Climatic Adaptation and Ecological Descriptors of 42 Mexican Maize Races

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ABSTRACT

To better understand the range of adaptation of maize (*Zea mays* L.) landraces, climatic adaptation intervals of 42 Mexican maize races were determined. A database of 4161 maize accessions was used to characterize altitudinal and climatic conditions where the 42 maize races grow, yielding ecological descriptors for each race. Using the geographical coordinates of the collection sites of each accession, their climatic conditions were characterized using the geographic information system IDRISI and a national environmental information system. Analyses of variance and cluster analyses of the racial ecological descriptors were performed to determine possible environmental groupings of the races. We found a very high level of variation among and within Mexican maize races for climate adaptation and ecological descriptors. The general overall climatic ranges for maize were 0 to 2900 m of altitude, 11.3 to 26.6°C annual mean temperature, 12.0 to 29.1°C growing season mean temperature, 426 to 4245 mm annual rainfall, 400 to 3555 mm growing season rainfall, and 12.46 to 12.98 h mean growing season daylength. These climatic ranges of maize surpass those from its closest relative, teosinte (*Z. mays* ssp. *parviglumis* Iltis and Doebley), indicating that maize has evolved adaptability beyond the environmental range in which ancestral maize was first domesticated.

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Abbreviations: GIS, geographic information systems; PC, principal component score.

Maize (*Zea mays* L.) is the most important crop for the economy of Mexico. It is the staple food of most ethnic groups and constitutes the main source of proteins and carbohydrates; about 6.5 million Mg of maize are consumed as tortillas each year in Mexico (INEGI, 2003). Mexico is also the center of origin and center of diversity of maize. Besides maize, many other crop plants also originated in Mexico, thus, Mexico is considered one of the most important centers of origin of agriculture (Vavilov, 1931). Hernández (1993) estimated that more than 105 economically important species were utilized by peoples of Mexico before the Spanish conquest. Furthermore, the morphological variability and genetic diversity of maize in Mexico have been of surpassing interest for many researchers (Vavilov, 1931; Welhausen et al., 1952; Sánchez et al., 2000). Maize of the Americas has been studied for over 100 years, in numerous national and international efforts, resulting in the description of about 300 races and subraces (LAMP, 1991).

Published in Crop Sci. 48:1502–1512 (2008).
doi: 10.2135/cropsci2007.09.0518

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The contribution of genetic diversity of Mexican races of maize to private and public breeding programs has been very important. During the 1940s, in the early stages of the cooperation of the Mexican government and the Rockefeller Foundation, seed multiplication and distribution of the better landraces and crosses between races of different regions gave important increases in yield. Tuxpeño in the humid tropical lowlands; Celaya, Bolita, and Cónico Norteño in the midaltitude lands (1000–1800 m); Cónico and Chalqueño in the highlands of Mexico; and Comiteco and Olotón in Chiapas represent the most important Mexican races in terms of production (Timothy et al., 1988; Ruiz et al., 2002).

Characterization of plant genetic resources and exchange of breeding materials and information led to identification of very important germplasm and spectacular increases in maize yield and improvement of other traits during the 1940s and 1950s. Improved germplasm from national and international breeding programs replaced landraces in some areas of Mexico (Smith et al., 2001). Nevertheless, the indigenous landraces are known to contain favorable alleles for agricultural production that have gone largely unused (Tarter et al., 2003, 2004). Furthermore, the accessions used in the breeding programs and landraces cultivated by farmers have evolved as a result of human selection during many generations at a site and often demonstrate location-specific adaptation superior to improved germplasm (Smith et al., 2001).

Detailed ecogeographical analysis to identify differences among racial collection sites and determine the climatic ranges of adaptation for races or accessions is important for understanding the genetic diversity of maize, planning future collecting missions, and supporting in situ conservation programs. Patterns of genetic variation are often coincident with environmental conditions, because of the processes of adaptation for germplasm to environmental factors (Lobo et al., 2003). Therefore, characterization of the environmental conditions of the sites is required to understand the climatic conditions to which different races are adapted. Environmental data from germplasm collecting sites were called ecological descriptors by Steiner and Greene (1996). The standardization of ecological descriptors is greatly facilitated when such descriptors are obtained through the use of environmental maps and databases in geographic information systems (GIS) (Lobo et al., 2003). Through the use of environmental maps in GIS, it is possible to estimate environmental conditions of the collecting sites (Lobo et al., 2003). Steiner and Greene (1996) named this kind of GIS-based classification, applied after germplasm collecting, "retro-classification" of accessions. The advantage of retro-classification is that no new germplasm collection is required; previously established germplasm collections are enhanced with ecological descriptors to facilitate their characterization and classification.

A specific example of application of retro-classification is the identification of genes for resistance to abiotic stresses, based on the hypothesis that resistance to abiotic stresses may be found in accessions previously exposed to the specific environmental stress (Hawtin et al., 1996). Guarino et al. (2002) provided a complete description of the importance and contribution of GIS in the conservation and utilization of plant genetic resources.

Using GIS, Hijmans and Spooner (2001) studied the geographical distribution and diversity of wild potato (*Solanum* spp.). Ruiz et al. (2001) also used GIS and environmental systems to determine the climatic and topographic ranges as well as the geographical distribution for the species of teosinte (wild *Zea* spp.) in Mexico. López et al. (2005) used databases in GIS to obtain the ecological descriptors and climatic adaptation of 25 wild bean species (*Phaseolus* spp.) of Mexico.

To date, no retro-classification has been performed for any large-scale maize collections. The purpose of this study was to determine the climatic adaptation and ecological descriptors for 42 Mexican maize races as a necessary first step to depict the potential geographical distribution of this species. Specific objectives included analysis of this data to determine if there are significant differences among maize races for climate adaptation and to relate racial clustering based on ecological descriptors and climatic adaptation to previously described clusters based on morphology, isozymes, and geography (Sánchez and Goodman, 1992; Sánchez et al., 2000).

MATERIALS AND METHODS

Databases

Data on altitude, latitude, and longitude of the sites where collections originated were obtained from the passport studies of the accessions published by the Latin-American Project Volume I and II (LAMP, 1991), which were checked and revised as needed. From the database of about 10,000 accessions, only those with both geographical information and racial classification were chosen; thus, 4161 accessions from 42 Mexican races were used for this study. The list of races and number of accessions per race is shown in Table 1. The agronomic characteristics of these races may be consulted in Welhausen et al. (1952) and Sánchez et al. (2000).

