozyme variation resided within populations and 23% between populations. This result suggested that breeders should identify one or a few Chinese populations with the best agronomic performance, and exploit the genetic variation within these selected populations. Cluster analysis classified the 29 populations into four main groups. Groupings based on allozyme data could be useful for classifying the populations into different heterotic groups and, consequently, exploiting them in hybrid breeding.

Keywords Maize · Allozyme · Genetic variation · Southwestern China

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Introduction

Maize (*Zea mays* L.) is one of the most-important food crops in southwestern China, which includes the provinces of Sichuan, Yunnan, Guizhou, southern part of Shanxi, and western parts of Guangxi, Hunan, and Hubei. These subtropical and temperate hill and mountain areas, with altitudes ranging from 100 to 2,500 m, have very complex climates. Average temperatures range from 10 to 25°C in April, whereas annual rainfall ranges from 800 to 1,300 mm (Dong 1992). Slopes, valleys, and gorges isolate the people and their maize crops in this area.

Commercial hybrid cultivars are not widely used because of limitations imposed by the special and complex environments in southwestern China. Local cultivars of maize were grown in more than 50% of the 4-million hectares in this area (Dong 1992), and the average grain yield per hectare in this area was only 2.25–4.50 t ha^{-1}. These cultivars were developed by different farmers over decades of planting and harvesting, and have become adapted to the hot and humid growing seasons in southwestern China. These open-pollinated populations have been geographically isolated and may have accumulated many mutant genes.

A total of 3,913 local maize populations had been collected from southwestern China during the 1950s–1980s

(Liu 1992) when many indigenous maize populations existed and few commercial varieties were available. However, except for agronomic and morphological data (Hsu 1988; Huang 1991; Lu et al. 1994), there have been no reports on the genetic diversity among these populations. Since the 1970 s, allozymes have been extensively used to examine the genetic variability in breeding material (Brown 1979; Tanksley and Orton 1983). Allozyme assay is a useful tool to detect genetic variation (Dubreuil and Charcrosset 1998; Sanchez et al. 2000), and is particularly suitable for developing countries because it is relatively simple, rapid, and inexpensive. It also provides an efficient approach for directly comparing the magnitude and distribution of genetic diversity between different populations and species. We used allozymes in this study to allow a direct comparison with previous studies on allozyme polymorphisms in U.S. (Smith 1984; Smith et al. 1985; Kahler et al. 1986), Bolivian (Goodman and Stuber 1983), and Mexican (Doebley et al. 1985) maize populations.

Our objectives in this research were to: (1) assess the level of allozyme polymorphism of maize populations from southwestern China, and (2) classify the populations into groups on the basis of allozyme variation.

Materials and methods

Maize populations

Twenty seven open-pollinated maize populations (Table 1) were selected from about 2,000 populations collected by the Tian Chishan Agricultural Research Institute (Enshi, Hubei, China). Two U.S. maize populations, BS13(S)C2 and Lancaster, were maintained in the maize research laboratory at Huazhong Agricultural University, Wuhan, China. Lancaster was provided by Dr. L.L. Darrah at the University of Missouri in 1984. BS13(S)C2 was provided by Dr. A.R. Hallauer at Iowa State University in 1984. It was a second cycle of inbred progeny selection from BS13(HT)C7 that was developed from seven cycles of half-sib family selection from Iowa Stiff Stalk Synthetic (BSSS) with Ia13 as the tester (Hallauer et al. 1988).

Isozyme assays

A total of 110 kernels of each population were grown in a growth chamber at 25°C for 7 days. Enzyme extraction methods, electrophoresis procedure, and gel scoring were performed according to Stuber et al. (1988). Inbreds Mo17 and Oh43 were considered as standards and their samples were loaded on each gel to aid allele scoring. About 90–105 seedlings of each population were genotyped at 18 isozymic loci of eight enzyme systems. The 18 isozymic loci were randomly distributed across eight out of ten maize chromosomes (Table 2). All alleles and genotypes for each locus were denoted with the method described by Stuber et al. (1988), but Acp4 was denoted according to Kahler (1983). All the isozyme assays were conducted in the Maize Research Laboratory at Huazhong Agricultural University in Wuhan, China.

