MAIZE ◆ PROGRAM ◆ SPECIAL ◆ REPORT

# Maize Genetic Resources

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CIMMYT is an internationally funded, nonprofit scientific research and training organization. Headquartered in Mexico, the Center is engaged in a worldwide research program for maize, wheat, and triticale, with emphasis on improving the productivity of agricultural resources in developing countries. It is one of 17 nonprofit international agricultural research and training centers supported by the Consultative Group on International Agricultural Research (CGIAR), which is sponsored by the Food and Agriculture Organization (FAO) of the United Nations, the International Bank for Reconstruction and Development (World Bank), and the United Nations Development Programme (UNDP). The CGIAR consists of some 40 donor countries, international and regional organizations, and private foundations.

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*Abstract:* This publication documents the origin and worldwide spread of maize from Mesoamerica, and describes the characterization, use, and conservation of maize genetic resources, including the crop's nearest wild relatives, teosinte and *Tripsacum*. Results of an international survey on the continued use of maize landraces in developing countries are reported, along with progress on the work of Latin American maize banks, in concert with CIMMYT, USAID, and USDA-NSSL, to regenerate their endangered holdings of maize landraces. An update is provided on collaborative research by CIMMYT and the French National Research Institute for Development Cooperation (ORSTOM) to transfer apomixis from *Tripsacum* to maize.

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# Contents

*Foreword*

# Characterizing Maize Genetic Diversity: The Key to Utilization

Maize is arguably Mesoamerica's greatest gift to the world. Farmers outside the Americas have been sowing the crop since the arrival of Colombus, and scientists in our century have dramatically increased the productivity of temperate maize, largely through exploiting heterosis.

## Information Unlocks Diversity

To marshall the genetic resources of *tropical* maize, though, scientists first had to gather information about its enormous diversity. International specialists, supported by the US National Research Council and the Rockefeller Foundation and in coordination with the ministries of agriculture of each country, systematically collected diverse samples of maize from the Americas during the early 1940s to mid-1950s. The samples were characterized as rigorously as possible and a series of bulletins were published that provided racial classifications for the samples. Researchers in the Office of Special Studies, a joint initiative of the Rockefeller Foundation and the Mexican Ministry of Agriculture, used elite selections from this huge cache of genetic diversity to develop breeding populations, synthetics, and hybrids. This effort evolved into the CIMMYT Maize Program, which has distributed both improved germplasm and seed of landrace accessions to interested researchers worldwide.

Information continues to be the key to the genetic vault of maize. Landraces are still grown on 54% of Latin American maizelands, excluding Argentina. If they are to be properly conserved and utilized, there is an obvious need to relate local use of maize landraces to their preservation ex-situ in germplasm banks. In the last several years staff in the CIMMYT maize germplasm bank have characterized several large maize race collections, using agronomic and morphological data obtained in multilocation trials, to designate core subsets. The Maize Program has collaborated in the Latin American Maize Evaluation Project (LAMP), and is coordinating efforts of banks throughout Latin America to regenerate endangered accessions of landraces. Information on landrace accessions comprises a valuable by-product of both initiatives. Less has been done to characterize the performance of landraces still sown throughout Latin America, though in 1995 the head of the CIMMYT maize germplasm bank conducted a general survey on the issue in which maize genetic resource specialists from eight countries participated. This Special Report carries more detailed descriptions of our work in the above areas.

## Wild Relatives and the Mystery of Maize's Origin

The subject of maize genetic resources extends considerably beyond the crop itself. The spread of improved varieties throughout the center of origin of maize, as well as the imminent release of genetically engineered maize in the USA and its consequently inevitable arrival in Mexico, has brought to the forefront the issue of geneflow between maize and its nearest wild relative, teosinte. Although the topic is not specifically addressed in this Report, the section herein describing teosinte's distribution and diversity should serve as useful background for related discussions. Also covered are efforts of scientists from the French National Research Institute for Development Cooperation (ORSTOM), in residence at CIMMYT to characterize and utilize the biodiversity of the maize wild relative, *Tripsacum.* The group is well along in research to transfer apomixis from *Tripsacum* to maize, and if they are able to obtain its expression in the crop, the consequences for poorer farmers in developing countries could be profound. Finally, since it is impossible to truly know someone unless you know something about the person's origin, distinguished experts in plant genetic resources, H. Garrison Wilkes, University of Massachusetts at Boston, and Major Goodman, North Carolina State University, briefly outline what is known and speculated about the origin of maize and how the crop's wild relatives figure in the scheme of its evolution.

## New Arrangements for Germplasm Conservation

Partly to ensure the unimpeded availability to researchers worldwide of genetic resources it conserves, the Consultative Group on International Agricultural Research (CGIAR, the system to which CIMMYT belongs) signed an agreement in 1994 with FAO that calls for the designation of specific accessions to be included in collections held in trust. Conditions of "in trust" storage specified in the agreement imply long-term storage and regeneration of holdings for the benefit of the international community. CIMMYT cannot store in trust any material which cannot subsequently be distributed under these terms, as specified in our materials transfer agreement, which insists on the free availability of the material for research and breeding and prohibits obtaining intellectual property rights on the material.

With regard to maize, all accessions except those defined as varieties have been designated as germplasm under the auspices of FAO and are considered to be held in trust. As stated in the CIMMYT germplasm acquisition agreement, all accessions currently being accepted for storage from institutions outside of CIMMYT will be held in trust. CIMMYT-developed germplasm being entered into the germplasm bank for storage will also be held in trust, except for varieties not deemed worthy of long-term storage.

Finally, CIMMYT and the USDA National Seed Storage Laboratory recently signed a memorandum of understanding that strengthens collaborative ties between the two institutions for the conservation of crop genetic resources. Duplicate samples of many maize accessions are preserved in the NSSL and in cooperating gene banks throughout Latin America and the Caribbean.

## Safekeeping for Future Use

Germplasm banks are precisely what their name suggests: a place where germplasm can be kept for security, yet withdrawn in time of need. The need is when a crop must be changed through the introduction of new traits – such as disease or pest resistance -- to meet challenges in its environment. Recall that, like other domesticated crops, maize is no longer capable of existing in the wild, and depends on humans for its existence and evolution.

We hope this Report provides a useful description of the vast gene pool of maize, and encourage you to contact the researchers cited herein or the directors of the CIMMYT Maize Program for further information. Finally, we would like to thank Cambridge University Press and the International Plant Genetic Resources Institute (IPGRI) for their cooperation in allowing our use of material that will also appear in *Biodiversity in Trust: The Status of Plant Genetic Resources Conservation and Use of CGIAR Mandate Species,* a co-publication by those two institutions which should be available in late 1996.

*D.C. Hess*
Director

*R.N. Wedderburn*
Associate Director

The CIMMYT Maize Program

### Chapter 1

# Mystery and Missing Links:
# The Origin of Maize

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## A Passport Without a Birth Certificate

We all carry passports that give our place of birth and origin on the assumption that, somehow, this better defines our identity. In the same way, people often ask about the origin of maize, a crop grown worldwide, as if knowing this would help them better understand and appreciate the plant. In truth, the place of origin of this international traveler is fairly well established, but the exact lineage of maize remains partially shrouded in mystery and, to some extent, controversy, even though scientists concur on many if not most of the facts of the matter. Three distinct camps within the scientific community hold differing hypotheses regarding the ancestor of maize, but all agree to a surprising extent on the basic circumstances surrounding its origin.

## The Origin of Maize

Maize appeared sometime between about 8,000 and 6,000 BC in Mesoamerica (i.e., Mexico, Guatemala), most probably along the western escarpment of central or southern Mexico in an arc within 500 km of Mexico City. The ecosystem that gave rise to maize was seasonal -- dry winters alternating with summer rains -- and highland (above 1,500 m), quite possibly mountainous and featuring steep slopes and limestone outcroppings. The above properties also describes the major area occupied by the closest plant relatives of maize, teosinte -- both the annuals and perennials -- and the genus *Tripsacum*. Maize and teosinte are unique among the grasses because the male and female flowers are borne in separate structures: the ear, or seed-bearing cob, is carried to the side of the stem and constitutes the female counterpart of the male flowered central spike of the tassel.

Unlike wheat and rice, maize has left an evolutionary trail obscured by complexity -- there are no extant intermediate forms between wild maize and the approximately 50 maize landraces that have evolved under farmer selection in Mexico and which, in many cases, are still cultivated there. Evolutionary missing links may have fallen prey to grazing animals -- cows, goats, and sheep -- introduced by the Spaniards during the 16th century colonization. Notwithstanding, early stages in the domestication of maize probably involved a small ear (1-3 cm) yielding no more than 50 small, hard seeds that would pop when heated. In fact, attempts to breed backwards to reconstruct the ancestor of cultivated maize have often used ladyfinger and/or "Argentine pop" maize as a starting point; not because these varieties are in themselves primitive, but because the grain size is in the ballpark for the primitive prototype.

The three most widely held views concerning the origin of maize are that it came from 1) a form of wild maize, 2) a wild teosinte, or 3) an unknown ancestor (i.e., neither wild maize nor teosinte) (Fig. 1). Each theory draws its supporting evidence from one or several fields of research, including archaeology, biochemical isozyme genetics, cytogenetics, morphology, and taxonomy. During the 1960s, there was widespread support for the idea of wild maize as the ancestor for the domesticated form. In contrast, in the 80s the theory holding greatest currency was that of teosinte as the progenitor of maize. Even today ample room exists for research that will ferret out the true ancestor of this productive cereal.

## The Place of Teosinte

That teosinte is the closest relative of maize is universally recognized; less clear, however, is the precise relationship between the two. Theories regarding the role of teosinte in the origin of maize vary according to how one interprets existing evidence. Most investigators agree that any construct for the origin of maize must *at least* account for teosinte as well. All recognize that teosinte has contributed significantly to both the racial diversity and heterotic nature of domesticated maize.

According to several experts -- Beadle (1980), Galinat (1978), de Wet and Harlan (1972), Iltis (1983), Kato (1976, 1984) and Doebley (1983, 1984) -- teosinte is the ancestor and wild form of maize, and differences in structure between the two (e.g., multi-rowed versus two-rowed ears, paired versus solitary spikelets, naked versus covered grain) have come about through domestication. Mangelsdorf (1986) argued that teosinte is a mutant form of maize and that, contrary to the teosinte-forebear theory, "corn was the ancestor of not only cultivated corn but also of teosinte." In 1983 this position was modified, positing maize as the ancestor of annual teosinte and describing perennial teosintes as more ancient wild plants (Wilkes 1979, Mangelsdorf 1986).

## Contrast and Consensus

Interestingly, although the maize- and teosinte-source explanations are diametrically opposed, both camps assume the same evolutionary events and morphological changes leading to domesticated maize, with slightly different slants. For instance, regarding the question of how maize and teosinte have managed to maintain separate identities -- that is, they coexist and even intercross without genetically "swamping" each other -- each expert invoked differering processes. Galinat, for example, emphasized disruptive selections, where the hybrid intermediates were selected against, forcing the population toward the parental extremes. Beadle, in contrast, focused on the importance of human guidance in the evolution of maize. Iltis' explanation springs from the rational taxonomic imperative.[1] And Mangelsdorf cites spatial isolation as a means to enforce the barrier to genetic exchange.

No matter what the exact lineage of maize, two things are clear: 1) Mexico is one of the major centers for the development of agriculture and 2) maize, the third most important food grain after rice and wheat, is one of Mexico's greatest gifts to the world.

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[1] The tassel and ear of maize and teosinte are essentially identical except for one difference that changes the entire biology of the plant. In maize the ear is based on the polystichous (many-ranked) single central spike, whereas the seeds of teosinte are borne in numerous distichous (two-ranked) spikes which are the counterpart of the abundant lateral branches of the tassel. The imperative is realizing that the radically different structures (one central and the other lateral) vary not in a fundamental pattern but in degree of emphasis in a commonly held structure. Since both have the structure, both are taxonomically related and co-specific.