Environmental Data

The environmental information system of the Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias (Medina et al., 1998), which is compiled in the GIS IDRISI, was used to characterize the environmental conditions of the collecting sites, and to provide the ecological descriptors for each maize race as described by Steiner and Greene (1996). The information system is composed by raster images with 900 by 900 m cells. From this system, images regarding altitude, annual and seasonal

Table 1. Number of accessions of 42 maize races used in this study.

Maize race	Accessions	Maize race	Accessions	Maize race	Accessions
Ancho	61	Cristalino de Chihuahua	65	Pepitilla	72
Apachito	15	Dulce	13	Ratón	15
Arrocillo	106	Dulcillo del Noroeste	26	Reventador	29
Azul	5	Dzit Bacal	55	Tabloncillo Perla	77
Blando de Sonora	20	Elotes Cónicos	137	Tablilla de Ocho	11
Bofo	24	Elotes Occidentales	38	Tabloncillo	136
Bolita	52	Gordo	11	Tehua	8
Cacahuacintle	32	Jala	22	Tepecintle	51
Celaya	273	Mushito	61	Tuxpeño Norteño	23
Chalqueño	368	Nal-Tel	59	Tuxpeño	565
Chapalote	18	Olotillo	139	Vandeño	49
Comiteco	52	Olotón	78	Zamorano Amarillo	16
Cónico	971	Onaveño	19	Zapalote Chico	34
Cónico Norteño	317	Palomero Toluqueño	18	Zapalote Grande	20

Table 2. Possible climatic types of Mexico (adapted from Medina et al., 1998).

No.	Climate type	Mean temp. of coldest month	No. of wet months	Mean annual temp.†
		°C		°C
5	Temperate arid temperate	<5	0 (<30 d)	5–18
6	Temperate semi-arid temperate	<5	1–3 (30–119 d)	5–18
7	Temperate subhumid temperate	<5	4–6	5–18
8	Temperate humid temperate	<5	>6	5–18
9	Subtropical arid temperate	5–18	0 (<30 d)	5–18
10	Subtropical semi-arid temperate	5–18	1–3 (30–119 d)	5–18
11	Subtropical subhumid temperate	5–18	4–6	5–18
12	Subtropical humid temperate	5–18	>6	5–18
13	Subtropical arid semi-hot	5–18	0 (<30 d)	18–22
14	Subtropical semi-arid semi-hot	5–18	1–3 (30–119 d)	18–22
15	Subtropical subhumid semi-hot	5–18	4–6	18–22
16	Subtropical humid semi-hot	5–18	>6	18–22
17	Subtropical arid hot	5–18	0 (<30 d)	22–26
18	Subtropical semi-arid hot	5–18	1–3 (30–119 d)	22–26
19	Subtropical subhumid hot	5–18	4–6	22–26
20	Subtropical humid hot	5–18	>6	22–26
21	Tropical arid semi-hot	>18	0 (<30 d)	18–22
22	Tropical semi-arid semi-hot	>18	1–3 (30–119 d)	18–22
23	Tropical subhumid semi-hot	>18	4–6	18–22
24	Tropical humid semi-hot	>18	>6	18–22
25	Tropical arid hot	>18	0 (<30 d)	22–26
26	Tropical semi-arid hot	>18	1–3 (30–119 d)	22–26
27	Tropical subhumid hot	>18	4–6	22–26
28	Tropical humid hot	>18	>6	22–26
29	Tropical arid very hot	>18	0 (<30 d)	>26
30	Tropical semi-arid very hot	>18	1–3 (30–119 d)	>26
31	Tropical subhumid very hot	>18	4–6	>26
32	Tropical humid very hot	>18	>6	>26

†Mean annual temperature calculated as the average of mean annual maximum and minimum temperature.

(May–October) mean temperature, annual and seasonal mean accumulated precipitation, seasonal photoperiod, and climate type were considered. Climate images represent normal data calculated from 1961 to 1995 series. In this system, the climate type is derived from the country climatic classification by Medina et al. (1998), according to whom there are 28 possible climatic variants in Mexico (Table 2).

Ecological Descriptors

Ecological descriptors were determined for each race in terms of climatic ranges. Climatic ranges were established once the values for each variable were specified in every accession site. These values were searched with the GIS IDRISI, using the raster images and the geographical coordinates for each accession site. The extreme values for each variable were taken to establish the climatic ranges.

Statistical Analysis

Differences among races for the various environmental variables were analyzed by one-way analysis of variance using SAS PROC GLM (SAS Institute, 1999) with races treated as class variables.

Numerical Taxonomy

To determine the relationships among races, similarities were calculated between races from data regarding the ecological descriptors (Table 3), using maximum and minimum values as well as mean values per each ecological parameter. Six additional variables (not shown) regarding minimum, maximum, and mean values of annual and seasonal rainfall/temperature ratio were also considered in this analysis; thus 24 variables were used for numerical taxonomy.

The product moment correlation between races was calculated after standardization of each variable in the data matrix to zero mean and variance 1, that is,

$$Z_{i.k} = (Y_{i.k} - Y_{..k})/S_k$$

where $Y_{..k}$ and S_k represent the mean and standard deviation for the kth character, respectively.

From the product moment correlation matrices, a cluster analysis was conducted using the Unweighted Pair Group (UPGMA) procedure of NYSYS-PC (Rohlf, 2000). In addition, the correlation matrix of ecological descriptors was subjected to a principal component analysis and principal component scores (PCs) were extracted from it with PROC PRINCOMP of SAS (SAS Institute, 1999).

Table 3. Ecological descriptors for 42 Mexican maize races (climate data values were characterized based on 1961–1995 series).