Table 1 The U.S. and Chinese maize populations, their origins, and the latitudes, longitudes, and elevations of their origins

Population	Origin	Endosperm		Latitude (north)	Longitude (east)	Elevation (meters)
		Color	Type			
U.S. populations						
BS13(S)C2	Iowa	Yellow	Dent			
Lancaster	Missouri	Yellow	Dent			
Chinese populations						
Ba Shizao	He Feng	Yellow	Flint	29.9	110.0	980
Bai Rizao	Yi Chang	Yellow	Flint	30.7	111.2	115
Bai Shaodi	Xuan En	White	Dent	30.0	109.4	532
Bang Chuihu	Fang Xian	Yellow	Dent	32.1	110.6	427
BD Yejizho	Ba Dong	Yellow	Flint	31.1	110.4	141
Da Pigu	Zhu Xi	Yellow	Dent	32.4	109.6	448
Da Zibai	Wu Feng	White	Dent	30.2	110.6	560
Er Jizao	Yun Xi	White	Flint	33.0	110.4	249
Er Man	Zi Gui	Yellow	Flint	30.9	110.9	98
Hua Liushi	Chang Yang	Mixed	Dent	30.5	111.1	118
Jin Bangchui	Zhu Shan	Yellow	Dent	32.3	110.2	407
Jin Zihuang	Xin Shan	Yellow	Dent	31.4	110.8	121
LC Yejizho	Li Chuan	Yellow	Flint	30.3	108.9	1,180
Liu Shinan	Yi Chang	White	Wax	30.7	111.2	115
Liu Shizao	Wu Feng	Yellow	Flint	30.2	110.6	560
Qin Kehuang	Zhu Xi	Yellow	Dent	32.4	109.6	448
Shen Lihong	Yuan An	Red	Flint	31.1	111.7	203
Tie Zibai	Ying Shan	White	Dent	30.9	115.7	113
Wu Yuehuang	Yi Chang	Yellow	Dent	30.7	111.2	115
Xia Zhibaogu	En Shi	White	Dent	30.3	109.4	437
Xiao Jinzi	Yun Xian	Yellow	Flint	32.9	110.8	202
Xiao Zibai	Yuan An	White	Dent	31.1	111.7	203
Xiao Zihuang	En Shi	Yellow	Dent	30.3	109.4	437
YA DaZihu	Yuan An	Yellow	Dent	31.1	111.7	203
XY Ziezihu	Yun Xian	Yellow	Dent	32.9	110.8	202
ZG DaZihu	Zi Gui	Yellow	Dent	30.9	110.9	98
ZX Tiezihu	Zhu Xi	Yellow	Dent	32.4	109.6	448