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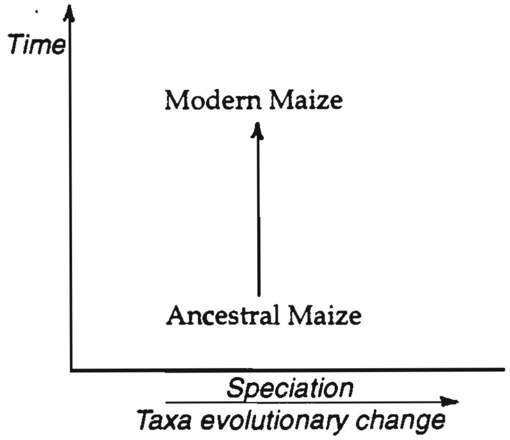
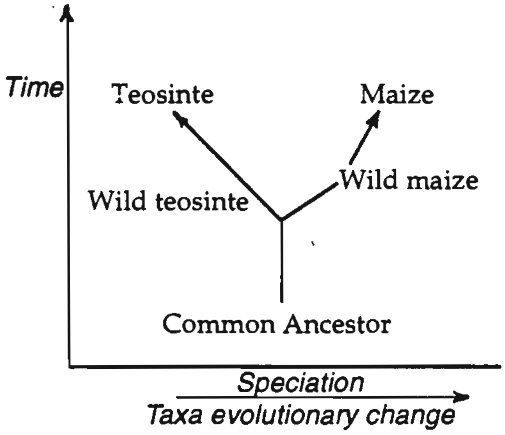
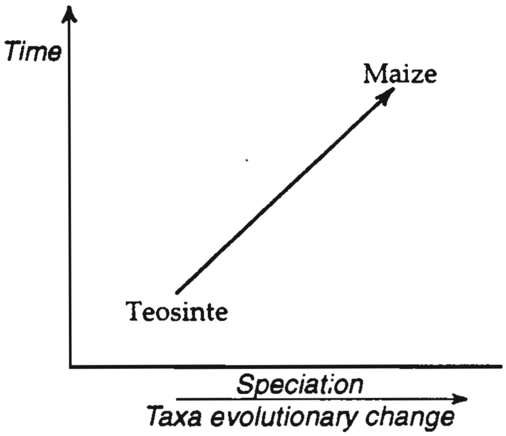
**Vertical Evolution: Maize from Wild Maize**
Kempton 1937
Mangelsdorf 1974, 1986
Wilkes 1989
Goodman 1988



**Vertical Evolution: Maize and Teosinte from a Common Ancestor but the Domestication of Maize from Wild Maize**
Montgomery 1906
Weatherwax 1918, 1919, 1954



**Progressive Evolution: Maize from Teosinte**
Vavilov 1931
Beadle 1972, 1980
de Wet and Harlan 1972
Galinat 1971, 1983, 1985, 1988, 1992
Iltis 1972, 1983
Doebley 1983
Kato 1984



**Hybrid Origin of Maize**
Harshberger 1896, 1899
Collin 1912, 1918

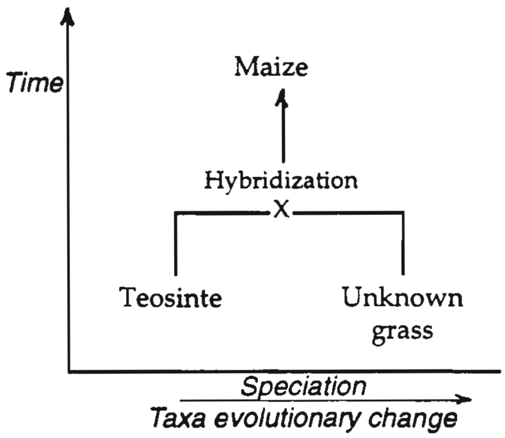


**Figure 1. Theories regarding the evolution of maize.**
Adapted from Wilkes 1979.

## *Chapter 2*

# Maize Germplasm: Its Spread, Use, and Strategies for Conservation

*S. Taba*

## The Cultigen and its Spread Worldwide

Maize: *Zea mays* L. (Species Plantarum 971. 1753) or *Zea mays* L. ssp *mays* Iltis (Iltis and Doebley 1980) is an American cultigen, domesticated in south-central Mexico. Maize goes by different names in various languages: *maize* or *corn* in English , *maïs* in French, *mais* in German/Italian, *maíz* in Spanish, *milho* in Portugese, *yùmí* in Chinese, *Khao phot* in Thai, *Jagung* in Indonesia, *Tomorokoshi* in Japanese, *Bokolo* in Ethiopia, *Chimanga* in Malawi, and *Zorrat* in Persian, to name a few.

Geographical movements of maize in the Americas occurred before and after the Spanish Conquest. The spread of maize races in the Americas and interrelationships among them have been studied and summarized (Goodman and Brown 1988; Sanchez G. 1994; Wellhausen et al. 1952; Goodman and Bird 1977; Bird and Goodman 1978; Anderson and Cutler 1942; Brown and Anderson 1947, 1948; McClintock 1978; Kato 1976, 1984). Adapted maize landraces have evolved from introductions and subsequent interbreeding in many parts of the world. Systematic collection efforts in the mid-20th century revealed enormous variation in these landraces (Wellhausen et al. 1952, 1957; Brieger et al. 1958; Brown 1953; Paterniani and Goodman 1977; Grobman et al. 1961; Grant et al. 1963; Hatheway 1957; Roberts et al. 1957; Timothy et al. 1961, 1963; Brandolini 1968; Suto and Yoshida 1956; Mochizuki 1968; Avila and Brandolini 1990; Costa-Rodrigues 1971). The first catalogue of maize genetic resources (NAS-NRC 1954, 1955) deals with original strains of maize in the Americas. These are partly preserved in national germplasm banks and largely at CIMMYT (Taba 1994). Updated lists of current collections from Latin America, including CIMMYT holdings, were published on CD-ROM by LAMP in 1992 and updated in 1995.

### Evolution and spread in the Americas

Remarkably, the present great diversity of maize types has arisen in less than 4,000 years. Corn was domesticated well before 4,000 B.C. in Tehuacán, Puebla State, Mexico (MacNeish 1985). In Mesoamerica maize became the dietary staple by about 1,500 BC (Goodman 1988a). The oldest known archaeological samples of maize were found in caves near Tehuacán (Mangelsdorf et al. 1964, 1967). Original dating based on analysis of surrounding strata placed their origin as far back as 5,000 BC, but recent direct analyses of the samples using accelerator mass spectrometry (AMS) suggest a more likely date of around 3,600 BC (dendro-calibrated in calendric years; Long et al. 1989). This early maize had very small, fragile, eight-rowed ears, but there is a debate about whether it was wild or domesticated (Benz 1994; Bird 1980, 1984; Mangelsdorf 1974; Wilkes 1989) and concerning its subsequent evolution. According to Bird (1980), a small-eared early domesticate reached Central America within 1,000 years of domestication and there hybridized with the teosinte *Zea luxurians*. Then a variable set of more productive types, including a lineage that led to Olotillo, was spread back to Mexico. By 2,000 years ago, a new complex of archaeological types, precursors to Nal-Tel and Chapalote, became abundant in Mexico (Benz 1994; Mangelsdorf 1974). Not only did teosinte introgression cause the explosive evolution of maize, but hybridization between maize races containing varying amounts of teosinte germplasm and various teosinte races has continued to contribute to the development of new maize races (Wellhausen et al. 1952; Wilkes 1977, 1979, 1989). Kato (1984), postulating the origin of maize from teosinte, suggested that genetic introgression between maize and teosinte could have taken place in the early domestication periods, but has been limited since by the rapid development of genetic barriers.

Central American maize could have reached South America at about 2,000 BC, where agricultural, ceramic-using cultures had already developed (Bird 1980, personal communication; Grobman et al. 1961). However, Pearsall (1994) claims the possible introduction of maize to northern South America from lower Central America around 5,000 BC, based on maize pollen remains and phytoliths in archaeological strata at various sites in Colombia and Ecuador. In North America, maize reached the southwest before 1,000 BC (Adams 1994) and appeared as a food in the New England and eastern New York areas around 1,000 AD (Bendremer and Dewar 1994). Archaeological remains from the West Indies site of En Bas Saline, northern Haiti, comprise pop and floury corn types and date to as early as about 1,250 AD (Newson and Deagan 1994).

### Migration to the four corners of the globe

Columbus found maize in Cuba and introduced it in Europe upon his return in 1493 (Mangelsdorf 1974). The following year it was planted in fields near Seville, Spain. Introductions continued from Central America, the Andean region, and the Mexican highlands, and germplasm better adapted to European conditions was bred from these materials during the 17th century. Subsequent introductions of early flint types from Canada and northern USA in the 18th century and of Corn Belt temperate dent maize in the late 19th and early 20th centuries added to already adapted gene pools

(Trifunovic 1978; Brandolini 1968). Flint maize was the predominant type in Europe until the introduction of Corn Belt dent in the late 19th century.

In the 16th century maize spread into Asia via the Mediterranean trade route, the Atlantic and Indian Ocean sea routes, and Magellan's voyage in the Pacific (the Philippines and eastern Indonesia) (Brandolini 1970). West Indian maize races were brought to Shikoku, Japan, in about 1,580 by Portuguese sailors (Suto and Yoshida 1956). Maize entered Africa from Spain and Italy through the Atlantic navigation routes, and was already grown in West Africa in 1560. Lowland tropical races from Brazil, the Guyanas, and the Paraná basin were also introduced to West African coastal regions by traders. Dutch settlers in southern Africa brought flint floury types early in the 17th century and new introductions came from the southern USA and northern Mexico to southern and eastern Africa in the late 19th and early 20th centuries (Brandolini 1970). Southern dent and northern flint from the USA were introduced by European settlers in the Southern Cone of South America in the 19th century (Paterniani and Goodman 1977; Timothy et al. 1961).

## Tropical Maize Landraces: Their Characterization and Conservation

Conservation of tropical maize landraces from the Americas has been the main activity of CIMMYT maize germplasm bank for the last three decades. Systematic collection, characterization, and utilization of tropical maize landraces began in Mexico in the early 1940s, as part of cooperative breeding research between the Rockefeller Foundation and the Mexican Ministry of Agriculture (Wellhausen 1988). This work was the model for similar efforts by the US National Academy of Sciences-National Research Council throughout the Americas during the 1940s and 50s (NAS-NRC 1954, 1955). The original collections were characterized, documented, and preserved in the national and regional banks. In the early 1960s an outgrowth of the Rockefeller-Mexico collaboration, the Inter-American Maize Program (forerunner of CIMMYT's Maize Program), formally assumed responsibility for preserving maize landrace collections for the international community and established a maize germplasm bank in Mexico for accessions from Mexico, Central America, the Caribbean, and South America. Initially the bank occupied itself with regeneration and seed storage; subsequently it undertook documentation of its maize landrace collections. After CIMMYT was founded in the mid-1960s and established its germplasm bank, the center assumed responsibility for the collections of the former Inter-American Maize Program. Additional acquisitions from previously non-collected areas by national maize or genetic resources programs, in collaboration with the International Board of Plant Genetic Resources (IBPGR; now International Plant Genetic Resources Institute, IPGRI), augmented the number of Latin

American maize accessions (Reid and Konopka 1988) in the 1970-80s. The last decade has seen extensive collaboration among institutes throughout the region, including CIMMYT, the US Department of Agriculture and its National Seed Storage Laboratory (NSSL), Pioneer Hi-Bred International, and national germplasm banks to characterize, document, regenerate, and preserve seed collections. Examples include the Latin American Maize Evaluation Project (LAMP; Salhuana 1988; Eberhart et al. 1995), and a project coordinated by CIMMYT whereby 13 national banks in the Americas are regenerating some 7,000 endangered accessions of maize landraces they hold.

### Use of maize landraces in breeding

Elite germplasm sources identified since the initial collections in the Americas have been incorporated into breeding composites, groups, gene pools, and populations by the CIMMYT Maize Program and national maize breeding programs worldwide (Pandey and Gardner 1992; Gracen 1986; Gerdes et al. 1993; CIMMYT 1982, 1992; Vasal and McLean 1994; Bjarnason 1994). These in turn have been used to develop improved varieties and hybrids. In temperate regions Corn Belt germplasm predominates and in the tropics Mexican white dents and Caribbean yellow dents and flints have been successfully utilized in national and international maize breeding programs. Sweetcorn and popcorn have undergone advanced breeding in temperate regions and often remain important at certain locations in the tropics. Other locally important landraces have been improved to the extent possible. Further use of maize landraces is expected, as breeders seek genetic diversity and higher yield in future products. In addition, unimproved landraces are still grown locally by many subsistence farmers (for example, tropical floury and morocho maize; CIMMYT 1994). These circumstances point up the importance of ex-situ and in situ conservation of native American maize germplasm.

Landrace accessions were first characterized and superior accessions then selected for direct release by Mexico's incipient breeding program, in the form of varieties such as V520 (San Luis Potosí 20), V520c (Capitaine), and Rocamex V-7 (Hidalgo 7) (Wellhausen 1950). Synthetics and hybrids were also developed directly from selected accessions. Further development and improvement of landrace-based breeding populations has occurred for various maize types (CIMMYT 1974, 1982; Eagle and Lothrop 1994; Taba 1995; Pandey and Gardner 1992). Inbred lines and hybrids that possess excellent plant type, seed quality, and inbreeding tolerance, as well as broad adaptation and high yield potential, have been developed from improved germplasm at CIMMYT, much of which is derived from tropical landraces (Vasal and McLean 1994; Bjarnason 1994).

Germplasm bank collections can provide genetic diversity for use by breeders concerned with genetic vulnerability and seeking unique genetic variation. Doebley et al. (1985) reported high levels of isozymic variation in 34 maize races from Mexico. Seventy-two percent of this variation resided within accessions, 27% among accessions, and for the 13 enzyme system encoded by 23 loci, an average of 7.09 alleles per locus was recorded, which indicated a level of variation comparable to that of the maize wild relative, teosinte (Doebley et al. 1984). Plant breeding tends to narrow the genetic diversity of a crop (Goodman 1990, 1988b). Germplasm development strategies should include the introgression of genetic variation from landrace cultivars or older varieties, as attempted in LAMP (Eberhart et al. 1995). Access to useful diversity in landrace materials will be further unlocked through their improved characterization and through databases that put key information on accessions at the fingertips of potential users, including both scientists and, possibly, farmer-breeders. As this progresses, we can expect a broadening of maize genetic diversity in farmers' fields.

**The case of Tuxpeño** -- The use of maize landraces at CIMMYT is exemplified by breeding work with the race Tuxpeño and related Mexican dent racial complexes. In 1963, the synthetic population La Posta was formed from intercrosses among $S_2$-to-$S_6$ lines developed from Capitaine (collected in 1952 at the farm of Pedro Capitaine, San Rafael, Veracruz, and used directly as V520c in Mexico); Oaxaca 12; Veracruz 39, Veracruz 15, Veracruz 8; San Luis Potosí 20, San Luis Potosí 21; Coahuila 8; and Eto[1] Blanco (line ETO 244) (Field book, E. Johnson). Five lines were derived from Capitaine, which contributed about 30% to the germplasm base of La Posta. Hybrids (H502, H507) from parental lines from the above collections were involved in the original intercrosses.

In 1965, a breeding population called Tuxpeño Crema I was formed from landrace collections of Veracruz 48, Veracruz 143, Veracruz 174; V520c (Capitaine), Michoacán 137, Michoacán 166; Colima Group 1 (Colima 2, 4, 14, 17, 23); Mix 1 from Guatemala; and selected families from La Posta (synthetic population) at the experiment station in San Rafael, Veracruz, Mexico, in the 1965B planting season. The population Tuxpeño Crema I was maintained under mass selection for high yield for three cycles. It then underwent modified full-sib family selection for reduced plant height in 1967B (cycle 1) at San Rafael (Johnson et al. 1986).