Race	Photoperiod			Altitude			Temperature						Rainfall						Climate types‡
	Seasonal†						Annual			Seasonal†			Annual			Seasonal†			
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	
	h			m			°C						mm						
Ancho	12.54	12.59	12.57	895	2100	1509	16.8	23.1	20.1	17.8	24.6	21.3	789	1224	970	735	1163	915	11, 15, 23, 27, 30, 31
Apachito	12.79	12.95	12.90	1900	2510	2340	12.1	15.2	13.2	15.2	18.4	16.1	493	1108	742	423	867	591	6, 7, 10, 11
Arrocillo	12.58	12.63	12.61	1660	2814	2225	11.9	19.4	15.9	12.7	20.2	16.7	462	2515	1290	400	2146	1018	9–12, 14
Azul	12.59	12.95	12.79	1900	2579	2182	13.6	15.2	14.6	14.7	18.4	16.9	493	1240	733	423	1143	635	10, 11
Blando de Sonora	12.82	12.95	12.89	115	947	455	19.6	23.0	21.4	23.5	27.3	25.6	526	1031	674	419	840	543	14, 17, 18
Bofo	12.67	12.81	12.71	400	1440	844	19.5	23.9	22.2	21.8	27.2	24.9	547	1189	855	477	1002	760	14, 15, 18, 26, 27
Bolita	12.51	12.81	12.59	1500	2465	2012	14.4	20.4	17.2	15.1	21.2	18.2	447	1432	788	400	1185	699	5, 9–11, 14, 15
Cacahuacintle	12.57	12.63	12.61	1960	2700	2472	12.7	17.6	14.3	13.6	18.3	15.2	471	1855	865	400	1407	726	9–12
Celaya	12.50	12.93	12.66	1120	2389	1765	14.8	21.5	18.4	16.4	23.6	20.0	447	2506	784	402	1899	713	9–16, 23, 26, 27
Chalqueño	12.53	12.95	12.61	1780	2900	2322	11.3	18.7	15.2	12.2	20.0	16.3	436	2506	793	400	1899	698	9–16, 20, 26
Chapalote	12.74	12.92	12.82	70	750	399	21.4	24.4	22.4	24.9	28.1	26.3	560	1182	858	419	957	700	14, 17, 18, 26, 27
Comiteco	12.46	12.54	12.50	820	2100	1529	16.9	23.6	20.2	17.5	24.1	20.6	959	4245	1361	880	3555	1165	11, 12, 15, 16, 23, 24, 27, 28, 31, 32
Cónico Norteño	12.54	12.95	12.71	1700	2670	2026	12.6	18.8	16.6	14.0	17.3	16.9	426	2110	580	400	1580	515	7, 9–15, 26
Cónico	12.50	12.72	12.61	1700	2900	2372	11.3	18.9	15.0	12.2	20.3	15.9	462	2506	837	400	1899	716	9–16, 23
Cristalino de Chihuahua	12.78	12.98	12.91	1610	2510	2104	12.1	17.5	14.4	15.2	20.3	17.4	456	1257	688	406	990	547	5–7, 9–11
Dulce	12.6	12.8	12.7	1284	2090	1730	16.2	21.2	18.4	18.8	24.6	21.1	489	911	691	421	850	619	9–11, 13, 14, 18, 26
Dulcillo del Noroeste	12.69	12.95	12.85	20	947	463	19.6	25.0	21.9	23.5	28.5	25.9	552	1475	807	437	1394	691	6, 10, 14, 17, 18, 26
Dzit Bacal	12.51	12.74	12.62	0	782	125	22.2	26.2	25.4	26.3	26.8	26.5	822	2581	1242	686	2143	990	11, 13, 19, 20, 23, 27, 28, 30, 31
Elotes Cónicos	12.54	12.73	12.61	1760	2700	2269	12.7	18.5	15.6	13.6	20.1	16.6	471	2169	772	400	1580	669	9–15
Elotes Occidentales	12.58	12.81	12.67	705	2170	1634	15.9	23.7	18.9	17.8	26.1	20.8	489	2506	854	421	1899	741	9–15, 26–28
Gordo	12.79	12.98	12.90	1900	2510	2126	12.6	16.4	14.4	15.3	19.1	17.3	493	1257	692	423	990	554	5–7, 9–11
Jala	12.62	12.67	12.66	1042	1850	1221	18.0	21.9	21.1	20.0	24.3	23.4	789	1147	956	701	1060	891	15, 26, 27
Mushito	12.58	12.67	12.61	1705	2600	1970	13.5	19.1	17.5	14.1	19.9	18.4	555	2386	1727	482	1927	1420	10–12, 15, 16
Nal-Tel	12.46	12.84	12.56	10	1286	265	21.5	26.4	25.2	22.4	28.3	26.0	574	3364	1380	435	3116	1159	11, 17, 23, 27, 28, 30–32
Olotillo	12.47	12.78	12.54	10	1870	731	18.4	26.1	23.6	18.7	28.6	24.7	778	3637	1433	649	2899	1267	11, 12, 14–16, 20, 23, 26–28, 30–32
Olotón	12.47	12.66	12.52	950	2303	1739	15.6	23.1	18.9	16.3	23.4	19.4	710	3582	1623	659	2978	1370	10–12, 15, 16, 23, 24, 27, 28
Onaveño	12.82	12.95	12.92	200	820	460	20.0	23.0	21.0	24.0	27.2	25.4	552	804	642	419	558	502	10, 13, 14, 17, 18
Palomero Toluqueño	12.52	12.98	12.64	2140	2887	2548	11.4	15.9	13.5	12.0	16.9	14.6	486	1960	847	406	1494	704	5, 9–12, 16
Pepitilla	12.55	12.83	12.59	514	2050	1211	16.9	24.6	21.5	17.9	26.5	22.9	522	2169	918	461	1667	851	9–15, 18, 23, 27, 30, 31
Ratón	12.62	12.85	12.77	84	1300	446	20.7	24.7	22.9	22.9	27.6	25.7	543	2738	878	400	2064	717	9–11, 14, 15, 18, 23, 26, 27, 31
Reventador	12.55	12.95	12.78	20	1100	366	20.6	26.1	22.9	24.2	28.7	26.6	526	1615	935	419	1436	797	13–15, 17, 18, 20, 26
Tablilla de Ocho	12.67	12.75	12.71	1400	1950	1686	17.0	20.0	18.5	19.0	22.2	20.5	513	742	625	451	676	557	10, 13, 14
Tabloncillo	12.55	12.91	12.66	10	2050	1285	16.5	26.1	20.6	18.4	28.7	22.8	453	1930	926	402	1828	833	11, 14, 17, 18, 26, 27, 30, 31
Tabloncillo Perla	12.63	12.95	12.79	10	1460	479	18.9	25.3	22.4	21.7	28.7	26.1	526	1930	989	426	1828	869	13–15, 17, 18, 26, 27, 30, 31
Tehua	12.47	12.52	12.51	500	1000	784	23.0	24.8	23.8	23.2	25.6	24.2	959	1708	1215	832	1512	1065	15, 23, 27, 28, 31
Tepecintle	12.46	12.67	12.51	8	1400	493	21.0	26.5	24.7	21.3	28.3	25.7	538	3320	1468	500	3076	1353	15, 17, 23–27, 30–32
Tuxpeño	12.46	12.91	12.59	0	1950	641	16.6	26.6	23.6	18.2	29.1	25.0	456	3637	1404	409	3135	1203	9, 11–20, 23, 25–28, 30–32
Tuxpeño Norteño	12.59	12.87	12.85	1400	1701	1529	17.1	19.4	18.0	19.7	21.2	20.6	432	953	494	400	895	454	10, 13, 23, 26
Vandeño	12.47	12.66	12.55	9	1645	410	19.4	26.6	24.8	20.9	28.7	26.8	706	3376	1238	639	3135	1108	10, 11, 15, 26, 27, 30–32
Zamorano Amarillo	12.58	12.66	12.62	1436	2070	1718	16.8	20.2	18.9	18.4	22.1	20.5	724	1150	897	670	1072	833	10, 11, 14, 15, 23
Zapalote Chico	12.48	12.52	12.51	50	880	171	23.4	26.4	26.0	23.7	28.3	27.3	563	1755	1195	506	1659	1107	26, 27, 30, 31
Zapalote Grande	12.47	12.54	12.50	50	830	410	23.6	26.5	25.2	24.1	27.8	26.1	736	3364	1583	706	3116	1414	26, 27, 31, 32