Table 2 Number of alleles detected at 18 isozyme loci in 29 populations

Population	Allozyme locus[a]																		Average number of alleles	Percentage of polymorphic loci	Expected hetero-zygosity
	Acp1 (9)	Acp4 (1L)	Adh1 (1L)	Cat3 (4)	Est1 (7L)	Est3 (3)	Est8 (8S)	Got1 (3L)	Got2 (5L)	Got3 (5S)	Mdh1 (8)	Mdh2 (6L)	Mdh3 (3L)	Mdh5 (5S)	Mmm (1L)	Pgd1 (6L)	Pgd2 (3L)	Phi1 (1L)			
Chinese populations																					
Bang Chuihu	2	3	1	5	4	2	2	2	2	1	2	2	2	2	1	2	1	1	2.1	72	0.20
Bai Rizao	2	3	2	3	2	2	3	3	1	1	1	2	2	1	1	2	2	2	1.9	72	0.24
Bai Shaodi	3	4	2	2	2	2	1	1	1	1	2	1	2	2	1	3	3	1	1.9	61	0.19
Ba Shizao	3	2	1	3	2	2	2	3	2	1	2	2	2	1	2	1	1	1	1.8	67	0.22
Da Pigu	4	4	1	4	3	2	3	2	3	2	1	2	2	1	1	2	3	1	2.3	72	0.29
Da Zibai	3	3	1	4	2	1	3	3	4	2	3	2	2	1	1	3	2	2	2.3	78	0.27
YA Dazihu	1	4	1	5	2	2	2	2	3	2	2	2	2	1	1	1	2	2	2.1	72	0.27
ZG Dazihu	3	1	1	3	2	1	1	2	2	2	2	1	2	2	1	1	1	1	1.6	50	0.15
Er Jizao	3	4	3	2	2	1	2	1	1	2	3	2	1	1	1	2	2	1	1.9	61	0.18
Er Man	3	1	1	4	2	1	3	2	2	2	5	3	1	1	1	2	1	1	2.0	56	0.19
Hua Liushi	4	3	1	4	2	2	2	3	2	2	2	2	2	2	1	2	2	1	2.2	83	0.26
Jin Bangchui	3	3	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1.6	50	0.17
Jin Zihuang	3	1	1	5	2	1	2	2	2	2	2	2	2	1	1	1	2	2	1.9	67	0.20
Liu Shinan	2	2	2	3	2	1	2	1	1	1	1	2	2	1	1	3	3	2	1.8	61	0.20
Liu Shizao	3	3	1	3	2	3	3	2	1	1	3	2	1	1	1	2	1	1	1.9	56	0.20
Qin Kehuang	3	3	3	4	2	1	1	1	1	1	4	3	1	1	1	2	1	1	1.9	44	0.16
Shen Lihong	4	4	1	3	2	2	3	1	1	1	3	3	1	1	1	2	2	1	2.0	56	0.25
Tie Zibai	2	1	1	1	2	1	3	2	3	3	3	2	1	1	1	2	1	1	1.7	50	0.13
ZX Tiezihu	1	3	1	1	3	2	3	2	2	2	2	1	1	1	2	1	1	1	1.7	50	0.14
YX Tiezihu	3	2	1	4	2	2	2	2	2	2	3	2	2	1	1	2	2	1	2.0	78	0.23
Wu Yuehuang	3	4	1	3	3	2	2	2	2	2	2	1	1	1	1	2	2	1	1.9	67	0.14
Xiao Jinzi	2	3	1	2	2	2	2	2	2	2	1	1	2	1	1	3	1	1	1.7	61	0.16
Xia Zhibaogu	3	3	1	4	2	2	2	2	2	2	2	1	1	1	1	2	1	1	1.8	61	0.17
Xiao Zihuang	3	3	1	4	2	2	2	3	2	2	1	1	1	1	1	1	1	1	1.8	50	0.20
Xiao Zibai	2	4	2	3	2	1	2	1	1	1	2	2	3	2	1	1	1	2	1.8	61	0.19
LC Yejizho	3	3	1	3	2	1	1	1	1	1	2	2	2	2	1	2	2	1	1.7	56	0.18
BD Yejizho	3	3	2	4	3	2	2	3	2	2	1	2	2	1	1	1	1	2	2.1	72	0.24
Total	5	6	3	7	4	3	4	3	4	3	5	4	3	2	2	3	4	2	3.7	94	0.28[b]
U.S. populations																					
BS13(S)C2	3	3	2	3	3	2	2	2	2	2	1	2	2	1	1	3	2	1	2.1	72	0.25
Lancaster	3	3	2	3	3	2	4	2	2	1	3	3	2	1	1	5	3	3	2.7	83	0.31
Total	3	4	2	4	3	2	4	3	2	2	3	3	2	1	1	5	3	3	2.8	100	0.32[c]

[a] The chromosomal location of each allozyme locus (from Stuber et al. 1988) is included in parentheses. L=long arm, S=short arm

[b] The total expected heterozygosity of 27 Chinese populations

[c] The total expected heterozygosity of the two U.S. populations

Analysis of genetic diversity

Expected heterozygosity within and between populations was estimated according to Nei (1975). The gene diversity in the total population (H_T) was partitioned into gene diversity within (H_S) and between (D_{ST}) populations, and

$H_T=H_S+D_{ST}$.

The relative (G_{ST}) degree of gene differentiation measures the portion of genetic variation in the whole population that is attributable to genetic differentiation among subpopulations (Hartl 1980, pp 160–168), and $G_{ST}=D_{ST}/H_T$ (Nei 1975). Genetic distances among populations were assessed using modified Rogers distance (Wright 1978). The matrix of modified Rogers distances was used for average cluster analysis on PC-SAS (SAS 1987).