**Reducing plant height** -- Certain productive tropical maize races, such as Tuxpeño, Olotillo, Chalqueño, and Montaña, have very tall plants and high ear placement. A common practice among subsistence maize farmers that is relevant to the evolution of

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[1] Maize race developed at the Tulio Ospina experiment station (Estación Tulio Ospina, or ETO), Medellín, Colombia.

maize plant morphology is to bend the mature plants to dry in the field before harvest. In contrast, modern maize farming -- and thus, breeding -- favors a reduced plant architecture for greater per-plant production efficiency. Excess plant and ear height can be reduced without significant changes to other agronomic traits, in both temperate and tropical maize (Russell 1991; Johnson et al. 1986). Russell (1985) showed simple correlation coefficients for 18 plant, ear, and grain traits with grain yield for 28 maize cultivars of four open-pollinated varieties and four single cross hybrids representing each 10-year period from 1930 to 1980 in the USA. His results showed that ear and plant height had r values of 0.03 and 0.09, respectively. Higher r values were for days from silk emergence to black layer (r = 0.71), harvest index (r = 0.83), ear length (r = 0.63), kernel depth (r = 0.57), Ear diameter (r = 0.42), pollen and silk interval (r = -0.76), shelling % (r= 0.68), and total plant weight (r = 0.94). Lower r values were for days to pollen shed (r= 0.19), days to silk emergence (r = -0.32), and ear per plant (r = 0.28). These parameters then describe the architecture of a productive plant type.

In the early-to-mid-1970s, CIMMYT researchers conducted extensive work to reduce plant height in Tuxpeño Crema I (Johnson et al. 1986). A similar procedure could be used now for in-situ conservation and improvement of landraces. Some 300 full-sib families were selected and planted in each cycle. At flowering about 50% of the families which were shorter than or equal to the mean were identified and plant-to-plant crosses among the selected families were made to generate the next cycle of full-sib families. As many as five selected plants per family were intercrossed among the selected families. At harvest ears from all plants of the intercrossed family in the breeding nursery were harvested and placed at the base of each plant and family performance was evaluated visually for grain yield, quality, lodging, and disease reaction. Some families and pollinated plants were rejected in the selection process at harvest. Two or three ears were saved from each selected family and the same number of families of about 300 ears were planted in the next generation. Thus, selection and recombination were done in the same cycle. A modified full-sib selection procedure as described was used from selection cycle 1 to 12 at Poza Rica Station, Mexico (60m elevation; 21° N latitude, under 180 kg N per ha per cycle). After cycle 12, the companion nurseries were planted a couple of weeks earlier at two other locations to provide plant height data before recombination at Poza Rica Station. The plant density was changed from the initial cycle of 30,000 plants per ha to 50,000 plants per ha at cycle 7, and to 104,000 plants per ha at cycle 12. Pollinations were made among short plants that had a short anthesis- to-silking interval under high density. After cycle 11, one random recombination cycle was practiced before the next cycle of selection. Selection cycles 0, 6, 9, 12, and 15 were evaluated for plant height, grain yield, harvest index, ears per plant, lodging, and other traits at three locations over two years in Mexico (Table 1). Plant density was adjusted over cycles of selection as plant size changed to calculate grain yields at optimum density. Plant height was reduced 2.4% per cycle as a result of reductions in the number of nodes and in internode length below the ear. Ear height was reduced about 50%. Lodging was minimal (5%) by cycle 15, compared with 43% for cycle 0. Grain yield increased 4.4% per cycle, despite the fact that yield was not a selection criterion. Harvest index and ears per plant increased significantly. Finally, the last cycle was as much as 11.8 days earlier to silk than cycle 0. Thus, it is evident that Tuxpeño Crema I $C_{15}$ was much improved over the original version of the population, as a result of selection for reduced plant height.

**The genetic composition of Tuxpeño Crema I** -- Judging from the accessions included, Tuxpeño Crema I probably contains Tuxpeño karyotypic groups of the races Tuxpeño, Vandeño and Celaya (Bretting and Goodman 1989; Kato 1984) and minor introgressions of Cónico Norteño and Eto Blanco. Tuxpeño Crema I includes a variation of Coahuila which is shorter and relatively earlier maturing than the race from Veracruz, with a possible introgression of Cónico Norteño (Taba et al. 1994). Michoacán and Colima accessions include Celaya and Vandeño. Studies of chromosome knob patterns of 57 Tuxpeño accessions (Kato 1988) placed the materials in four groups corresponding to north central Mexico (the States of Chihuahua, Coahuila, Durango, San Luis Potosí), the Gulf of Mexico (Tamaulipas, Veracruz, Yucatán), western Mexico (Colima, Jalisco, Michoacán), and southern Mexico (Oaxaca, Chiapas) and Guatemala. Certain unique knobs (2S, 3L1, 6L1, 7L1, 10 L2) of the Mesa Central complex (Cónico, Cónico Norteño) were found in accessions from north central and western regions of Mexico. The northern Gulf Coast accessions have a knob at 10 L2, indicating introgression of Mesa Central Complex germplasm. Accessions from southern Mexico and Guatemala and southern Veracruz have knobs at 4S2, 5S1and 6L2, characteristic of the Zapalote complex (Zapalote Chico, Zapalote Grande). Apparently, Tuxpeño germplasm characterized by a large knob at 9L2 came into contact in different regions of Mexico with maize races having the Mesa Central and Zapalote chromosome knob patterns, resulting in the current Tuxpeño race complex. The Pepitilla chromosome knob pattern (6L3) was not encountered, suggesting that this material is not present in Tuxpeño. The similar ear anatomy of Mexican dent Tuxpeño, Vandeño and Celaya races was noted by Benz (1986), who placed them with Tepecintle in the "unaffiliated" category of the Mexican narrow ear complex.

**Additional breeding with Tuxpeño materials** -- Tuxpeño Crema I, La Posta, and their derivatives were used to form breeding populations at CIMMYT. Population 21 (Tuxpeño Crema 1 cycle 11 and some families from Pool 24) is called Tuxpeño 1. Population 49 (Tuxpeño Crema 1 cycle 17) is called Blanco Dentado-2. Population 43 is a full-sib family selection from La Posta. These populations have been widely distributed in 43 countries in tropical Asia, Africa, and Latin America (CIMMYT 1986).

CIMMYT researchers collaborated extensively with scientists from the International Institute of Tropical Agriculture (IITA), Nigeria, in the early 1980s to develop populations of maize based on La Posta that would possess resistance to streak virus, an important maize disease in sub-Saharan Africa (Tang and Bjarnason 1993). Their efforts were largely successful, except for the fact that Tuxpeño is susceptible to *Striga hermonthica*, a parasitic flowering plant whose economic importance in maize cropping areas of sub-Saharan Africa has greatly increased in recent years (Kim 1994).

The CIMMYT maize physiology unit has developed drought tolerant maize populations based on Tuxpeño Crema I cycle 11 (Edmeades et al. 1992; Bolaños and Edmeades 1993; Bolaños et al. 1993) and using reduced anthesis-silking interval as a phenotypic marker for increased yield under drought. Again, this methodology would apply for the in-situ conservation and improvement of landraces. After eight cycles of full-sib recurrent selection for drought tolerance at flowering, increased partitioning of the photosynthate to the ear -- manifested as an increased rate of ear growth prior to anthesis, rapid silk growth, reduced growth of the tassel and surface roots, and higher harvest index -- was associated with higher grain yield in the Tuxpeño Sequía population. Drought tolerant genotypes did not show deeper rooting, which could be desirable for water uptake under severe drought. Improved cycles of selection ($C_6$ and $C_8$) under water stress at the CIMMYT experiment station at Tlaltizapán outyielded non-tolerant cultivars and were more stable over a range of environments, including irrigation, rainfed conditions, and limited irrigation (Byrne et al. 1995). Anthesis-silking-interval (ASI), which when short serves as a selection criterion for drought tolerance, was significantly reduced in improved Tuxpeño Sequía selections.

Between 1966 and 1990, national program cooperators released 147 varieties and hybrids developed from CIMMYT and IITA's mainly Tuxpeño populations. These releases cover approximately 3.8 million hectares worldwide (CIMMYT 1992). Tuxpeño germplasm figures in the pedigrees of many CIMMYT gene pools and populations (CIMMYT 1982). Tuxpeño accessions are also included in Thai Composite 1 (later called Suwan 1), a downy-mildew-resistant variety developed by Thai researchers and subsequently used in breeding research worldwide (Sriwatanapongse et al. 1993).

CIMMYT has also developed hard- and soft-endosperm, opaque-2 versions of La Posta and Tuxpeño-1. The development of this quality protein maize (QPM) employed selection to accumulate modifier genes that act on the opaque-2 gene for vitreous endosperm. Some modifier genes have been shown to reduce protein quality, as compared with that of soft endosperm opaque-2 (QPM with 8-9% protein, 2.6-2.9% lysine and 0.68-0.78% tryptophan in protein) (Villegas et al. 1992). Galinat (1995) discussed the importance of adaptive gene complexes in breeding for biotechnology-derived quality traits such as high lysine, high oil, sweetness, etc., drawing on the natural diversity of maize. QPM modifiers come from diverse germplasm sources used at CIMMYT, and QPM is used in China, South America, a few countries in Africa, and the USA (Mertz 1992). Research on QPM at CIMMYT resulted in many quality protein pools, populations, and inbreds (Bjarnason and Vasal 1992; Pixley and Bjarnason 1993).

## Regeneration and Preservation of Bank Accessions

### Preservation approaches

Maize is an out-breeding crop in nature. Modern maize genetics and breeding have created inbreds and hybrids (East 1908; Shull 1909; Russell 1991; Gracen 1986; Vasal and McLean 1994; Bjarnason 1994). To maintain maize seed in germplasm banks, there are two forms of population structure: outbreeding and inbreeding. For open pollinated varieties, landraces, synthetics, and populations, we generally use outbreeding strategies based on population genetics for preservation and regeneration (Crossa 1989a; Crossa et al. 1994; Breese 1989; NRC 1993). Maintenance of inbred lines requires inbreeding or within-line sibbing, seed conservation approaches similar to those used for self-pollinating crops such as rice and wheat (NRC 1993).

### Types of collections

Landrace collections are open pollinated populations from farmers' fields or seed collected in local markets. As per a 1992 survey (CIMMYT 1994), they still account for some 42% of developing country maize area. Local landraces are still grown widely in Mexico and Central America, the Andean region (less in Venezuela), parts of the Southern Cone of South America, and in certain countries of Asia and Africa. However, certain recycled seed sources may have also been included in the "unimproved" category of the survey, due to the difficulties of distinguishing them from pure landraces. In 1992, only about 21% of commercial seed sales in developing countries except China were open-pollinated varieties (OPVs), attesting to the demand for hybrid seed. Erosion of local landraces is occurring as they are replaced by improved OPVs or hybrids. Original strains of local landraces, if not properly preserved either in situ, ex situ, or both, will be lost. In addition to landraces, current and obsolete elite germplasm (inbred lines, synthetic varieties, populations, etc.) from breeding programs should be preserved in national and, in some cases, international germplasm banks. Enhanced materials from breeding programs can be accessioned in germplasm banks by registering the germplasm in Crop Science or with the American Society of Agronomy (ASA).

## Seed Conservation in the CIMMYT Maize Germplasm Bank

Current CIMMYT maize accessions total more than 13,200 and new introductions are constantly being added from the cooperative regeneration project (see below). Passport data on CIMMYT maize germplasm bank accessions have been compiled and published (CIMMYT 1988; LAMP 1992). Similar data for accessions in national germplasm banks in Latin America and the Caribbean have been partially compiled for accessions evaluated under the LAMP project. To safeguard our collections, duplicate samples of about four-fifths the accessions are kept at the National Seed Storage Laboratory (NSSL), Colorado.

We classify our materials into two collections, base and active. Base collection seed is kept in sealed containers at subzero temperatures and low humidity, allowing it to remain viable for 50-100 years. Seed in the active collection is kept at just above freezing (0-2°C) and constitutes the "working" bank from which seed requests are filled. The current bank storage facility was built in 1972. We will begin construction of a new bank facility in 1995, with funding from the government of Japan.

To facilitate day-to-day bank activities, such as seed shipment, regeneration, characterization, and maintaining passport and seed storage information, we have an in-house database system developed in 1986-87. This is constantly updated. In addition, with help from CGNet and IPGRI, in 1989-91 we developed a PC-operated global database system that has been distributed worldwide to interested users. Finally, we cooperate with the national programs of Mexico and Guatemala to monitor teosinte populations in situ in those countries.

### Regenerating accessions

A significant function of a maize germplasm bank is to replenish seed samples when their germination falls below acceptable levels or their size is reduced by distribution. This can be accomplished either by collecting additional seed at the original site or by growing out viable seed from a sample, a process known as regeneration.

In regenerating bank accessions, bank managers should avoid as much as possible contamination via outcrossing or mixtures of seeds, and any loss of genetic diversity due to population bottlenecks and subsequent inbreeding. An optimum sample size for regenerating non-inbred accessions is determined by the gene frequencies of rare alleles present in the accession (Crossa 1989a; Breese 1989; NRC 1993). For landrace collections or other panmictic maize populations, we have recommended that 100 or more ears be produced per accession, to include genotypes or alleles that occur at frequencies of 5% (Crossa, 1989a). In addition, depending on the contribution of gametes of individual plants to the next generation, the genetic structure of the accession can change according to the effective population size (Ne; Crossa, et al. 1994). When the numbers of seed and pollen parents are controlled during regeneration, the effective population size is twice that of the original population (N). When the accession to be regenerated is treated as monoecious, each plant can serve as both a male and female parent. There are three modes of pollination and seed preparation:

- *Case* 1. To represent equal numbers of male and female plants in the next generation, plant-to-plant crosses (with or without reciprocal crosses) or chain crosses within an accession are made and equal numbers of seeds are taken from each ear to make up a seed lot for preservation and utilization. Ne = 2N and pollination is not random.
- *Case* 2. Pollination occurs at random (or bulk pollination), therefore there is no control on the numbers of pollen plants, but equal numbers of seeds from each ear will make up the seed lot for the next generation. Ne = (4/3)N.
- *Case* 3. Pollination occurs randomly and different numbers of seeds will make up seed lots for the next generation (no control on male and female gametes). Ne = N.