†May to October.

‡Climate types description as in Table 2.

RESULTS AND DISCUSSION

Figure 1 illustrates the geographical distribution of maize accession collection sites and climate types in Mexico. Maize was collected from a very broad and diverse range of Mexican regions. According to the ecological descriptors for the 42 races studied, *Z. mays* is present in 24 of the 28 climatic types of Mexico (Table 3). Ranges of altitude and climate variables among and within races are wide, indicating that maize has evolved substantial climatic adaptability (Fig. 1). Currently, maize may grow from arid to humid environments and from temperate to very hot environments, mostly in the tropical and subtropical areas of Mexico (Tables 2 and 3). Tuxpeño has the greatest adaptability among Mexican races; Tuxpeño accessions were found in 19 climatic types (Table 3). A number of outstanding varieties were developed from Tuxpeño during the 1960s by the International Maize and Wheat Improvement Center (Timothy et al., 1988). The worldwide success of Tuxpeño in maize breeding programs is likely related to its broad adaptability. The next most widely adapted races were Olotillo, Pepitilla, and Celaya, which were found in 13, 12, and 11 climate types, respectively (Table 3). In contrast, some races have very restricted distributions; Azul was found only in two climatic types, while Blando de Sonora, Jala, and Tablilla de Ocho were each reported in three climatic types (Table 3). The climate types containing the greatest number of maize races and accessions were subtropical subhumid temperate (with 28 races), subtropical semi-arid temperate (25 races), subtropical subhumid semi-hot (23 races), subtropical semi-arid semi-hot (23 races), tropical subhumid hot (21 races), and tropical subhumid semi-hot (20 races) (Table 3).

Mexican maize was collected from altitudes ranging from sea level (Dzit Bacal and Tuxpeño) to 2900 m (Cónico and Chalqueño; Table 3). These values are similar to the range 0 to 3300 m reported by Purseglove (1985) as the altitudinal limits for maize worldwide. The races with the widest altitudinal range were Tabloncillo (2040 m), Tuxpeño (1950 m), and Olotillo (1860 m). These landraces encompass very different thermal conditions over the altitudinal range. For example, Tabloncillo grows in environments with mean annual temperatures ranging from 16.5 to 26.1°C, and mean growing season temperatures ranging from 18.4 to 28.7°C seasonally; Tuxpeño grows in environments with mean annual temperatures of 16.6 to 26.6°C and mean seasonal temperatures of 18.2 to 29.1°C seasonally; and Olotillo grows in environments with mean annual temperatures of between 18.4 and 26.1°C and with mean seasonal temperatures 18.7 and 28.6°C (Table 3).

Based on the range of seasonal mean temperature for the accessions (Table 3), some races can grow under rather cool temperature conditions. Ancho, Apachito, Arrocillo, Azul, Bolita, Cacahuacintle, Celaya, Chalqueño, Comiteco, Cónico, Cónico Norteño, Cristalino de Chihuahua, Elotes Cónicos, Elotes Occidentales, Gordo, Mushito, Olotón, Palomero Toluqueño, and Pepitilla are all able to develop in growing seasons under 18.0°C, which is the limit of subtropical conditions (Medina et al., 1998). Most of these races belong to the racial groups Cónico and Sierra de Chihuahua, as defined by Sanchez and Goodman (1992), and apparently have developed improved adaptation to colder temperature environments (Eagles and Lothrop, 1994; Ruiz et al., 1998). Further support for this idea is that the base temperature values for these racial groups ranges from 2 to 6.5°C (Ruiz et al., 1998), in contrast to the typical subtropical and tropical maize base temperature of 10°C (Shaw, 1975; Ruiz et al., 2002).