Results and discussion

Number of allozyme alleles

We found a total of 69 alleles at 18 allozyme loci with an average of 3.8 alleles per locus across all 29 populations. There were 67 alleles in the 27 Chinese populations with an average of 3.7 alleles per locus, and 50 alleles in the two U.S. populations with an average of 2.8 alleles per locus. The average number of alleles was significantly lower ($p<0.01$) in the U.S. than in the Chinese populations. Forty eight out of sixty nine alleles (70%) were present in both the Chinese and U.S. populations, two (3%) alleles (*Pgd1–7* and *Pgd1–9*) were present only in the U.S. populations, and 19 (28%) alleles were present only in the Chinese populations (Table 3).

Comparisons with previous studies, using the same set or subset of allozyme markers, indicated that the average number of alleles observed in the 27 Chinese local populations was significantly higher ($p<0.01$) than in 72 historically important U.S. inbreds (Smith et al. 1985), 111 U.S. hybrids (Smith 1984), and 12 open-pollinated U.S. populations (Kahler et al. 1986) (Table 3). For example, at the same set of eight allozyme loci there was an average of 4.0 alleles per locus among the 27 Chinese populations, but only 2.8 alleles per locus among the 12 U.S. open-pollinated populations (Kahler et al. 1986). These U.S. populations included Reid Yellow Dent, Lancaster, Leaming, Minneasota 13 and Krug, which have been widely used in maize breeding in the U.S.A. (Troyer 1999). We therefore conclude that there is abundant allozyme polymorphism in maize populations from southwestern China, and these populations might be valuable germplasm for broadening the genetic base of U.S. Corn Belt breeding germplasm.

Maize was first introduced into China only about 500 years ago (Burtt-Davy 1914; Liu 1992). Several factors might have contributed to the generation, preservation, and accumulation of new genes in maize populations from southwestern China. These factors include the complex climate conditions, hundreds of years of natural and artificial selection, varied cropping systems and rotations, and lack of intercrossing with commercial hybrids in this mountainous area of southwestern China. The discovery of waxy maize (*Z. mays sinensis*) in the Yunnan province (a part of southwestern China), and that an original cultivar of waxy maize only had a four-row ear (Zeng 1992), which was a typical character of wild corn (Weatherwax 1955), are good examples of such a valuable gene pool. In contrast, we also noted that there were more allozyme alleles among 31 Bolivian races (Goodman and Stuber 1983) and 34 Mexican races (Doebley et al. 1985) than in 27 Chinese populations at the same set of loci (Table 3). This result was expected if we consider that Mexico and Bolivia were the centers of origin of maize (Burtt-Davy 1914; Galinat 1988).

Distribution of allozyme alleles

The number of allozyme alleles per locus varied between the 18 allozyme loci in the 27 Chinese populations we studied. Three loci (Mdh5, Mmm and Phi1) had only two alleles. Cat3, the most-variable locus, had seven alleles. If a locus is considered polymorphic only when the frequency of the most-common allele is less than 0.99 (Nei 1975; Gottlieb 1981), then 17 of the 18 loci examined (94%) were polymorphic. Among 34 Mexican races of maize, 91% loci were polymorphic by this criterion (Doebley et al. 1985). In our study, the percentage of polymorphic loci ranged from 44% in Qin Kehuang to 83% in Hua Liushi. It was 72.2% for BS13(S)C2 and 83% for Lancaster (Table 2).

Fourteen out of sixty seven (21%) alleles in the 27 Chinese populations were rare, having frequencies of 0.01 or less. Sanchez et al. (2000) investigated 1,080 accessions representing more than 300 maize races of the Americas on 23 isozyme loci, and found that 81% of the 329 allozyme alleles were rare. The inclusion of 27 Chinese populations in this study (versus 1,080 accessions in the Sanchez et al. report) limited the finding of more rare alleles.

At 14 of 18 (77.8%) allozyme loci, the distributions of allozyme alleles within each locus were similar between the 27 Chinese populations and the U.S. germplasm (data not shown). But they were very different at Acp4, Est1, Pgd1 and Pgd2. In the U.S. germplasm, which included the two U.S. populations in this study, 72 U.S. inbreds (Smith et al. 1985), 111 U.S. hybrids (Smith 1984) and 12 U.S. populations (Kahler et al. 1986), the most-frequent alleles were *Acp*4–2, *Est*1–2 and *Pgd*1–3.8. These three alleles were not the most-frequent alleles in the 27 Chinese populations (Table 4). At Pgd2, the Chinese germplasm had a much higher frequency (20.5%) of *Pgd*2–6 than the U.S. germplasm (Table 4). We do not know the phenotypic effects associated with these most-common alleles. But the differences in the most-common alleles between the Chinese and the U.S. germplasm indicated that the Chinese populations might be a valuable germplasm for complementing the U.S. Corn Belt breeding germplasm.