When the accession to be regenerated is treated as dioecious -- that is each plant can serve either as male or female, but not both -- the effective population size can vary according to the numbers of male and female plants used, with or without controlling the number of male and female gametes to be included in the next generation.

- *Case* 1. When male and female gametes are controlled by plant-to-plant crosses, then Ne = 8NmNf/(Nf + Nm), where Nf = the number of female parents and Nm = the number of male parent.
- *Case* 2. When only female gametes are controlled (i.e., pollination is random or bulk), then Ne = 16NmNf/3(Nf + Nm).
- *Case* 3. When pollination is random and unequal numbers of seeds are saved per individual, then Ne = 4NmNf/(Nf + Nm) (Hallauer and Miranda 1981).

Population genetics has been used to derive practical procedures for regenerating germplasm bank accessions (Crossa et al. 1994). An ideal procedure is to place two seeds from each of the 100 or more ears in individual regeneration packets. Plant the seeds of each packet in a regeneration plot, possibly planting another plot with duplicate seed packets for the same accession, and make plant-to-plant crosses in each plot. Harvest 100 or more ears from the main plot and duplicate plot and make the regeneration packets as before. Using more ears (150-350) will capture alleles at frequencies of 3-5% in each of 150 loci with a 90-95% probability. A less desirable option involves bulking equal numbers of seeds from each ear (e.g., 40-50 seeds), planting a large sample (260) from the balanced seed bulk, and making plant-to-plant (dioecious mode) or chain crosses (monoecious mode). This method is practical and requires fewer resources than the first procedure, but presents some drawbacks. A sampling from the balanced seed bulk usually represents fewer of the families that went into the seed bulk. For example, if equal numbers of seeds of the original 150 ears are bulked and a sample of 100 seeds is taken from the bulk, the sample will contain seed from only 73 of the original families, on average (Crossa 1989a). In addition, unequal numbers of plants from each original family may be included in seed regeneration. Both factors will impair the estimation of effective population size at each regeneration. Over many regeneration cycles it is important to maintain more or less equal effective population sizes to avoid genetic drift, increased inbreeding, and a subsequent loss of genes. Inbreds can be maintained by selfing or sib-mating within a line.

Regeneration requires artificial pollination when no isolation field plots are available. In the case of older seed samples whose germination capacity has significantly diminished, it may be difficult to establish enough plants for pollination. In some cases, the accessions' lack of adaptation to the site may cause failure. These difficulties can be partially addressed by estimating the percent germination of the sample prior to planting and by using passport data to choose a site to which the materials will likely be adapted. Seed from regeneration should be fully mature, as clean as possible from ear rot organisms, and free from mechanical damage.

### Regenerating Latin American maize landraces

Regeneration is one of the more expensive aspects in the ex situ conservation of maize genetic resources, and germplasm banks in developing countries often lack the resources to perform this task. A dramatic example is provided by the case of banks in Latin America and the Caribbean. In international meetings at CIMMYT in 1988, bank representatives and leading authorities on maize genetic resources noted that unique landrace samples, many collected as part of Rockefeller and NAS-NRC initiatives during the 1940s and 50s, were in dire need of regeneration, or worse, already beyond recuperation, due mainly to the region's straitened economic circumstances. With funding from USAID through Project Noah and from the USDA National Seed Storage Laboratory (NSSL), staff of CIMMYT and of banks from 13 countries in the region mounted a massive effort to regenerate some 7,000 endangered accessions during 1992-97 (Listman 1994; see also Chapter 6 of this Special Report). CIMMYT and the NSSL are keeping backup samples of regenerated seed under long-term storage at subzero centigrade temperatures, and basic information about the accessions is being compiled in a database that will be available to all cooperators. In addition to saving the landraces, the project is seen as laying the groundwork for a hemisphere-wide maize conservation network. The case serves to illustrate the principle that, just as benefits from genetic resources transcend national borders, so also must their conservation often depend on international cooperation.

## Core Subsets and Conserving Latin American Maize Germplasm

Partly to open access to the tremendous biodiversity represented in vast germplasm collections and partly to enhance the efficiency of maintaining them, maize genetic resource specialists have used the approach of forming core subsets. These basically comprise small collections of seed that fairly represent the genetic diversity of accessions of a large race complex from which they are drawn. Core subsets facilitate germplasm use by providing ready access to the range of variation in entire bank collections. They can be preserved in active collections and distributed as widely as requested, since they contain a maximum of genetic variability with a minimum of redundancy. The larger collections from which they are formed can be kept in long-term storage in a base collection, enabling access if necessary. Finally, core subsets offer a potential avenue for breeders to introgress landrace diversity into improved lines and hybrids, and serve as back-ups for the in situ conservation of landraces.

For crop germplasm collections, Brown (1989a and 1989b) used statistical theory on neutral alleles to suggest that a subset containing 10% of the original accessions could represent over 70% of the genetic variation in the collection. For example, the estimated number of maize landrace accessions in germplasm banks throughout Latin America and the Caribbean is some 26,000 (CIMMYT 1994), so a sampling of 2,600 accessions, if properly chosen, could fairly represent the genetic diversity of maize landraces in the region. To arrive at this 10% subset, the CIMMYT maize germplasm bank has developed stratifying methods that help avoid duplication and ensure a representative sampling. These are 1) classifying accessions into races, 2) forming subgroups within each race, 3) grouping these by homologous area of adaptation, 4) conducting field evaluations, and 5) eliminating possibly closely related accessions by checking information on their original collection sites. Each criterion serves to identify non-overlapping genetic diversity in the accessions studied.

**Racial classification** -- Anderson and Cutler (1942) used short, descriptive race names to group maize accessions that possess recognizable, common features. Since then, these common features have been accepted as characteristics of particular races by maize germplasm collectors and germplasm bank managers (NAS-NRC 1954, 1955;

Bird 1982; Gutierrez 1974). A particular race may be associated with a range of production environments. The site of origin of an accession can serve as a rough indicator of race or race complex.

**Racial sub-groups** -- In some cases a race has different grain colors and/or textures. Often, each form has been maintained separately on-farm. Thus, racial subgroups constitute non-overlapping classes within a race.

**Homologous area of adaptation** -- Another way to develop the initial, non-overlapping clusters is to group the accessions by habitat, based on altitude and latitude. This step is necessary when a number of races can be dealt with as a group within a well-defined growing habitat. LAMP evaluation trials grouped the accessions based on the region within each homologous area (Eberhart et al. 1995; LAMP 1992). Thus, the trials often consisted of several taxonomic maize races.

**Field evaluation** -- The above stratifying methods basically involve the use of already existing information. In contrast, field evaluations generate new data and are therefore more expensive. Evaluation/characterization trials are conducted, and data on plant and ear morphology and the maturity of accessions can be used to group similar accessions. A SAS program -- Ward's Minimum Variance Cluster Analysis -- is used at CIMMYT to group accessions based on multiple traits considered stable over environments (Goodman and Paterniani 1969; Sanchez et al. 1993). The program statistically determines the number of different groups present in the data set, based on the continuous variables, and lists them by group.

**Collection-site data** -- To supplement cluster analysis and choose a subset from each non-overlapping cluster by avoiding closely related accessions from the same site, agronomic performance is collated with information on the collection site from passport data. Accessions with superior agronomic performance (i.e., high yield, good seed quality, and good standability) are chosen for the core subset.

Mexican and Caribbean races were the first materials evaluated by CIMMYT maize germplasm bank staff. The resulting datasets have been used to establish breeder-targeted core subsets of the Tuxpeño and Cónico complexes (Taba et al. 1994; Crossa et al. 1994; Silva 1992). From 848 Tuxpeño accessions and accession composites from the bank passport database, 175 were selected, based on lodging and adaptation in multilocation trials in 1988-90, and evaluated at two sites in Mexico to obtain characterization data for cluster and principal component analyses. Figures 1 and 2 show the results of principal component analysis and cluster analysis on 80 accessions of a core subset chosen from homogenous substrata created by the cutting point applied to a dendrogram from classification analysis (cluster analysis) on 175 accessions. These accessions are expected to represent the genetic diversity of the Tuxpeño collection preserved at CIMMYT. We will continue to evaluate major maize races of Latin America and the Caribbean, as samples are introduced. Characterization data of LAMP trials published in 1992 are also being examined with the idea of establishing core subsets. Finally, we believe it would be useful to identify and preserve core subsets of major maize landraces still grown by farmers, both as a back-up for their in-situ use and as a starting point for working with farmers to improve selected landraces for traits of local interest, thereby promoting their in-situ preservation.

## Use of Maize Races in Latin America: Implications for Conservation

It has been a close to a half century since the great diversity of Mexican races of maize was systematically sampled and studied (Wellhausen et al. 1952). The collections were initially stored in the bank of the Inter-American Maize Program and by collaborating institutions such as the Mexican National Institute of Forestry, Agriculture, and Livestock Research (INIFAP; then INIA), the Cooperative Maize Research Program (PCIM), Peru; the Colombian Agriculture and Livestock Institute (ICA), Tulio Ospina, Colombia; and Piracicaba, San Paulo, Brazil. Samples from the original collections were widely distributed, and seed exchange among the collaborating institutions has continued in recent times (Reid and Konopka 1988, Taba 1994:). International collaboration on the regeneration, storage, characterization, and evaluation of Latin American landraces is still needed. Work under LAMP has only accomplished part of this objective (LAMP 1992; Eberhart et al. 1995). Given the continued importance of certain landraces to food production in the region (CIMMYT 1994), future efforts must entail both ex-situ conservation of the original collections and in-situ preservation of locally important maize races.

To obtain more current information on the use of landraces in Latin America, in spring 1995 we sent a questionnaire to managers of the 13 germplasm banks participating in the cooperative Latin American maize regeneration project. They were asked to characterize landrace use according to four categories: 1) landraces which are extant and have been cultivated in the community or region for long time, 2) landraces cultivated continuously for special and determined uses or food preparations, 3) landraces or racial complexes cultivated because they are higher yielding or better adapted than improved varieties, and 4) landraces employed by maize breeding programs in the country (Tables 2-5). The results showed that many landraces are cultivated, and that the same taxonomic races are often found in different countries, but they may be specially adapted to local growing conditions or farmer requirements.

Special food preparations are the motive behind the continued use of certain landraces, as has been reported before (Goodman and Bird 1977). Such locally adapted varieties may have acquired special properties from farmer selection over the many generations they have been grown and can be targets of in-situ (on-farm) conservation, as defined in Article 2 of the Convention on Biological Diversity that followed the United Nations Conference on Environment and Development (UNCED) in 1992 (Krattiger et al. 1994).

The sampling strategy for collecting germplasm and choosing core subsets of bank collections is designed to cover rare and widespread, as well as common and localized, classes of alleles (Marshall and Brown 1975; NRC 1993). In-situ conservation of locally adapted maize races utilizes the most common and localized class of genes or gene complexes, with a probable geneflow of useful genes or gene complexes from other germplasm sources. Some races in Tables 3-5 are common in a given country, which facilitates their conservation on-farm. Once such a landrace has been monitored in situ, a core subset can be developed; enhancement of the race can begin as part of forming the subset (Taba 1994, Crossa et al. 1994). One can include bank accessions of the landraces, as well as new accessions collected during in-situ monitoring, in characterization trials. To enhance unique genetic traits of a landrace, additions from other germplasm sources can be considered. Contamination can cause degradation of genetic traits; so, in some cases, sophisticated monitoring may be required to know a foreign genetic component which might be recombinant DNA. Ex-situ seed conservation of the core subset will ensure the availability of seed that is "true" to the race.

Finally, a database on landrace utilization and conservation could be developed and distributed widely for use by genetic resource specialists and breeders. Most productive maize races, such as Tuxpeño, Celaya, Vandeño, Común, Cuban Flint, Coastal Tropical Flint, Tuzón, Cateto, Cónico, Chalqueño, Cacahuacintle, Cuzco, Sabanero, Montaña, and Corn Belt Dent, have been used extensively in breeding, but in fact they and their derivatives (experimental lines, populations, and gene pools) should be better represented in bank collections.

## Landrace Enhancement to Conserve Biodiversity

Landrace diversity comes from long-time cultivation by farmers who utilize as much as possible of the genetic potential manifested under their particular growing conditions. Farmer accessions of landraces are constantly subjected to selection, migration (mixing with other farmers' accessions), and mutation. A landrace's hallmark is that it maintains the genetic properties that meet farmers' needs (Ortega-Paczka 1973, Brush

1991). About 10% of Mexican maize races are utilized in breeding programs; the rest are condemned to extinction in the long run unless they are also improved (Marquez-Sanchez 1993). Soleri and Smith (1995) found that both genetic shift and genetic drift had occurred in populations of Hopi maize conserved ex situ, as compared with those conserved in situ.