With respect to rainfall, maize was collected in sites with annual rainfall of 426 mm (race Cónico Norteño) to 4245 mm (race Comiteco). From Table 3, 14 races grow in environments with more than 2000 mm of precipitation in the growing season and more than 2500 mm of precipitation annually. These races include Arrocillo, Comiteco, Dzit Bacal, Nal-Tel, Olotillo, Olotón, Ratón, Tepecintle, Tuxpeño, Vandeño, and Zapalote Grande, which seem to have evolved to grow under very humid environments. However, maize more typically seems to have evolved to adapt to drier environments, since most of the races studied (31) can survive with <580 mm of annual precipitation and <500 mm precipitation for the growing season of May to October. Races adapted to very dry conditions include Apachito, Arrocillo, Azul, Blando de Sonora, Bofo, Bolita, Cacahuacintle, Celaya, Chalqueño, Chapalote, Cónico, Cónico Norteño, Cristalino de Chihuahua, Dulce, Dulcillo del Noroeste, Elotes Cónicos, Elotes Occidentales, Gordo, Mushito, Nal-Tel, Onaveño, Palomero Toluqueño, Pepitilla, Ratón, Reventador, Tablilla de Ocho, Tabloncillo, Tabloncillo Perla, Tepecintle, Tuxpeño, and Tuxpeño Norteño. Accessions from these races could represent useful sources of genes for drought tolerance in maize. However, care must be taken when searching for sources of drought resistance based on these climatic adaptation variables, because some accessions collected from sites with these low levels of seasonal precipitation may have been cultivated under irrigation, as was reported by López et al. (2005) for wild beans in Mexico.

Mean growing season (May–October) daylength was 12.46 to 12.98 h, indicating little variation about this factor among all collecting sites analyzed (Table 3). This explains why most Mexican races are unadapated to long daylengths, which has restricted their use in temperate breeding programs (Holland and Goodman, 1995).

Analysis of variance demonstrated significant variation among races for mean values of all ecological variables (Table 4), which supports the thesis that maize has evolved a wide climatic adaptation almost all over Mexico. This also supports the idea that racial classification reflects true phylogenetic relationships among maize collections and is useful for characterizing maize germplasm.

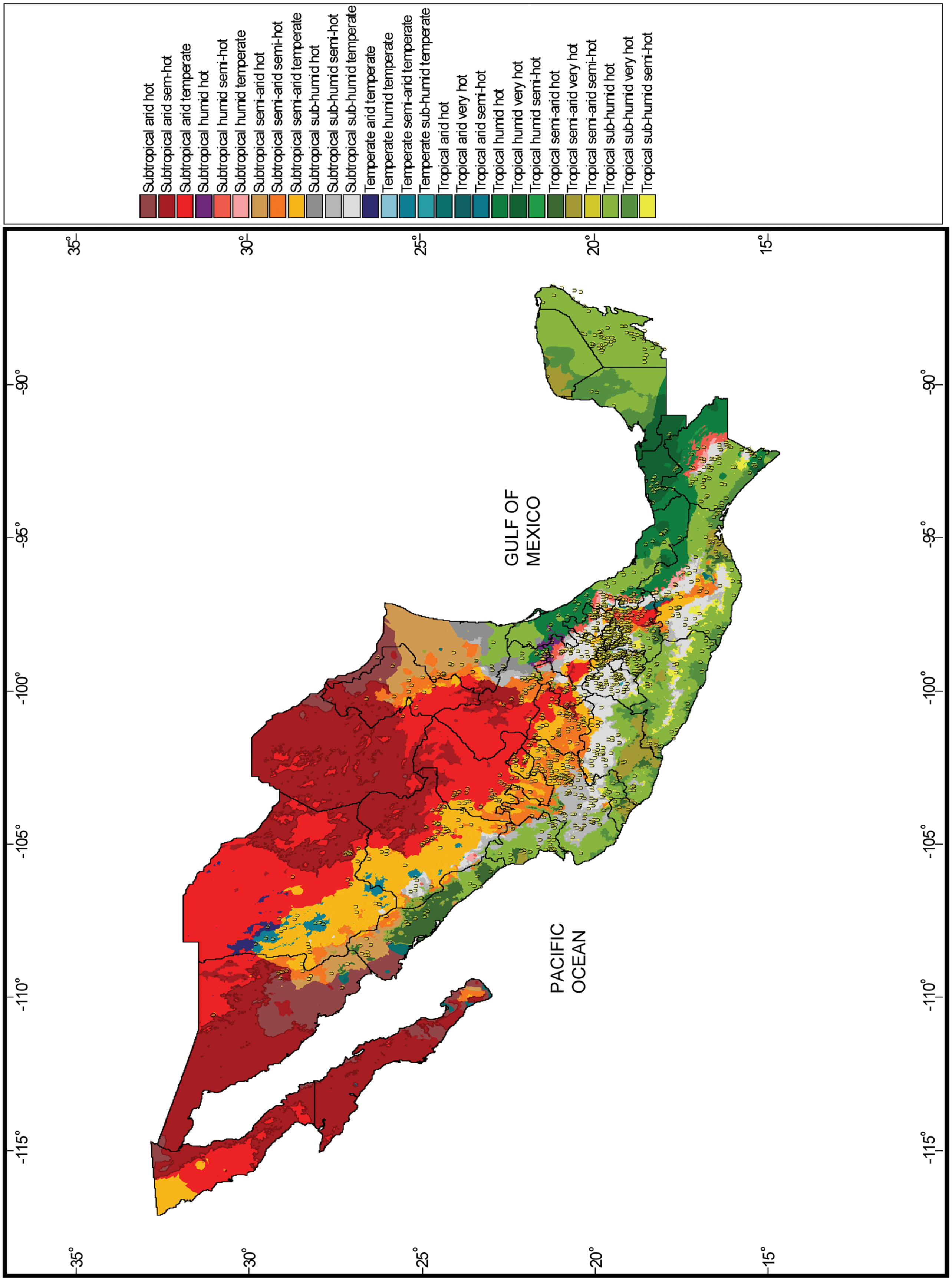

Figure 1. Geographical and climatic distribution of *Zea mays* in Mexico.

Racial Classification

Cluster analysis for the 42 Mexican races of maize based on ecological variables is presented in Fig. 2. Four major divisions can be identified, which mostly match with geographical racial groups from Sánchez and Goodman (1992), morphological-isozymatic racial groups (Sánchez et al., 2000), and simple sequence repeat racial complexes (Reif et al., 2006).