Table 3 Comparisons of allele numbers and expected heterozygosities between 27 Chinese populations and other germplasms. [1] and [2] Results from this study, [3] Smith et al. 1985, [4] Smith 1984, [5] Kahler et al. 1986, [6] Goodman and Stuber 1983, [7] Doebley et al. 1985

Germplasm	Allele numbers at each allozyme locus																		Average number of allele	
	Acp1	Acp4	Adh1	Cat3	Est1	Est3	Est8	Got1	Got2	Got3	Mdh1	Mdh2	Mdh3	Mdh5	Mmm	Pgd1	Pgd2	Phi1	Common loci[a]	All loci[b]
27 Chinese populations[1]	5	6	3	7	4	3	4	3	4	3	5	4	3	2	2	3	4	2	3.7	
2 US populations[2]	3	4	2	4	3	2	4	3	2	2	3	3	2	1	1	5	3	3	3.7	2.8**
72 US inbreds[3]	4	–	3	3	–	–	–	2	2	1	2	4	2	2	1	3	2	4	3.6	2.5**
111 US hybrids[4]	5	–	2	1	–	–	–	2	2	1	2	3	2	2	2	2	2	3	3.6	2.2**
12 US populations[5]	3	6	2	–	3	–	–	2	–	–	–	2	–	–	–	2	2	–	4.0	2.8**
31 Bolivian races[6]	6	–	4	8	–	–	6	4	3	2	7	5	4	6	2	5	5	6	3.6	4.9**
34 Mexican races[7]	9	–	4	8	–	–	7	7	3	6	9	12	6	6	3	6	6	5	3.6	6.5**
Germplasm	Expected heterozygosity at each allozyme locus																		Average expected heterozygosity	
	Acp1	Acp4	Adh1	Cat3	Est1	Est3	Est8	Got1	Got2	Got3	Mdh1	Mdh2	Mdh3	Mdh5	Mmm	Pgd1	Pgd2	Phi1	Common loci[c]	All loci[d]
27 Chinese populations[1]	0.58	0.60	0.08	0.49	0.47	0.23	0.30	0.15	0.08	0.06	0.49	0.41	0.44	0.04	0.00	0.27	0.34	0.08	0.28	
2 US populations[2]	0.64	0.66	0.38	0.34	0.56	0.18	0.50	0.09	0.06	0.03	0.25	0.53	0.50	0.00	0.00	0.59	0.16	0.09	0.28	0.32
72 US inbreds[3]	0.63	–	0.24	0.13	–	–	–	0.11	0.11	0.00	0.24	0.63	0.15	0.06	0.00	0.49	0.13	0.30	0.25	0.21
111 US hybrids[4]	0.54	–	0.04	0.00	–	–	–	0.10	0.04	0.00	0.21	0.55	0.08	0.02	0.02	0.40	0.21	0.31	0.25	0.18
12 US populations[5]	0.56	0.66	0.43	–	0.60	–	–	0.10	–	–	–	0.50	–	–	–	0.41	0.04	–	0.36	0.46
31 Bolivian races[6]	0.51	–	0.06	0.42	–	–	0.15	0.44	0.04	0.01	0.21	0.49	0.09	0.36	0.03	0.52	0.04	0.12	0.25	0.23
34 Mexican races[7]	0.63	–	0.03	0.08	–	–	0.18	0.20	0.02	0.06	0.19	0.64	0.21	0.26	0.02	0.47	0.02	0.19	0.25	0.21

** Significant at the 0.01 probability level

[a] Average number of alleles in 27 Chinese populations at the same subset of allozyme loci as other germplasms

[b] Average number of alleles in other germplasms at all available loci

[c] Expected heterozygosity of 27 Chinese populations at the same subset of allozyme loci as other germplasms