Geneflow from improved germplasm to landraces can be achieved without diminishing biodiversity. Marquez-Sanchez (1993) reported a method of improving maize landraces in Mexico via limited backcrossing. He was able to change plant type toward the donor parent with recovery of the landrace ear type. In a cross combination, a residual heterotic effect remained in the backcross generations in which 7/8 of the original landrace genome is expected to be recovered in $BC_2$. Regarding heterotic patterns in Mexican maize races, Crossa et al. (1990) reported that narrow ear races and their derivatives, such as Tabloncillo, Chapalote, Jala, and Harinoso de Ocho, had better combining ability than other landraces studied. Selection for the recombinant plant and ear type was practiced on individual plants in selected female rows (20-25%) in a half-sib family recombination plot. The recurrent landrace was planted in male rows in $BC_1$ and $BC_2$ generations (Marquez-Sanchez 1993). Original crosses were 200 full-sib families between the landrace and the donor parent (V-424 or cycle 17 of Tuxpeño 1). To improve the race Jala, the recovered $BC_1$ (3/4 genome of Jala) gave 28.5% higher yields than Jala, with a 10% reduction in plant height, 20% reduction in ear height, 5% reduction in ear length (18.2 cm for BC1), and 9% increase in ear diameter, based on the means of four trials in the Bajio region and Jalisco, Mexico, in 1991. A core subset of a race usually contains several sub-racial diversity groupings (Taba et al. 1994; Silva 1992). Selected geneflow of the type described above, even into individual sub-racial groups, adds useful biodiversity to a race, assists farmers, and thus contributes to the likelihood of the race's conservation in situ. Soleri and Smith (1995) suggested that a central goal of in-situ conservation is to maintain both the genetic diversity and population structure that farmers can exploit through local adaptation. Some 250 Latin American maize races could benefit from enhancement (Goodman and Brown 1988) and some are already in the process (Marquez-Sanchez 1993). The on-farm conservation of maize landrace biodiversity requires further assistance, not only from conservationists and germplasm banks but also from maize breeders and research scientists.

In other parts of the world where landraces are utilized extensively, they can be improved in a similar manner (Brown and Robinson 1992). The unique properties of a race may be genetically analyzed for characterization and database development. Modern biotechnology should play an important role in characterizing landraces and developing a methodology to help them "evolve" in their habitats. Such work could begin with a locally important race -- for example, race Bolita, in Mexico (Tables 4 and 5). Efforts are under way in the USA to broaden the germplasm base of Corn Belt dent, through the introgression of tropical germplasm (Troyer 1990; Goodman 1988b, 1992; Tiffany et al. 1992; Hallauer 1978; Michelini and Hallauer 1993).

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**Table 1. Results of modified full-sib recurrent selection for reduced plant height in Tuxpeño Crema I (Johnson et al. 1986).***

| Cycle | Plant height (cm) | Grain yield (Mg ha) | Harvest index | Ears /plant | Lodging (%) | Days to silking |
|---|---|---|---|---|---|---|
| 0 | 282 | 3.17 | 0.30 | 0.70 | 43 | 73.4 |
| 6 | 219 | 4.29 | 0.40 | 0.87 | 12 | 67.1 |
| 9 | 211 | 4.48 | 0.40 | 0.90 | 14 | 66.7 |
| 12 | 202 | 4.93 | 0.41 | 0.93 | 9 | 65.7 |
| 15 | 179 | 5.40 | 0.45 | 0.98 | 5 | 61.6 |
| LSD (p=.05) | 22 | 0.30 | 0.04 | 0.12 | - | 0.6 |
| Change per cycle (%) | -2.39** | 4.43** | 3.10** | 2.50** | 6.70** | 1.0** |

* Data are from trials grown at or near optimum plant density at two or three locations in Mexico, 1978-79.

** Significant at P = 0.01. Percent change is based on cycle 0.

**Table 2a. Extant maize landraces and their distribution in Argentina (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations* |
|---|---|---|
| 1 | Cristalino Colorado | 1, 2, 3, 4, 6, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 |
| 2 | Dentado Blanco | 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 19 |
| 3 | Pisingallo | 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 20 |
| 4 | Avatí Morotí | 3, 4, 5, 6, 7, 8, 9, 18 |
| 5 | Complejo Tropical | 4, 5, 7, 8, 9, 10, 12, 13 |
| 6 | Amarillo de Ocho | 8, 9 |
| 6 | Calchaquí | 1, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16 |
| 7 | Perlita | 3, 4, 5, 6, 7, 8, 11, 12, 13, 17, 18, 20 |
| 8 | Dentado Amarillo | 1, 2, 4, 5, 6, 7, 8, 10, 13, 14, 15, 16, 17 |
| 9 | Cristalino Amarillo | 1, 2, 15, 18, 20 |
| 10 | Amarillo Ocho Hileras | 1, 14, 15, 16, 17, 18 |
| 11 | Venezolano | 4, 5, 6, 7, 8, 9, 10, 11 |
| 12 | Canario de Formosa | 3, 5, 6, 7, 8 |
| 13 | Blanco Ocho Hileras | 1, 14, 16, 17, 18, 19 |
| 13 | Capia Blanco | 8, 9, 10, 12 |
| 13 | Tusón | 3, 4, 6, 7, 8, 9, 10, 11, 13 |
| 14 | Dulce | 1, 7, 14, 15, 16, 17, 18, 19, 20 |

| | | |
|---|---|---|
| 15 | Cristalino Amarillo Anaranjado | 1, 3, 4, 5, 6, 7, 8, 12, 13, 14, 17 |
| 16 | Cristalino Blanco | 1, 2, 14, 15, 18, 19 |
| 16 | Perla | 5, 7, 8, 9, 10, 11, 12, 13, 16 |
| 17 | Morochito | 6, 7, 9, 12, 16 |
| 18 | Avatí Morotí Tí | 3, 4, 5, 14, 16, 17 |
| 18 | Socorro | 10, 12 |
| 19 | Capia Garrapata | 8, 9, 10 |
| 19 | Dentado Blanco Marlo Fino | 3, 8, 12, 13 |
| 20 | Amargo | 3, 6, 16 |
| 20 | Avatí Pichingá | 4, 5, 6, 7 |
| 20 | Camelia | 3, 4 |
| 20 | Capia Variegado | 8, 9 |
| 20 | Cravo | 5 |
| 20 | Pericarpio Rojo | 1, 7, 14, 15 |
| 21 | Chaucha Blanco | 8, 10, 12 |
| 22 | Altiplano | 8, 9 |
| 22 | Capia Rosado | 8, 9, 12 |
| 22 | Culli | 8, 9 |
| 23 | Chaucha Amarillo | 8, 10 |
| 24 | Chulpi | 9 |
| 24 | Cuzco | 8, 9 |
| 24 | Dentado Amarillo Marlo Fino | 5 |
| 25 | Avatí Morotí Mita | 4, 5 |
| 25 | Azul | 8, 9 |
| 25 | Catete Oscuro | 5 |
| 25 | Colita | 12 |
| 25 | Dentado Blanco Rugoso | 1 |
| 26 | Marrón | 8, 9 |
| 26 | Negro | 8 |

Source: Ing. Lucio Roberto Solari, INTA, Pergamino, Argentina.

* Province codes: 1 = Buenos Aires; 2 = Santa Fe; 3 = Entre Rios; 4 = Corrientes; 5 = Misiones; 6 = Chaco; 7 = Formosa; 8 = Salta; 9 = Jujuy; 10 = Tucuman; 11 = Santiago del Estero; 12 = Catamarca; 13 = La Rioja; 14 = Córdoba; 15 = Mendoza; 16 = San Luis; 17 = La Pampa; 18 = Neuquen; 19 = Rio Negro; 20 = Chubut.

**Table 2b. Extant maize landraces and their distribution in Bolivia (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Hualtaco | Cochabamba valley |
| 1 | Morocho 8 hileras | Inter-Andean valley |
| 1 | Kellu | Chuquisaca,Cochabamba, and Tarija valleys |
| 1 | Cubano Amarillo | Tropical area |
| 2 | Kajbia | Chuquisaca valley |
| 2 | Huillcaparu | Cochabamba valley |
| 2 | Kellu Huillcaparu | Cochabamba valley |
| 2 | Kulli | Inter-Andean Valley |
| 2 | Aizuma | Central temperate valley |
| 2 | Morocho Grande | Lower valleys, east Andean slope |
| 2 | Uchuquilla | Temperate valleys |
| 2 | Aperlado | Tarija valley |
| 3 | Paru | La Paz, Potosí, Chuquisaca, and Cochabamba |
| 3 | Chuspillo | Inter-Andean temperate valley |
| 3 | Checchi | Inter-Andean temparate valley |
| 3 | Tuimuru | High altitude Andean valley |
| 3 | Oke | Southern valley |
| 3 | Karapampa | Chuquisaca valley |
| 3 | Morocho Chico | Chuquisaca and Tarija valley |
| 3 | Morocho Chaqueño | Chuquisaca and Santa Cruz valleys |
| 3 | Blando Amazónico | Beni, Pando, eastern slope of La Paz |
| 3 | Blando Cruceño | Central plain of Santa Cruz |
| 3 | Chake Sara | Chuquisaca valley |
| 3 | Perla | Lower valley of Santa Cruz |
| 3 | Perola | Santa Cruz and Tarija (Province of Gran chaco) |
| 4 | Huaca Songo | High altitude valley |
| 4 | Jampe Tongo | La Paz, Potosí |
| 4 | Harinoso de 8 hileras | Inter-Andean temperate valley |
| 4 | Concebideño | Cochabamba valley |
| 4 | Colorado | Southern valley, Yungas |
| 4 | Morochillo de Tarija | Tarija valley |
| 4 | Duro Amazónico | Beni, Pando, and Santa Cruz |

| | | |
|---|---|---|
| 4 | Bayo | Amazonean plains and Yungas (warm valleys) |
| 4 | Canario | Department of Chuquisaca (Monteagudo) |
| 4 | Morocho de 14 hileras | Santa Cruz and Chuquisaca |
| 4 | Blanco Mojo | Santa Cruz |
| 4 | Cordillera | Santa Cruz |
| 5 | Pura | Tarija Valley |
| 5 | Pasanckalla | Highland valley, La Paz, Lago Titicaca area |
| 5 | Pisanckalla | Central inter-Andean valleys |
| 5 | Purito | Santa Cruz, Beni, Chalco, and Tarija |
| 5 | Achuchema | Transition zone from valley to plain |
| 5 | Blanco Yungueño | Yungas zone |
| 5 | Enano | Pando |
| 5 | Perla Primitivo de los Llanos | Santa Cruz (Province of Ibanes) |
| 5 | Perla Amarillo | Temperate region. This includes Perla (flint) and Morocho |

Source: Dr. Gonzalo Avila, Pairumani, Cochabamba, Bolivia.

**Table 2c. Extant maize landraces and their distribution in Chile (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Araucano | 9, 10, and 8* |
| 2 | Ocho Corridas | 9, 10, and 8 |
| 3 | Camelia | 4, 5, 6, 7, 8, and Metroplitan region |
| 4 | Cristal Chileno | 7, 8, and 5 |
| 5 | Diente de Caballo | Metropolitan region, 5, 6, 7, and 4 |
| 6 | Choclero | Metropolitan region, 5, 6, 7, and 4 |
| 7 | Curagua | 7, 8, and 2 |
| 8 | Capio Chileno Grande | 1 and 2 |
| 9 | Harinoso Tarapaqueño | 1 and 2 |
| 10 | Capio Chileno Chico | 1 and 2 |
| 11 | Maíz de Rulo | 7 |
| 12 | Morocho Blanco | 3, 2, 5, and 7 |
| 13 | Semanero | 7 and 6 |
| 14 | Amarillo de Nuble | 8 |

| | | |
|---|---|---|
| 15 | Pisankalla | 7, 8, and 5 |
| 16 | Limeño | 1 |
| 17 | Chutucuno | 2 and 1 |
| 18 | Chulpi | 1 |
| 19 | Amarillo de Malleco | 9 |
| 20 | Polulo | 1 and 2 |
| 21 | Morocho Amarillo | 2 |
| 22 | Negrito Chileno | 2 and 1 |
| 23 | Marcame | 2 and 1 |

Source: Ing Orlando Paratori, INIA, Santiago, Chile.

* Province codes: 1 = Arica, Iquique, Tarapaca; 2 = El Loa, Tocopilla, Antofagasta; 3 = Huasco, Copiapo, Atacama; 4 = Limari, Elqui, Choapa, Cochimbo; 5 = Petorca, Quillota, San Felipe, Los Andes, Valparaiso, Aconcagua; 6 = Cachapoal, Colchagua, Rancagua, Ohiggins; 7 = Curico, Linares, Talca, Maule, Cauquenes; 8 = Nuble, Bio Bio, Arauco; 9 = Mallelco, Cautin, Temuco, Valdivia, Bio Bio; 10 = Valdivia, Osorno, Llanquihue.

**Table 2d. Extant maize landraces and their distribution in Colombia (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Puya | RC* (Antioquia, Santander, Magdalena, Guajira) |
| 2 | Sabanero | RA (Cundinamarca, Boyacá, Nariño) |
| 3 | Costeño | RC (Córdoba, Bolívar, Magdalena, Atlántico) |
| 4 | Montaña | RA (Antioquia, Nariño) |
| 5 | Andaqui | Orinoquia (Meta) |
| 6 | Amagaceño | RA (Nariño, Antioquia, Valle, Huila, Caladas, C/Marca, Boyacá, S/Der) |
| 7 | Común | VI (Valle, Cauca, Huila, Caldas, Quindio, Risaralda) |
| 8 | Cacao | RA (Santanderes, Cundinamarca, Boyacá) |
| 9 | Cariaco | RC (Córdoba, Atlántico, Magdalena) |
| 10 | Chococeño | RP (Chocó, Nariño, Valle, Cauca) |
| 11 | Clavo | VI (Tolima, Caldas, Norte Santander) |
| 12 | Pira Naranja | RA (Nariño, Cundinamarca, Boyacá) |
| 13 | Pollo | RA (Nariño, Cundinamarca, Boyacá) |
| 14 | Pira | RA (Cundinamarca) |
| 15 | Negrita | RC (Atlántico, Magdalena, Guajira) |
| 16 | Guirua | RA (Magadalena) |

Source: Dr. Carlos Diaz, ICA, Medellín, Colombia. * R = Region; A = Andean; C = Caribbean; V = Valley; I = Inter-Andean.