Group 1: Temperate to Semi-Hot Environment

This group mainly includes races growing in environments with a mean temperature growing season between 14 and 21°C (Table 5), and three subgroups are clearly defined. The first subgroup is composed of races that are cultivated in a semi-dry growing season with mean rainfall from 540 to 640 mm (Tables 3 and 5) and includes Apachito, Cristalino de Chihuahua, Gordo, and Azul, which match with racial group Sierra de Chihuahua (Sánchez and Goodman, 1992) and with a subdivision of the group Central and Northern Highlands (Sánchez et al., 2000). A second subgroup is represented by races Bolita, Cacahuacintle, Cónico, Elotes Cónicos, Chalqueño, Palomero Toluqueño, Celaya, and Cónico Norteño, which grow with a seasonal precipitation generally over 650 mm, that basically correspond to racial group Cónico (Sánchez and Goodman, 1992), with the exception of Bolita and Celaya, which belong to the eight-rowed group (Sánchez and Goodman, 1992). A third subgroup is characterized by a wet growing season with more than 1000 mm and includes races Arrocillo, Mushito, Comiteco, and Olotón; the first two races correspond to group Cónico and the latter two to the late maturity group (Sánchez and Goodman, 1992).

Group 2: Semi-Hot to Hot Environment

This group comprises races that are cultivated under a mean growing season temperature from 20 to 27°C, and three subdivisions can be differentiated. The first subgroup is characterized by growing season that is hot and semi-dry to semi-wet, with mean temperature near or higher than 25°C and 500 to 870 mm of precipitation. Races included in this subgroup are Blando de Sonora, Onaveño, Chapalote, Dulcillo del Noroeste, Bofo, Reventador, Tabloncillo Perla, and Ratón, which are members of the eight-rowed racial group (Sánchez and Goodman, 1992) except Chapalote, Dulcillo del Noroeste, and Ratón, which correspond to the early maturity group (Sánchez and Goodman, 1992; Sánchez et al., 2000). A second subgroup includes races Dulce, Tablilla de Ocho, and Tuxpeño Norteño, which grow in a semi-hot (20–22°C) and semi-dry (450–620 mm) growing season (Tables 3 and 5). These races are classified in group Cónico (Dulce), group eight-rowed (Tablilla de Ocho), and tropical Dents (Tuxpeño Norteño) according to geographical groupings (Sánchez and Goodman, 1992). Alternatively, these racial groups have been classified as Central and Northern Highlands group (Dulce), eight-rowed group (Tablilla de Ocho), and tropical Dents (Tuxpeño Norteño; Sánchez et al. (2000). A third subgroup is represented by races Elotes Occidentales, Pepitilla, and Tabloncillo, which grow under a semi-hot to hot (20.5–23°C) and semi-wet (740–855 mm) growing season. Elotes Occidentales and Tabloncillo belong to the eight-rowed group and Pepitilla is included in the tropical Dents group by Sánchez and Goodman (1992) and Sánchez et al. (2000).

Group 3: Very Hot Environment

Races grouped here typically develop under a very hot (24.5–27.5°C) and wet (990–1360 mm) growing season. These races include Dzit Bacal, Tehua, Olotillo, Zapalote Chico, Nal-Tel, Tepecintle, Tuxpeño, Vandeño, and

Table 4. Average, coefficient of variation, and *F*-values testing for variation among 42 maize races for six key climate variables.

Variable	Average	Coefficient of variation	*F*-value†
Photoperiod	12.71	0.415	195.44**
Altitude	1619.65	20.62	511.91**
Mean annual temperature	18.68	9.03	474.26**
Mean seasonal temperature	20.09	8.84	489.10**
Mean annual rainfall	994.78	41.27	53.69**
Mean seasonal rainfall	860.31	39.39	55.96**

**Significant at $P < 0.01$.

†Value of *F*-test of null hypothesis of no variation among races.

Table 5. Minimum, maximum, and mean levels of ecological descriptors in racial groups of maize.

Racial group‡	Photoperiod			Altitude			Temp.† Annual			Temp.† Seasonal			Rainfall Annual			Rainfall Seasonal		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
	h			m			°C						mm					
Temperate to semi-hot environment	12.46	12.98	12.67	820	2900	2125	11.3	23.6	15.9	12.0	24.1	17.3	426	4245	945	400	3555	796
Semi-hot to hot environment	12.55	12.95	12.76	10	2170	928	15.9	26.1	20.9	17.8	28.7	23.9	432	2738	796	400	2064	688
Very hot environment	12.46	12.91	12.54	0	1950	448	16.6	26.6	24.7	18.2	29.1	25.8	456	3637	1351	409	3135	1185
Jala	12.54	12.67	12.62	8954	2100	1483	16.8	23.1	20.0	17.8	24.6	21.7	724	1224	941	670	1163	880

†Characterization of climate variables based on 1961 to 1995 series.

‡Groups based on cluster analysis of ecological descriptor data (Fig. 2).

Zapalote Grande. The first three races are considered part of the late maturity group; Zapalote Chico and Nal-Tel are included in the early maturity group, and the remaining races are members of the tropical Dents group (Sánchez and Goodman, 1992; Sánchez et al., 2000)

Group 4: Jala

This group is composed of races Ancho, Jala, and Zamorano Amarillo, distributed mostly in western Mexico at mid-elevations (1200–1800 m, Table 5) and are recognized by their unusual kernel size and number. Ears of plants in the Zamorano Amarillo and Jala races can have 12 to 14 rows of very large kernels of width 9 to 12 mm and length 11 to 15 mm (Sánchez et al., 2000). This group coincides exactly within a subdivision of the eight-rowed group based on the morphological-isozymatic classification by Sánchez et al. (2000).

The results of the principal component analysis are presented in Fig. 3. The first PC accounted for 42%, the second for 37%, and the third for 10.5% of the total variation in ecological parameters. In Fig. 3, the first PC clearly separates races from very hot environments (Group 3) from the rest of races; the second PC separates races adapted to temperate and semi-hot environments (Group 1) from races adapted to semi-hot to hot environments (Group 2).

The grouping of some races, such as Olotón, Dulce, Bolita, Celaya, and Tuxpeño Norteño, on the basis of climate variables contradicts previous work based on morphology and isozymes (Sánchez et al., 2000). However, when cluster analysis and principal component analysis of ecological descriptors were combined, several of the relationships can be explained, supporting most of the previous studies. In Fig. 3, Comiteco and Olotón are closer to Group 3 based on the first PC; these races grow in regions with temperatures and annual rainfall/temperature ratios (not shown in Table 3) higher than the rest of races of Group 1 (Table 3). Bolita and Celaya are between Group 1 and 2 in Fig. 3; their values of temperature and rainfall/temperature ratios are similar to races of Group 2.