[d] Expected heterozygosity of other germplasms at all available loci

Table 4 Allele frequencies (%) at four allozyme loci in 27 Chinese populations and U.S. germplasms

Allozyme allele	27 Chinese populations[a]	Two U.S. populations[b]	72 U.S. inbreds[c]	111 U.S. hybrids[d]	12 U.S. populations[e]
Acp4–1	12.7	25.5	–	–	31.3
Acp4–2	15.7	48.5	–	–	46.8
Acp4–4	9.7	6.0	–	–	0.2
Acp4–5	59.5	20.0	–	–	12.2
Acp4–6	1.9	0.0	–	–	6.2
Acp4–7	1.0	0.0	–	–	0.0
Other alleles	0.0	0.0	–	–	3.3
Est1–1	2.9	21.5	–	–	27.5
Est1–2	27.8	60.0	–	–	53.6
Est1–4	67.3	18.5	–	–	19.0
Est1–6	1.9	0.0	–	–	0.0
Pgd1–2	84.9	42.5	41.0	27.9	28.5
Pgd1–2.8	5.8	4.0	0.0	0.0	0.0
Pgd1–3.8	9.2	47.0	59.0	72.1	71.5
Pgd1–7	0.0	5.0	0.0	0.0	0.0
Pgd1–9	0.0	1.5	0.0	0.0	0.0
Pgd2–2.8	0.3	6.5	7.4	11.8	1.8
Pgd2–5	78.9	91.5	92.6	88.2	98.2
Pgd2–6	20.3	2.0	0.0	0.0	0.0
Pgd2–7	0.5	0.0	0.0	0.0	0.0

[a] and [b] Results from this study
[c] Smith et al. 1985
[d] Smith 1984
[e] Kahler et al. 1986

Expected heterozygosity within and among populations

The expected heterozygosity (H), which is a function of both allele numbers and allele frequencies, ranged from 0.13 in Tie Zibai to 0.31 in Lancaster with an average of 0.21 among all 29 populations (Table 2). Each of the two U.S. populations had a higher H than the average H among the Chinese populations. This result demonstrated that each Chinese population is not necessarily more diverse; Lancaster is most abundant in allozyme variation among 29 populations. The total H was lower in the 27 Chinese populations (H=0.28) than in the two U.S. populations (H=0.32) (Table 2). The fact that 21% of the alleles among the 27 Chinese populations had a frequency of <1%, but no such alleles existed in the two U.S. populations (data not shown), may have contributed to the lower H of the 27 Chinese populations relative to the two U.S. populations.

Compared with other germplasms, the 27 Chinese populations had a much higher H at Mdh1 and Pgd2, but a much lower H at Pgd1 (Table 3). In contrast, four groups of U.S. germplasms (two U.S. populations in this study, 72 U.S. inbreds, 111 U.S. hybrids, and 12 U.S. populations) had a consistent H at each of the 18 allozyme loci.

Table 5 Measures of gene diversity at 18 allozyme loci in 27 Chinese populations

Locus	Number of alleles	H_S[a]	H_T[a]	G_{ST}[a]
Acp1	5	0.46	0.60	0.23
Acp4	6	0.43	0.65	0.34
Adh1	3	0.09	0.11	0.11
Cat3	7	0.37	0.44	0.15
Est1	4	0.38	0.54	0.29
Est3	3	0.16	0.24	0.33
Est8	4	0.28	0.29	0.04
Got1	3	0.09	0.15	0.39
Got2	4	0.09	0.10	0.16
Got3	3	0.06	0.06	0.11
Mdh1	5	0.29	0.47	0.39
Mdh2	4	0.33	0.43	0.25
Mdh3	3	0.28	0.44	0.36
Mdh5	2	0.03	0.03	0.03
Mmm	2	0.00	0.00	0.05
Pgd1	3	0.19	0.33	0.44
Pgd2	4	0.17	0.32	0.50
Phi1	2	0.07	0.07	0.04
Mean	3.72	0.21	0.29	0.23

[a] H_S, the gene diversity within populations; H_T, the gene diversity in the total populations; G_{ST}, the relative degree of gene differentiation (Nei 1975)

Analysis of gene diversity

Total gene diversity (H_T) for each locus varied from 0.00 at Mmm to 0.65 at Acp4. The average across all loci was 0.29 (Table 5). The H_T for Chinese populations was slightly higher than the H_T for Mexican maize (0.25) (Doebley et al. 1985). Gene diversity in the total populations can be apportioned within and between subpopulations. The mean gene diversity within populations (H_S) varied from 0.00 at Mmm to 0.46 at Acp1 (Table 5). The average over all loci was 0.21, which was also slightly higher than that of Mexican races of maize, 0.18 (Doebley et al. 1985).