**Table 2e. Extant maize landraces and their distribution in Cuba (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Cubano Amarillo | Central and western regions* |
| 2 | Tusón | Eastern and western regions |
| 3 | Argentino | Eastern and central regions |
| 4 | Chandelle | Eastern and western regions |
| 5 | Canilla | Eastern and central regions |
| 6 | Coastal Tropical Cristalino | Central and eastern regions |
| 7 | Cuban Flint | Central and western regions |

Ing. Cecilio Marcos Torres, Institute L. Dimitrova, El Tomeguin, Cuba.

*The eastern region is from Camaguey to Guantanamo; the central region is from Villa Clara to Ciego de Avila; the western region is Matanzas, La Habana, and Pinar del Rio.

**Table 2f. Extant maize landraces and their distribution in Ecuador (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Mishca | Pichincha, Cotopaxi, Tungurahua |
| 2 | Huandango | Imbabura, Carchi, Pichincha |
| 3 | Cuzco Ecuatoriano | Azuay, Cañar, Bolívar |
| 4 | Blanco Blando | Chimborazo, Bolívar, Cañar |
| 5 | Morochon | Carchi, Imbabura, Pichincha |
| 6 | Sabanero | Imbabura, Pichincha, Cotopaxi, Chimborazo |
| 7 | Chillos | Pichincha |
| 8 | Racimo de Uva | Pichincha, Cotopaxi, Chimborazo |
| 9 | Chulpi | Chimborazo, Pichincha, Cotopaxi |
| 10 | Canguil | Imbabura, Pichincha, Chimborazo |
| 11 | Kcello | Azuay, Loja, Bolívar |
| 12 | Blanco harinoso dentado | Loja |
| 13 | Uchima | Loja, Azuay |
| 14 | Cubano | Manabi, Esmeraldas, El Oro |
| 15 | Tuxpeño | Manabi, Los Rios |
| 16 | Chococeño | Esmeraldas, Manabi |
| 17 | Candela | Manabi |

| | | |
|---|---|---|
| 18 | Patillo | Chimborazo, Cañar |
| 19 | Pojoso Chico | Napo, Pastaza |
| 20 | Clavito | Chimborazo, Azuay |
| 21 | Gallina | El Oro |
| 22 | Yunquillano | Morona Santiago |
| 23 | Yungueño | Morona Santiago, Zamora, Chinchipe |

Source: Ing. Edison Silva, INIAP, Quito, Ecuador.

**Table 2g. Extant maize landraces and their distribution in Mexico (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Locations |
|---|---|---|
| 1 | Tuxpeño | All regions except 1, 27, 30* |
| 2 | Celaya | 1, 4, 5, 6, 8, 9, 11, 12, 13, 14, 16, 18, 19, 21, 23, 28, 30 |
| 3 | Cónico | 1, 4, 5, 8, 9, 11, 12, 13, 14, 16, 18, 19, 21, 23, 27, 28, 30 |
| 4 | Cónico Norteño | 1, 4, 6, 8, 9, 11, 12, 13, 14, 16, 17, 18, 19, 21, 23, 28, 30 |
| 5 | Chalqueño | 1, 4, 8, 9, 11, 12, 13, 14, 15, 18, 19, 21, 23, 27, 28, 30 |
| 6 | Elotes Cónicos | 1, 9, 10, 11, 12, 13, 14, 18, 19, 21, 23, 27, 28, 30 |
| 7 | Elotes Occidentalis | 5, 6, 8, 9, 10, 11, 12, 14, 16, 19, 23, 28, 30 |
| 8 | Olotillo | 5, 10, 11, 14, 15, 16, 18, 19, 20, 23, 25, 28, 29 |
| 9 | Tabloncillo | 4, 7, 8, 10, 12, 15, 16, 17, 22, 23, 24, 30 |
| 10 | Reventador | 4, 7, 8, 9, 10, 12, 14, 16, 22, 24 |
| 11 | Tabloncillo Perla | 2, 4, 5, 7, 8, 12, 16, 22, 24 |
| 12 | Bolita | 4, 8, 11, 12, 13, 18, 19, 28, 30 |
| 13 | Dzit-Bacal | 3, 5, 11, 14, 20, 23, 26, 28, 29 |
| 14 | Vandeño | 5, 7, 10, 12, 14, 15, 16, 18, 25 |
| 15 | Nal-tel | 3, 5, 10, 18, 20, 24, 25, 29, 28 |
| 16 | Pepitilla | 8, 10, 12, 13, 14, 15, 19, 28 |
| 17 | Maíz Dulce | 4, 9, 12, 14, 16, 22, 30 |
| 18 | Mushito | 9, 10, 11, 14, 18, 19, 28 |
| 19 | Cacahuacintle | 11, 13, 14, 19, 27, 28 |
| 20 | Harinoso de 8 | 4, 12, 16, 22, 23, 24 |
| 21 | Palomero | 4, 13, 14, 19, 27, 28 |
| 22 | San Juan | 4, 8, 12, 22, 24, 30 |
| 23 | Tepecintle | 5, 10, 18, 20, 28, 29 |
| 24 | Arrocillo Amarillo | 11, 13, 19, 27, 28 |

| | | |
|---|---|---|
| 25 | Dulcillo del Noroeste | 4, 8, 22, 24, 30 |
| 26 | Tuxpeño Norteño | 4, 6, 15 |
| 27 | Bofo | 8, 16, 21, 30 |
| 28 | Olotón | 5, 11, 18, 28 |
| 29 | Ancho | 10, 13, 15 |
| 30 | Arrocillo | 11, 19, 27 |
| 31 | Azul | 4, 12, 13 |
| 32 | Blandito de Sonora | 8, 22, 24 |
| 33 | Conejo | 10, 14, 18 |
| 34 | Jala | 7, 12, 16 |
| 35 | Lady Finger | 4, 22, 24 |
| 36 | Zapalote Chico | 5, 18, 29 |
| 37 | Zapalote Grande | 5, 18, 25 |
| 38 | Onaveño | 21, 22, 24 |
| 39 | Blandito | 4, 8 |
| 40 | Chapalote | 22, 24 |
| 41 | Clavillo | 3, 5 |
| 42 | Cristalino de Chihuahua | 4, 8 |
| 43 | Fasciado | 9, 21 |
| 44 | Gordo | 4, 8 |
| 45 | Tehua | 4, 6 |
| 46 | Tablilla de 8 | 16, 17 |
| 47 | Zamora | 12, 14 |
| 48 | Tablilla | 8, 30 |
| 49 | Apachito | 4 |
| 50 | Carmen | 26 |
| 51 | Comiteco | 5 |
| 52 | Complejo Serrano de Jalisco | 12 |
| 53 | Coscomátepec | 28 |
| 54 | Harinoso | 22 |
| 55 | Maizón | 4 |
| 56 | Xmejenal | 29 |
| 57 | Tunicata** | 8 |

Source: Dr. Francisco Cardenas, INIFAP, Mexico.

* Location codes: 1 = Aguascalientes; 2 = Baja California; 3 = Campeche; 4 = Chihuahua; 5 = Chiapas; 6 = Coahuila; 7 = Colima; 8 = Durango; 9 = Guanajuato; 10 = Guerrero; 11 = Hidalgo; 12 = Jalisco; 13 = Mexico; 14 = Michoacán; 15 = Morelos; 16 = Nayarit; 17 = Nuevo Leon; 18 = Oaxaca; 19 = Puebla; 20 = Quintana Roo; 21 = Queretaro; 22 = Sinaloa; 23 = San Luis Potosí; 24 = Sonora; 25 = Tabasco; 26 = Tamaulipas; 27 = Tlaxcala; 28 = Veracruz; 29 = Yucatán; 30 = Zacatecas.

** Probably no longer grown locally.

**Table 2h. Extant maize landraces and their distribution in Peru (listed according to the number of accessions in the national bank, from more to fewer).**

| | Race | Ecological zones | Latitude (° S) | Departments |
|---|---|---|---|---|
| 1 | San Gerónimo Huancavelicano | Highland 2500-3600m | 11-14 | Junín, Ayacucho, Huancavelica |
| 2 | Morocho | Highland 2500-3200m | 12-15 | Huancavelica, Ica |
| 3 | Cuzco Cristalino Amarillo | Highland 2800-3500m | 14-16 | Ica, Puno |
| 4 | Ancashino | Highland 2800-3500m | 8-10 | Ancash |
| 5 | Piscorunto | Highland 2800-3600m | 13-17 | Apurimac, Arequipa, Ayacucho |
| 6 | Piricinco | Jungle 0-800m | 6-13 | Lambayeque, San Martin, Madre de Dios |
| 7 | Cubano Amarillo | Jungle 0-1500m | 6-13 | Lambayeque, San Martin, Madre de Dios |
| 8 | Cuzco | Highland 2600-3500m | 5-17 | Cajamarca, Huanuco, La Libertad, Junín, Ayacucho, Huancavelica, Arequipa, Moquegua, Apurimac, Cuzco |
| 9 | Paro | Highland 2600-3300m | 12-17 | Arequipa, Moquegua, Apurimac, Cuzco |
| 10 | Perla | Coast 0-1500m | 8-15 | Ancash, Lima |
| 11 | Pardo | Coast 0-500m | 11-13 | Ancash, Lima |
| 12 | Huancavelicano | Highland 2900-3700m | 12-14 | Junín, Ayacucho, Huancavelica |
| 13 | Alazán | Coast 0-500m | 5-9 | Piura, Lambayeque, La Libertad |
| 14 | Chullpi | Highland 2500-3200m | 12-15 | Arequipa, Moquegua, Apurimac, Cuzco |
| 15 | Kculli | Highland 2000-3500m | 5-17 | Cajamarca, Huanuco, La Libertad, Junín, Ayacucho, Huancavelica, Arequipa, Moquegua, Apurimac, Cuzco |
| 16 | Arequipeño | Highland 2000-3000m | 13-17 | Arequipa, Moquegua, Apurimac, Cuzco |
| 17 | Cusco Gigante | Highland 2500-3000m | 12-14 | Junín, Ayacuhco, Huancavelica |
| 18 | Arizona | Coast 0-800m | 7-9 | Piura, Lambayeque, La Libertad |

| | | | | |
|---|---|---|---|---|
| 19 | Capio | Highland 2000-3000m | 5-9 | Cajamarca, Huanuco, La Libertad |
| 20 | Marañón | Highland 2000-2800m | 7-10 | Cajamarca, Huanuco, La Libertad |
| 21 | Mochero | Coast 0-500m | 5-7 | Piura, Lambayeque, La Libertad |
| 22 | Chuncho | Jungle 500-2000m | 10-14 | Apurimac, Cerro de Pasco |
| 23 | Huayleño | Highland 2800-3200m | 8-10 | Cajamarca, Huanuco, La Libertad |
| 24 | San Gerónimo | Highland 3000-3600m | 11-13 | Junín, Ayacuhco, Huancavelica |
| 25 | Uchuquilla | Highland 2800-3500m | 14-16 | Arequipa, Moquegua, Apurimac, Cuzco |
| 26 | Chaparreno | Coast 0-500m | 14-17 | Ica, Arequipa |
| 27 | Colorado | Coast 0-1000m | 6-9 | Piura, Lambayeque, La Libertad |
| 28 | Morocho Cajabambino | Highland 1800-2500m | 5-9 | Cajamarca, Huanuco, La Libertad |
| 29 | Sabanero | Highland 2000-3000m | 5-10 | Cajamarca, Huanuco, La Libertad |
| 30 | Shajatu | Highland 2500-3000m | 8-10 | Cajamarca, Huanuco, La Libertad |
| 31 | Tumbesino | Coast 0-500m | 4-5 | Piura, Lambayeque, La Libertad |
| 32 | Chimlos | Jungle 500-2000m | 12-14 | Apurimac, Cuzco |
| 33 | Granada | Highland 3000-3700m | 9-14 | Cajamarca, Huanuco, La Libertad, Junín, Ayacucho, Huancavelica |
| 34 | Chancayano Blanco | Coast 0-1000m | 11-13 | Ancash, Lima |
| 35 | Coruca | Coast 0-2000m | 17-18 | Ica, Arequipa |
| 36 | Amarillo Huancabamba | Highland 1500-2800m | 5-6 | Cajamarca, Huanuco, La Libertad |
| 37 | Pagaladroga | Coast 0-800m | 5-7 | Piura, Lambayeque, La Libertad |
| 38 | Tambopateño | Jungle 0-1000m | 11-13 | Madre de Dios |
| 39 | Aleman | Jungle 500-2000m | 10-12 | Junín |
| 40 | Blanco Ayabaca | Highland 2200-3000m | 5-6 | Cajamarca, Huanuco, La Libertad |
| 41 | Cabana | Highland 3000-3500m | 16-17 | Arequipa, Moquegua, Apurimac, Cuzco |
| 42 | Morado Canteño | highland 2200-3200m | 11-13 | Junín, Ayacucho, Huancavelica |
| 43 | Huarmaca | Highland 2200-2800m | 5-6 | Cajamarca, Huanuco, La Libertad |

| | | | | |
|---|---|---|---|---|
| 44 | Confite Puntiagudo | Highland 2200-3000m | 7-14 | Junín, Ayacucho, Huancavelica |
| 45 | Perlilla | Jungle 500-2000m | 9-14 | Huanuco |
| 46 | Confite Morocho | Highland 2800-3500m | 13-14 | Arequipa, Moquegua, Apurimac, Cuzco |
| 47 | Confite Puneño | Highland 3500-4000m | 15-16 | Arequipa, Moquegua, Apurimac, Cuzco |
| 48 | Chancayano Pintado | Coast 0-800m | 11-13 | Ancash, Lima |
| 49* | Rienda | Coast 0-1800m | 8-11 | Ancash, Lima |
| 50* | Huachano | Coast 0-1000m | 11-13 | Ancash, Lima |
| 51* | Jora | Coast 0-1000m | 8-10 | Ancash, Lima |
| 52* | Enano | Jungle 200-800m | 12-13 | Madre de Dios, Cuzco |

Source: Ing. Ricardo Sevilla, PCIM, Lima, Peru.