Tuxpeño Norteño, is closely associated with Tuxpeño and other components of Group 3 in most studies, it relates to races adapted to semi-hot and semi-dry environments. The ecological descriptors that explain the inclusion of Tuxpeño Norteño into Group 2 are photoperiod and rainfall; regions where Tuxpeño Norteño is planted receive <500 mm annual rainfall and have mean photoperiod of 12.9 h (Group 2 means are 1350 mm and 12.5 h, respectively).

Ecological descriptors for the four racial groups obtained in this study are presented in Table 5. From these data, environmental adaptation of each racial group can be inferred. Mean ecological descriptors of the

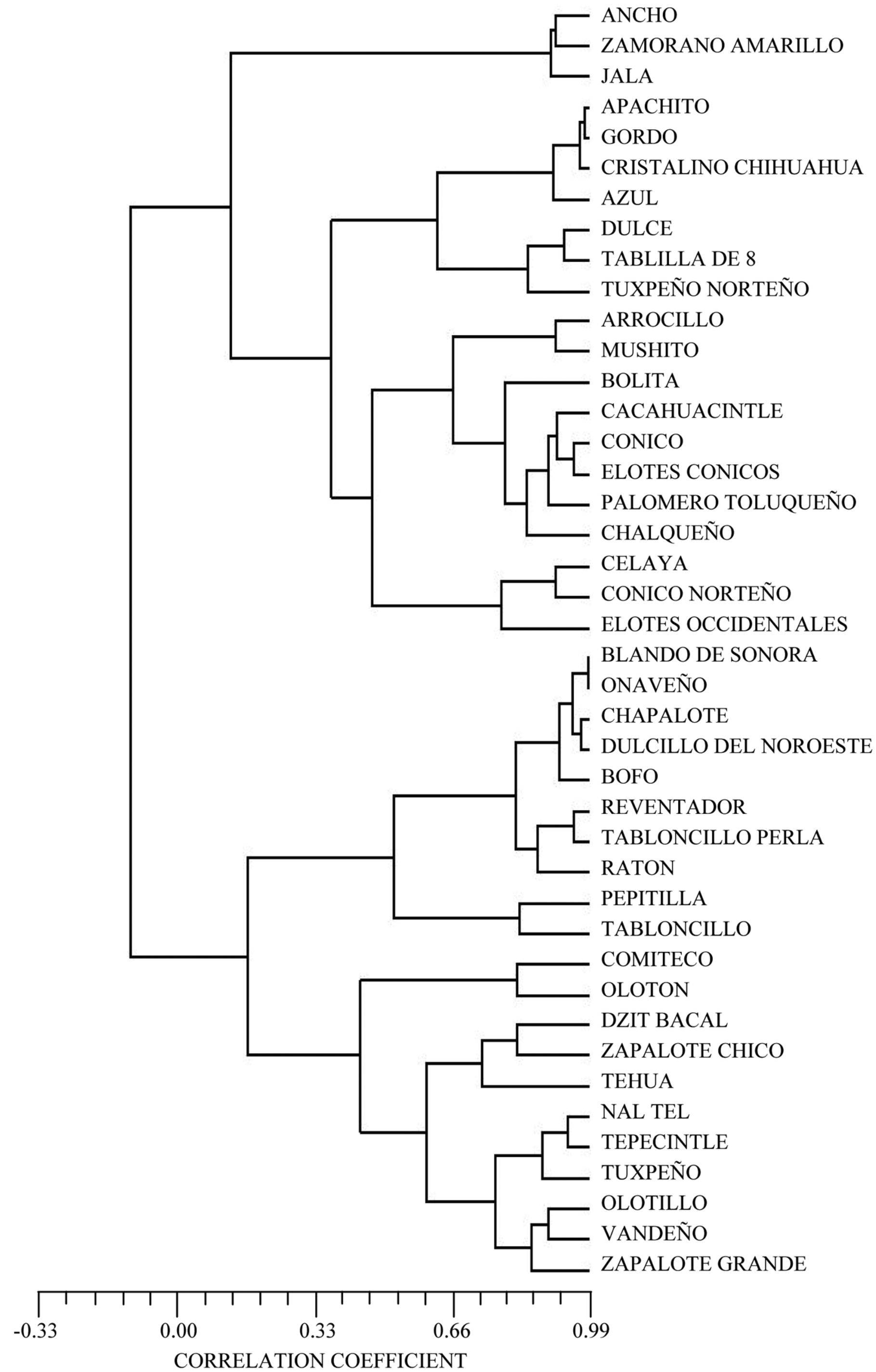

Figure 2. Dendrogram of 42 Mexican maize races, based on ecological variables.