The relative degree of gene differentiation among populations, G_{ST} (Hartl 1980; Nei 1975), varied from 0.03 at Mdh5 to 0.50 at Pgd2, with the average over all loci being 0.23 (Table 5). This means that 23% of gene diversity resided among populations, and 77% of gene diversity resided within populations. This result indicat-

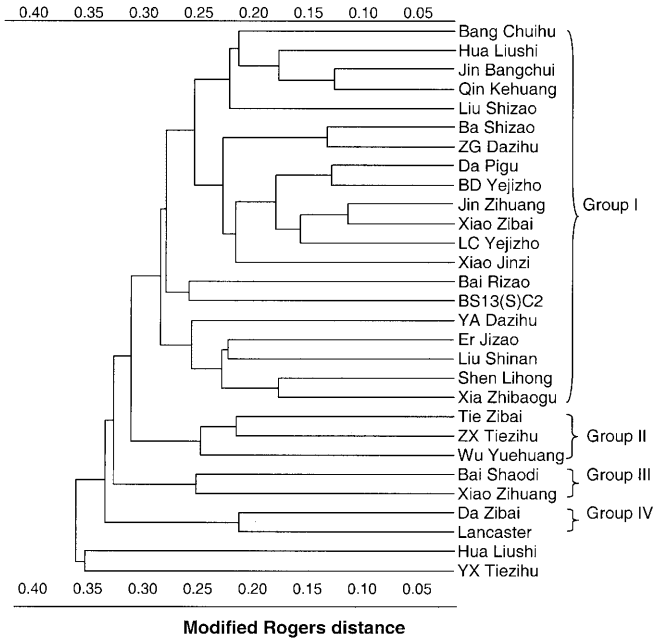

Fig. 1 Groupings of 29 maize populations based on 18 allozyme loci

ed that there was more genetic variation within, than among, maize populations from southwest China. Accordingly, maize breeders should concentrate their breeding efforts on only one or a few Chinese populations that have the best agronomic performance. A similar level of G_{ST} (0.28) was also found in Mexican maize (Doebley et al. 1985). This result also indicated that the local populations of maize from southwest China are well differentiated from each other.

Genetic distance and cluster analysis

At the modified Rogers distance of 0.30, the 29 populations were clustered into four groups (Fig. 1). Group I had 20 populations including BS13(S)C2, and was considered as a BSSS type. Group II had three populations, Tie Zibai, ZX Tezihu and Wu Yuehuang, and they all were flint type. However, Tie Zibai had white endosperm, whereas ZX Tiezihu and Wu Yuehuang had yellow endosperm. Group III had only two populations, Bai Shaodi and Xiao Zihuang. Group IV had one U.S. population (Lancaster) and one Chinese population (Da Zibai) that had a white endosperm. We considered this group as a Lancaster type. The populations Hua Liushi and YX Tiezihu remained ungrouped. Group I included the majority (69%) of the 29 populations in this study. This could be due to the weak power of genetic differentiation of allozymes as observed by Zhang et al. (1993) and Pogson et al. (1995). It also could be due to the real close genetic distances among those 20 populations, as Dubreuil and Charcosset (1998) observed that allozyme and RFLP markers had a similar relative magnitude of genetic differentiation. We could not distinguish these two cases in this study. Data on yield and agronomic performance are needed to validate the classifications.

Groupings on the basis of markers such as SSRs (Smith et al. 1997; Lu and Bernardo 2001), RFLPs (Dudley et al. 1991; Messmer et al. 1992) and allozymes (Goodman and Stuber 1983; Smith et al. 1985), have agreed well with pedigree information. The pedigree relationships among the 27 Chinese populations were unknown. Groupings based on allozyme data in this study thus provide a basis for classifying them into different heterotic groups and, consequently, exploiting them in hybrid breeding.

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