* Probably lost at the community level.

**Table 3a. Landraces, in order of priority, which are cultivated for specific uses in Argentina.**

| | Race | Primary use* | Secondary use | Tertiary use |
|---|---|---|---|---|
| 1 | Cristalino Colorado | Polenta, humita, locro | Feed grain and forage | |
| 2 | Dentado Blanco | Choclo, flour, semolas, mote | Feed grain forage | Tortas |
| 3 | Pisingallo | Flour, chilcan, ulpada, misko pitapi, pochoclo, pororo | Feed grain | |
| 4 | Avatí Morotí | Masa, bread | Paraguayan soup. Baipai, yapora, bori | Tortillas, croquettes, feed grain |
| 5 | Amarillo de Ocho | Choclo, caldo majao, anchi de semola | Calapi, sanco, chicha, tulpo, pire | Feed grain |
| 5 | Calchaquí | Cooked flour, frangollo, mazamorra | Locro chilcan, ulpada, soup, choclo | Feed grain |
| 6 | Dentado Amarillo | Glucose, starch, alcohol, choclo | Feed grain and forage | Tortas |
| 7 | Cristalino Amarillo | Locro, chichoca, polenta, choclo, humita | Feed grain | |
| 8 | Capia Blanco | Mote, biscochos, alfajor, turron, tamal | Tijtinchas, flour, tostadas, chilcon | Ulpada, soup, misko, pitapi, bread, pastel, choclos, chicha |

| | | | | |
|---|---|---|---|---|
| 9 | Capia Variegado | Mote, biscochos, alfajor, turron, tamal | Tijtinchas, flour, tostadas, chilcon | Ulpada, soup, misko, pitapi, bread, pastel, choclos, chicha |
| 10 | Capia Garrapata | Mote, biscochos, alfajor, turron, tamal | Tijtinchas, flour, tostadas, chilcon | Ulpada, sopa, misko, pitapi, bread, pastel, choclos, chicha |
| 11 | Altiplano | Choclo, masa | Biscochos, pire | Chicha |
| 11 | Capia Rosado | Mote, biscochos, alfajor, turron, tamal | Tijtinchas, flour, tostadas, chilcon | Ulpada, soup, misko, pipati, bread, pastel, choclos, chicha |
| 11 | Chulpi | Yupe, humita, guaycha | Choclo, locro | Mazamorra with cheese |
| 11 | Culli | Flour, masa, choclo | Chicha morada, soup | Feed grain |
| 12 | Cuzco | Flour, bread, masa | Starch, alcohol, choclo | Feed grain |

* Partial list of definitions: harina cocida = dough; mote = hominy; choclo = green ear; humita = sweet dough cooked; chichoca = cooked grits; polenta = cooked flour; tostada = toasted tortilla; alfajor = cake; chicha = corn beer; biscocho = sweet roll; mazamorra, turron = candy.

**Table 3b. Landraces, in order of priority, which are cultivated for specific uses in Bolivia.**

| | Race | Primary use* | Secondary use | Tertiary use |
|---|---|---|---|---|
| 1 | Hualtaco | Choclo, soup | Burritas, tamales | Mote |
| 1 | Morocho | Chicha | Soup | Mote |
| 2 | Kellu | Chicha | Mote | Soup |
| 3 | Huillcaparu | Chicha | Mote | Soup |
| 3 | Uchuquilla | Soup | Mote, choclo | |
| 3 | Kajbia | Choclo | Mote | |
| 3 | Aizuma | Chicha | Mote | |
| 3 | Karapampa | Chicha | Mote | Soup |
| 3 | Morocho grande | Soup | Chicha | Mote |
| 3 | Duro Amazónico | Choclo-tamal | | |
| 3 | Blando Cruceño | Repostería | Choclo-tamal | |
| 3 | Aperlado | Choclo | Soup | |
| 3 | Perola | Soup | Choclo | |
| 3 | Morocho 14 hileras | Chicha | Mote | |

| | | | | |
|---|---|---|---|---|
| 4 | Chuspillu | Chicha | Tostado (perched grains) | |
| 4 | Kulli | Chicha | Api (mazamorra) | |
| 4 | Perla | Soup | Mote | |
| 4 | Checchi | Tostado (parched grains) | Pito | |
| 4 | Hauca songo | Tostado, soup | Pito | |
| 4 | Jampe tongo | Tostado | Soup | |
| 4 | Paru | Mote | Soup | |
| 4 | Blanco Yungueño | Choclo | Mote | |
| 4 | Kellu Huillcaparu | Chicha | Mote | |
| 4 | Concebideño | Chicha | Mote | Soup |
| 4 | Morocho chico | Chicha | Mote | Soup |
| 4 | Morocho Chaqueño | Soup | Choclo | Mote |
| 4 | Blando Amazónico | Repostería | Choclo-tamal | |
| 4 | Bayo | Repostería | Choclo-tamal | |
| 4 | Cañario | Repostería | Choclo-tamal | |
| 4 | Chaquesara | Soup | Choclo | |
| 4 | Cordillera | Chicha | Mote | |
| 5 | Pisanckalla | Tostado (pop corn) | | |
| 5 | Pura | Tostado (popcorn) | | |
| 5 | Pasanckalla | Tostado (pop corn) | | |
| 5 | Purito | Tostado (pop corn) | | |
| 5 | Harinoso 8 hileras | Choclo | Mote | |
| 5 | Achuchema | Tostado | | |
| 5 | Tuimuru | Mote | Soup | |
| 5 | Oke | Soup | Mote | |
| 5 | Colorado | Chicha | Mote | |
| 5 | Morocho 8 hileras | Mote | Chicha | |
| 5 | Blanco mojo | Choclo | Mote | |

* Choclo = green ear; mote = hominy; chicha = corn beer; grano tostado = toasted grain; palomitas = pop corn; humitas = sweet masa cooked; tamal = steamed dough filled with meat and/or sauce; mazamorra = candy.

**Table 3c. Landraces, in order of priority, which are cultivated for specific uses in Chile.**

| | Race | Primary use* | Secondary use | Tertiary use |
|---|---|---|---|---|
| 1 | Choclero** | Choclo | Chuchoca | Humitas and guisos |
| 2 | Diente de Caballo** | Choclo | Chuchoca | Humitas and guisos |
| 3 | Araucano** | Choclo | Chuchoca | |
| 4 | Ocho corridas** | Chicken feed grain | | |
| 5 | Camelia** | Chuchoca | Chicken feed grain | |
| 6 | Harinoso Tarapaqueño** | Choclo | Humitas and guisos | |
| 7 | Capio Chileno Grande | Choclo | Humitas and guisos | |
| 8 | Curagua** | Harina tostada | | |
| 9 | Semanero** | Choclo | | |
| 10 | Polulo | Maíz reventon | | |
| 11 | Chutucumo | Maíz reventon | | |
| 12 | Cristalino Chileno** | Maíz reventon | | |
| 13 | Amarillo de Malloco** | Maíz reventon | | |

* Choclo = green ear; chuchoca = cooked grids; harina tostada = floury toasted; maíz reventon = pop corn; guisos = any main dish from maize.

** Noted for conservation of maize biodiversity by Ing. O. Paratori.

**Table 3d. Landraces, in order of priority, which are cultivated for specific uses in Colombia.**

| | Race | Primary use* | Secondary use |
|---|---|---|---|
| 1 | Puya | Grain | Arepas |
| 2 | Sabanero | Choclos | Forage |
| 3 | Costeño | Grain | Feed |
| 4 | Montaña | Choclos | |
| 5 | Andaqui | Grain | |
| 6 | Amagaceño | Grain | |
| 7 | Comun | Grain | |
| 8 | Cacao | Choclos | Grain |
| 9 | Cariaco | Drink with chocolate | |
| 10 | Chococeño | Grain | |

* Choclos = green ear; arepas = large, thick tortilla.

**Table 3e. Landraces, in order of priority, which are cultivated for specific uses in Cuba.**

| | Race | Primary use | Secondary use |
|---|---|---|---|
| 1 | Cubano Amarillo | Green ears | Grain |
| 2 | Tusón | Green ears | Grain |
| 3 | Argentino | Green ears | Grain |
| 4 | Chandelle | Green ears | Grain |
| 5 | Canilla | Green ears | Grain |
| 6 | Coastal Tropical Crystal | Green ears | Grain |
| 7 | Cuban Flint | Green ears | Grain |

**Table 3f. Landraces, in order of priority, which are cultivated for specific uses in Ecuador.**

| | Race | Primary use* | Secondary use | Tertiary use |
|---|---|---|---|---|
| 1 | Mishca | Toasted grain | Choclo | Mote |
| 2 | Huandango | Choclo | Grano tostado | Mote |
| 3 | Cuzco Ecuatoriano | Mote | Choclo | Flour |
| 4 | Blanco Blandito | Choclo | Mote | Toasted grain |
| 5 | Chillos | Grano tostado | Choclo | Mote |
| 6 | Morochon | Soups and drinks | Choclo | Flour |
| 7 | Chulpi | Toasted grain | Flour | Chicha |
| 8 | Canguil | Popcorn | | |
| 9 | Racimo de Uva | Atole | Flour | |

* Choclo = green ear; mote = hominy; reventado = pop corn; atole = sweet drink of corn flour with milk; chicha = maize beer

**Table 3g. Landraces, in order of priority, which are cultivated for specific uses in Mexico.**

| | Race | Primary use* | Secondary use | Tertiary use |
|---|---|---|---|---|
| 1 | Cacahuacintle | Bread, toasted grain | Elotes, pozole, memelas | Gordas de maíz |
| 2 | Elotes Cónicos | Elotes, pozole | Tlacoyos | |
| 3 | Elotes Occidentales | Elotes, pozole | | |
| 4 | Ancho | Pozole | | |
| 5 | Zapalote Chico | Totopos | | |
| 6 | Bofo | Toasted grain | Huacholes | Maíz crudo reposado |
| 7 | Reventador | Toasted grain, popcorn | Toasted grain, popcorn | Ponteduro con panela |
| 7 | Chapalote | Toasted grain, popcorn | Toasted grain | Ponteduro con panela |
| 7 | Palomero Toluqueño | Toasted grain, popcorn | Toasted grain | Ponteduro con panela |
| 7 | Apachito | Toasted grain, popcorn | Toasted grain | Ponteduro con panela |
| 7 | Arrocillo | Toasted grain, popcorn | Toasted grain | Ponteduro con panela |
| 8 | Azul | Tamales | Tortillas | |

* Partial list of definitions: elotes = green ears; pozole = whole grains in meat broth; totopos = a type of small tortilla; tamales = steamed, meat- and sauce-filled dough; tlacoyos = fried cakes with beans inside; memelas = large, flat fried corn cakes; ponteduro con panela = candy.

**Table 3h. Landraces, in order of priority, which are cultivated for specific uses in Peru.**

| | Race | Primary use* | Secondary use |
|---|---|---|---|
| 1 | San Gerónimo Huancavelicano | Mote | Choclo |
| 2 | Cuzco Cristalino Amarillo | Mote | Chicha |
| 3 | Paro-Piscorunto | Cancha | Mote |
| 4 | Ancashino-Huayleño | Cancha | |
| 5 | Cuzco | Choclo | Mote |
| 6 | Morocho | Mote | Chicha |
| 7 | Pardo-Chancayano | Choclo | |
| 8 | Alazán | Chicha | |
| 9 | Kculli | Chicha | |
| 10 | Chullpi | Cancha | |

* Mote = hominy; cancha = toasted grain; choclo = green ear; chicha = corn beer.

Table 4a. **Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Argentina.**

| | Race | Locations* |
|---|---|---|
| 1 | Cristalino colorado | 1, 2, 3, 4, 6, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 |
| 2 | Dentado Blanco | 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 19 |
| 3 | Pisingallo | 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 20 |
| 4 | Avatí Morotí | 3, 4, 5, 6, 7, 8, 9, 18 |
| 5 | Amarillo de Ocho | 8, 9 |
| 6 | Dentado Amarillo | 1, 2, 4, 5, 6, 7, 8, 10, 13, 14, 15, 16, 17 |
| 7 | Cristalino Amarillo | 1, 2, 15, 18, 20 |
| 8 | Capia Blanco | 8, 9, 10, 12 |
| 9 | Cristalino Blanco | 1, 2, 14, 15, 18, 19 |
| 10 | Capia Garrapata | 8, 9, 10 |
| 11 | Capia Variegado | 8, 9 |
| 12 | Capia Rosado | 8, 9, 12 |
| 13 | Chulpi | 9 |

* Location codes: 1 = Buenos Aires; 2 = Santa Fe; 3 = Entre Rios; 4 = Corrientes; 5 = Misiones; 6 = Chaco; 7 = Formosa; 8 = Salta; 9 = Jujuy; 10 = Tucuman; 11 = Santiago del Estero; 12 = Catamarca; 13 = La Rioja; 14 = Córdoba; 15 = Mendoza; 16 = San Luis; 17 = La Pampa; 18 = Neuquen; 19 = Rio Negro; 20 = Chubut.