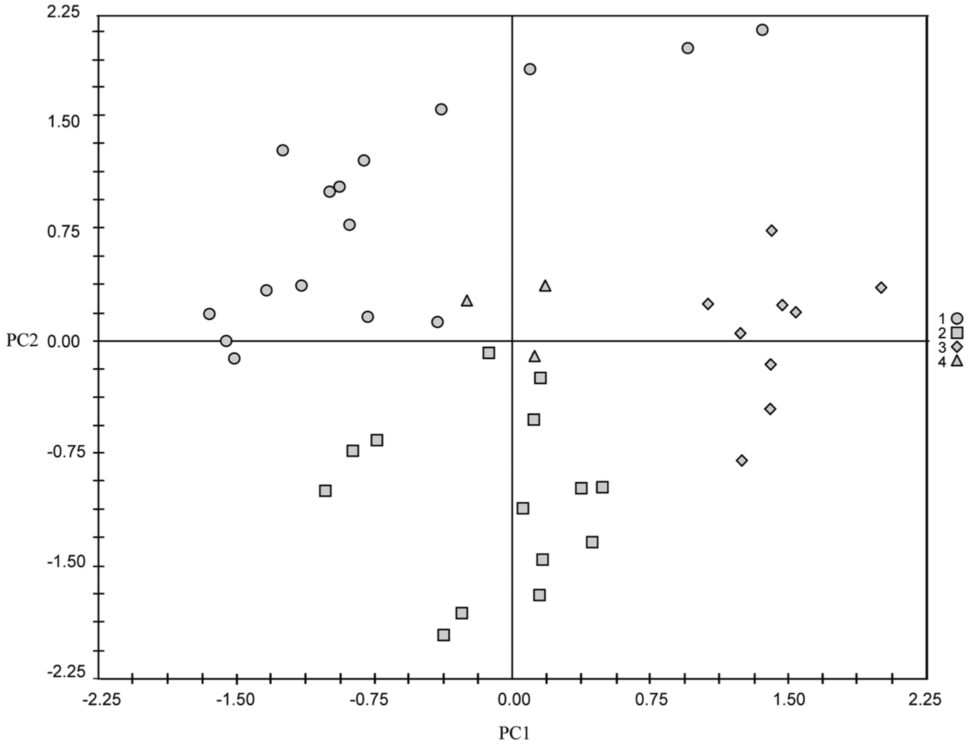

Figure 3. Graph of the first two axes from a principal component analysis of 24 ecological parameters representing the collecting sites of 42 Mexican races of maize. Symbols represent groups of Fig. 2.

racial groups could be used as the basis for synthesizing breeding populations or creating core collections.

Historical spread of early agricultural populations in Mexico through regions created many patterns in the distributions of maize genotypes that still exist today. Based on the varying levels of within-race diversity, archaeological, and paleoethnobotanical evidence, it is clear that dispersal out of the center of origin was not always uniform (Blake, 2006). Historical spread of maize may have resulted in morphological and genetic similarity among races located in closer geographic regions; these regions also tend to have more correlated ecological parameters. On the other hand, selection for similar ear and kernel traits and for ceremonial purposes within related materials under very different environmental conditions may have disrupted the relationship between taxonomic similarity and similar ecological adaptation. In addition, isolation mechanisms such as strict human selection or gametophyte factors (Kermicle, 2006) could be involved, resulting in evolutionary divergence between geographically close populations and races. Thus, when comparing racial groupings on the basis of ecological descriptors, morphology, and genetic markers, some differences among systems of classification are to be expected. Nevertheless, most of the 42 races of maize included in this work did fall into reasonably well-defined groups supporting relationships from previous studies.

Results reported here support Mexico as a very important center of maize diversity in which the species has been cultivated for millennia and is now found from sea level to elevations around 3000 m. Further, Mexican maize is planted in dry regions with average annual rainfall <430 mm to regions with annual rainfall greater than 4000 mm. Genetic diversity of the races and populations of maize in Mexico are a function of several evolutionary factors including human selection, gene flow, and genetic drift, especially in the form of bottleneck effect and mutation (Matsuoka, 2005). Environmental heterogeneity seems to be a major force for increasing genetic diversity within species (García et al., 1989; Linhart and Grant, 1996) and environmental differences are the driving force behind the overall patterns of maize diversity (Welhausen et al., 1952; Brush and Perales, 2007). Further, indigenous farmers are conscious of the environmental factors associated with maize production, such as climate regimes and their temporal changes, soil quality (especially water retention and fertility), and the biological nature of the maize populations they handle (Hernández X., 1985). This has led to tailoring of maize landraces to the local conditions in which they are found. These factors and their interactions have combined to produce the substantial genetic diversity maintained between and within the races and populations of maize in Mexico.

Genetic evidence indicates that maize originated from annual teosinte (*Z. mays* ssp. *parviglumis* Iltis and Doebley), whose distribution is centered in the Rio Balsas Region extending from Jalisco to Oaxaca (Matsuoka et al., 2002; Fukunaga et al., 2005). This region of high environmental diversity includes varied combinations of plant species and agricultural technologies. It is important to note that the range of annual rainfall in 22 maize races analyzed (Table 3) is wider than that for *Z. mays* ssp. *parviglumis*, which was reported to be 843 to 1758 mm (Ruiz et al., 2001). After several millennia, maize spread from its place of origin to much of the rest of the world following multiple dispersal paths. In many areas to which maize subsequently became adapted, very important environmental constraints were present, however, humans have created more optimal environment for a crop by clearing, weeding, fertilizing, and controlling water, expanding thereby the environmental range for maize (Pearsall, 1978). Current maize races have been able to grow far beyond the environmental range where maize wild relatives are known to grow, colonizing even environments that are judged not suitable for maize by several authors (Doorenbos and Kassam, 1979; Baradas, 1994; Ruiz et al., 1999), including some regions in the North of Mexico (Medina et al., 1998). Thus, most diversity found in maize races is the result of human selection and adaptation during the dispersal process from east to west and from south to north of *Z. mays* ssp. *parviglumis* and the first early maize types (Matsuoka, 2005; Fukunaga et al., 2005); in addition, these aspects may be associated with climatic changes that occurred in prehistoric times (Buckler et al., 2006).

CONCLUSIONS

The general overall climatic ranges for maize, based on 4161 field collections of 42 Mexican maize races were 0 to 2900 m of altitude, 11.3 to 26.6°C annual mean temperature, 12.0 to 29.1°C growing season mean temperature, 426 to 4245 mm of annual rainfall, 400 to 3555 mm of growing season rainfall, and 12.46 to 12.98 h of daylength during the growing season. These climatic limits of maize surpass those from its closest relative *Z. mays* ssp. *parviglumis*, indicating that maize has evolved greater adaptability and greatly expanded its geographic range.

Nowadays, maize may grow from arid to humid environments and from temperate to very hot environments, basically in tropical and subtropical lands. Tuxpeño is the most widely adapted Mexican race, as it is found in 19 climatic types. The highest diversity (in terms of highest number of races) is found in temperate subtropical climates with subhumid to semi-arid regimes.

Several races that apparently developed adaptability to high rainfall, low rainfall, hot, and cold environments are identified. This knowledge will contribute to a better understanding of the adaptation capabilities of maize, which could be useful in regional maize breeding programs. Results of this study will also help in depicting the actual and potential geographical distribution of maize in Mexico.

Classification of the Mexican races by ecological descriptors and using numerical taxonomic methods complements previously available classifications based on geography, morphology, and isozyme frequencies to enhance understanding of racial geographical distribution and environmental adaptation.

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