Table 4b. **Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Bolivia.**

| | Race | Ecological zone | Departments |
|---|---|---|---|
| 1 | Hualtaco | Temperate valley | Cochabamba, |
| 2 | Aperlado | Temperate valley | Tarija, Chuquisaca |
| 2 | Kellu | Temperate valley | Cochabamba, Chuquisaca, Potosí, La Paz |
| 3 | Aizuma | Temperate valley | Cochabamba, Chuquisaca, |
| 3 | Blando Amazónico | Amazonia | Beni, Pando, La Paz |
| 3 | Blando Cruceño | Tropical plains | Santa Cruz, Chuquisaca |
| 3 | Checchi | Temperate valley | Cochabamba, Chuquisaca, Potosí, Tarija |
| 3 | Huillcaparu | Temperate valley | Cochabamba |
| 3 | Kajbia | Temperate valley | Chuquisaca |
| 3 | Kulli | Temperate valleys | Cochabamba, Chuquisaca, Potosí, Tarija |

| | | | |
|---|---|---|---|
| 3 | Morocho Grande | Yungas | Santa Cruz, Cochabamba |
| 3 | Perla | Lower valley | Chuquisaca, Tarija |
| 3 | Perola | Tropical plains | Santa Cruz |
| 3 | Uchuquilla | Temperate valley | Cochabamba, Chuquisaca, Potosí, Tarija |
| 4 | Chaque Sara | Temperate valley | Chuquisaca |
| 4 | Chuspillo | Temperate valleys | Cochabamba, Chuquisaca, Potosí. |
| 4 | Colorado | Meridian yungas valley | Tarija, La Paz |
| 4 | Cordillera | Lower valley, Chaco | Santa Cruz |
| 4 | Duro Amazónico | Amazonia | Beni, Santa Cruz, Pando, La Paz |
| 4 | Duro Beniano | Tropical plains | Pando, Beni |
| 4 | Huaca songo | High altitude Andean | Cochabamba, La Paz, Potosí, Chuquisaca |
| 4 | Jampe Tongo | High altitude Andean | La Paz, Potosí, |
| 4 | Karapampa | Temperate valley | Chuquisaca |
| 4 | Kellu Huillcaparu | Temperate valley | Cochabamba |
| 4 | Morocho 8 Hileras | Temperate valley | Chuquisaca, Cochabamba, Potosí, Tarija |
| 4 | Morocho Chaqueño | Chaco | Santa Cruz, Chuquisaca |
| 4 | Morocho Chico | Temperate valley | Chuquisaca, Tarija |
| 4 | Oke | Temperate valley | Chuquisaca, Potosí, |
| 4 | Paru | High altitude Andean | La Paz, Potosí, Chuquisaca, Cochabamba, |
| 4 | Taimuru | High altitude Andean | Potosí, Cochabamba, Chuquisaca |
| 5 | Achuchena | Lower valley | Chuquisaca, Santa Cruz |
| 5 | Bayo | Chaco | Chuquisaca, Santa Cruz |
| 5 | Blanco Mojo | Tropical plains | Santa Cruz, Beni |
| 5 | Blanco Yungueño | Yungas (warm valley) | La Paz, Santa Cruz |
| 5 | Cañario | Chaco | Chuquisaca, Santa Cruz |
| 5 | Concebideño | Temperate valley | Cochabamba |
| 5 | Harinoso 8 hileras | Temperate valley | Chuquisaca, Tarija, |
| 5 | Morochillo de Tarija | Temperate valley | Tarija |
| 5 | Morocho 14 hileras | Chaqueña and Chiquitana plains | Santa Cruz |
| 5 | Pasanckalla | High Andean valley | La Paz, Potosí |
| 5 | Pisanckalla | Temperate valley | Cochabamba, Chuquisaca, Tarija |
| 5 | Pura | Lower valleys | Tarija |
| 5 | Purito | Tropical plains | Santa Cruz, Beni, Tarija |

**Table 4c. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Chile.**

| | Race | Locations* | | |
|---|---|---|---|---|
| 1 | Araucano | 9 | 10 | 8 |
| 2 | Choclero | Metropolitan region | | |
| 3 | Diente de Caballo | Metropolitan region | | |

* Location codes: 8=Nuble, BioBio, Arauco; 9=Malleco, Cautin, Temuco, Valdivia; 10=Valdivia, Osorno, Llanquihue.

**Table 4d. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Colombia.**

| | Race | Location/ecology |
|---|---|---|
| 1 | Puya | Hot climate |
| 2 | Sabanero | Cundiboyacense High plain (cold climate) |
| 3 | Costeño | Coastal plains of North (hot climate) |
| 4 | Amagaceño | Temperate climate |
| 5 | Montaña | Cool moderate climate |

**Table 4e. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Cuba.**

| | | Location | |
|---|---|---|---|
| | Race | Primary | Secondary |
| 1 | Cubano Amarillo | Central | West |
| 2 | Tusón | East | |
| 3 | Argentino | East | Central |
| 4 | Chandelle | East | West |
| 5 | Canilla | East | Central |
| 6 | Coastal Tropical Crystal | Central | West |
| 7 | Cuban Flint | Central | West |

**Table 4f. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Ecuador.**

| | Race | Location<br>Primary | Secondary | Tertiary |
|---|---|---|---|---|
| 1 | Huandango | Imbabura | | |
| 2 | Chaucho-Huandango | Imbabura | | |
| 3 | Mishca | Pichincha | Cotopaxi | |
| 4 | Cuzco Ecuatoriano | Azuay | Bolívar | Cañar |
| 5 | Blanco Blandito | Chimborazo | Bolívar | |
| 6 | Chillos | Pichincha | | |
| 7 | Morochón | Imbabura | Pichincha | Chimborazo |

**Table 4g. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Mexico.**

| | Race | Location (ecology) |
|---|---|---|
| 1 | Chalqueño | Highland, La Mesa Cental (wet) |
| 2 | Cónico | Highland La Mesa Central (less wet) |
| 3 | Olotón | Southern highland (very cloudy) |
| 4 | Cristalino de Chihuahua | Northeastern highland |
| 5 | Celaya | Intermediate elevations, 1000-1800m (wet) |
| 5 | Tabloncillo | Intermediate elevations, 1000-1800m (wet) |
| 5 | Pepitilla | Intermediate elevations, 1000-1800m (wet) |
| 5 | Tuxpeño Norteño | Intermediate elevations, 1000-1800m (wet) |
| 5 | Ratón | Intermediate elevations, 1000-1800m (wet) |
| 6 | Bolita | Intermediate elevations, 1000-1800m (dry) |
| 6 | Cónico Norteño | Intermediate elevations, 1000-1800m (dry) |
| 7 | Tuxpeño | Lowlands, 0-1000m (wet) |
| 7 | Vandeño | Lowlands, 0-1000m (wet) |
| 7 | Comiteco | Lowlands, 0-1000m (wet) |
| 8 | Zapalote Chico | Lowlands, 0-1000m (dry) |
| 8 | Nal-tel | Lowlands, 0-1000m (dry) |

**Table 4h. Landraces, in the order of priority, which are cultivated for grain production in their regions of adaptation in Peru.**

| | Race | Location (Department)<br>Primary | Secondary | Tertiary |
|---|---|---|---|---|
| 1 | San Gerónimo Huancavelicano | Junín, Pasco | Huancavelica, Ayacucho, Lima | |
| 2 | Morocho | Huanuco, Pasco | Ayacucho, Apurimac | |
| 3 | Cuzco Cristalino Amarillo | Cuzco | Apurimac | |
| 4 | Ancashino | Ancash | Huanuco | |
| 5 | Piscorunto | Cuzco, Arequipa | Ayacucho | Apurimac |
| 6 | Piricinco | San Martin, Loreto | Ucayali, Madre de Dios | |
| 7 | Cubano Amarillo | San Martin, Loreto, Ucayali | Pasco, Junín, Ayacucho | Apurimac, Madre de Dios |
| 8 | Cuzco | Cuzco, Apurimac | Ayacucho, Huancavelica | Junín, Cajamarca |
| 9 | Perla | Lima, Ancash | Ica | |
| 10 | Pardo | Lima | | |

**Table 5a. Landraces, in order of priority, used in breeding in Argentina.**

| | Race | Locations* |
|---|---|---|
| 1 | Cristalino Colorado | 1, 2, 3, 4, 6, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 |
| 2 | Dentado Blanco | 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 19 |
| 3 | Pisingallo | 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 20 |
| 4 | Calchaquí | 1, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16 |
| 5 | Dentado Amarillo | 1, 2, 4, 5, 6, 7, 8, 10, 13, 14, 15, 16, 17 |
| 6 | Cristalino Amarillo | 1, 2, 15, 18, 20 |
| 7 | Dulce | 1, 7, 14, 15, 16, 17, 18, 19, 20 |
| 8 | Cristalino Amarillo-Anaranjado | 1, 3, 4, 5, 6, 7, 8, 12, 13, 14, 17 |
| 9 | Cristalino Blanco | 1, 2, 14, 15, 18, 19 |
| 9 | Perla | 5, 7, 8, 9, 10, 11, 12, 13, 16 |
| 10 | Camelia | 3, 4 |
| 11 | Chulpi | 9 |

* Location codes: 1 = Buenos Aires; 2 = Santa Fe; 3 = Entre Rios; 4 = Corrientes; 5 = Misiones; 6 = Chaco; 7 = Formosa; 8 = Salta; 9 = Jujuy; 10 = Tucuman; 11 = Santiago del Estero; 12 = Catamarca; 13 = La Rioja; 14 = Córdoba; 15 = Mendoza; 16 = San Luis; 17 = Laq Pampa; 18 = Neuquen; 19 = Rio Negro; 20 = Chubut.

**Table 5b. Landraces, in order of priority, used in breeding in Bolivia.**

| | Race | Location/ecology |
|---|---|---|
| 1 | Morochos | Temperate valley |
| 1 | Hualtaco | Temperate valleys |
| 1 | Kajbia | Temperate valleys |
| 1 | Uchuquilla | Temperate valleys |
| 1 | Hualtaco Precoz | Temperate valleys |
| 1 | Cubano Amarillo (introduced variety) | Tropical plains |
| 2 | Kulli | Temperate valleys |
| 2 | Aperlado | Southern valleys |
| 2 | Kellu | Temperate valleys |
| 3 | Jampe tongo | Highland valleys |
| 3 | Huaca songo | Highland valleys |
| 3 | Chuspillo | Temperate valleys |
| 3 | Huillcaparu | Central valleys |
| 3 | Checchi | Temperate valleys |

**Table 5c. Landraces, in order of priority, used in breeding in Chile.**

| | | Region | |
|---|---|---|---|
| | Race | Primary | Secondary |
| 1 | Choclero | Metropolitan | 5, 6, 4, 7 |
| 2 | Diente de Caballo | Metropolitan | 5, 6, 4, 7 |
| 3 | Camelia | 4, 5, 6, 7, 8 | |
| 4 | Ocho Corridas | 9, 10, 8 | |

* Location codes: 4 = Limari, Elqui, Choapa, Cochimbo; 5 = Petorca, Quillota, San Felipe, Los Andes, Valparaiso, Acncagua; 6 = Cachapoal, Colchagua, Rancagua, Ohiggins; 7 = Curico, Linares, Talca, Maule, Cauquenes; 8 = Nuble, Bio Bio, Arauco; 9 = Malleco, Cautin, Temuco, Valdivia, Bio Bio; 10 = Valdivia, Osorno, Llanquihue.

**Table 5d. Landraces, in order of priority, used in breeding in Colombia.**

| | Race | Region/ecology |
|---|---|---|
| 1 | Sabanero | Andean (Cundinamarca and Boyacá) |
| 2 | Costeño | Caribbean (hot climate region) |
| 3 | Puya | Caribbean regions with high moisture (Darien Colombiano) |
| 4 | Montaña | Andean region (Eastern Antioqueño) |

**Table 5e. Landraces, in order of priority, used in breeding in Cuba.**

| | Race | Location |
|---|---|---|
| 1 | Cubano Amarillo | Lowland tropics |
| 2 | Tusón | Lowland tropics |
| 3 | Argentino | Lowland tropics |
| 4 | Chandelle | Lowland tropics |
| 5 | Canilla | Lowland tropics |
| 6 | Coastal Tropical Cristalino | Lowland tropics |
| 7 | Cuban Flint | Lowland tropics |

**Table 5f. Landraces, in order of priority, used in breeding in Ecuador.**

| | Race | Region<br>Primary | Secondary | Tertiary |
|---|---|---|---|---|
| 1 | Huandango | Imbabura | | |
| 2 | Cuzco Ecuatoriano | Azuay | Bolívar | Cañar |
| 3 | Mishca | Pichincha | Cotopaxi | |
| 4 | Blanco Blandito | Chimborazo | | |
| 5 | Morochon | Imbabura | Pichincha | Chimborazo |
| 6 | Chulpi | Chimborazo | Pichincha | Imbabura |

**Table 5g. Landraces, in order of priority, used in breeding in Mexico.**

| | Race | Region/ecology |
|---|---|---|
| 1 | Chalqueño | Central highlands (wet) |
| 2 | Cónico | Central highlands (less wet) |
| 3 | Celaya | Intermediate elevations, 1000-1800m (wet) |
| 3 | Tuxpeño | Intermediate elevations, 1000-1800m (wet) |
| 3 | Tabloncillo | Intermediate elevations, 1000-1800m (wet) |
| 4 | Bolita | Intermediate elevations, 1000-1800m (dry) |
| 4 | Cónico Norteño | Intermediate elevations, 1000-1800m (dry) |
| 4 | Cónico | Intermediate elevations, 1000-1800m (less wet) |
| 5 | Tuxpeño | Lowlands, 0-1000m (wet) |
| 5 | Tuxpeño Norteño | Lowlands, 0-1000m (wet) |
| 6 | Ratón (San Juan) | Lowlands, 0-1000m (dry) |

**Table 5h. Landraces, in order of priority, used in breeding in Peru.**

| | Race | Distribution by region | Purpose* |
|---|---|---|---|
| 1 | Cubano Amarillo | Jungle | Grain |
| 2 | Perla | Central Coast | Grain and forage |
| 3 | San Gerónimo Huancavelicano | Highland (very cold) | Choclo and grain |
| 4 | Ancashino | Highland (intermediate, north and central) | Cancha |
| 5 | Cuzco | Highland (from mid to the highest) | Choclo and mote |
| 6 | Morocho | Highland (north, central, and south) | Mote and grain |
| 7 | Kculli | Highland (low) and Coast | Pigmento |
| 8 | Cuzco Gigante | Highland | Choclo |
| 9 | Huayleño | Highland (medium, north and central) | Cancha |
| 10 | Arizona | Coast (north and central) | Flour |

* Choclo = green ear; cancha = toasted grain; mote = hominy; pigmento = pigment.

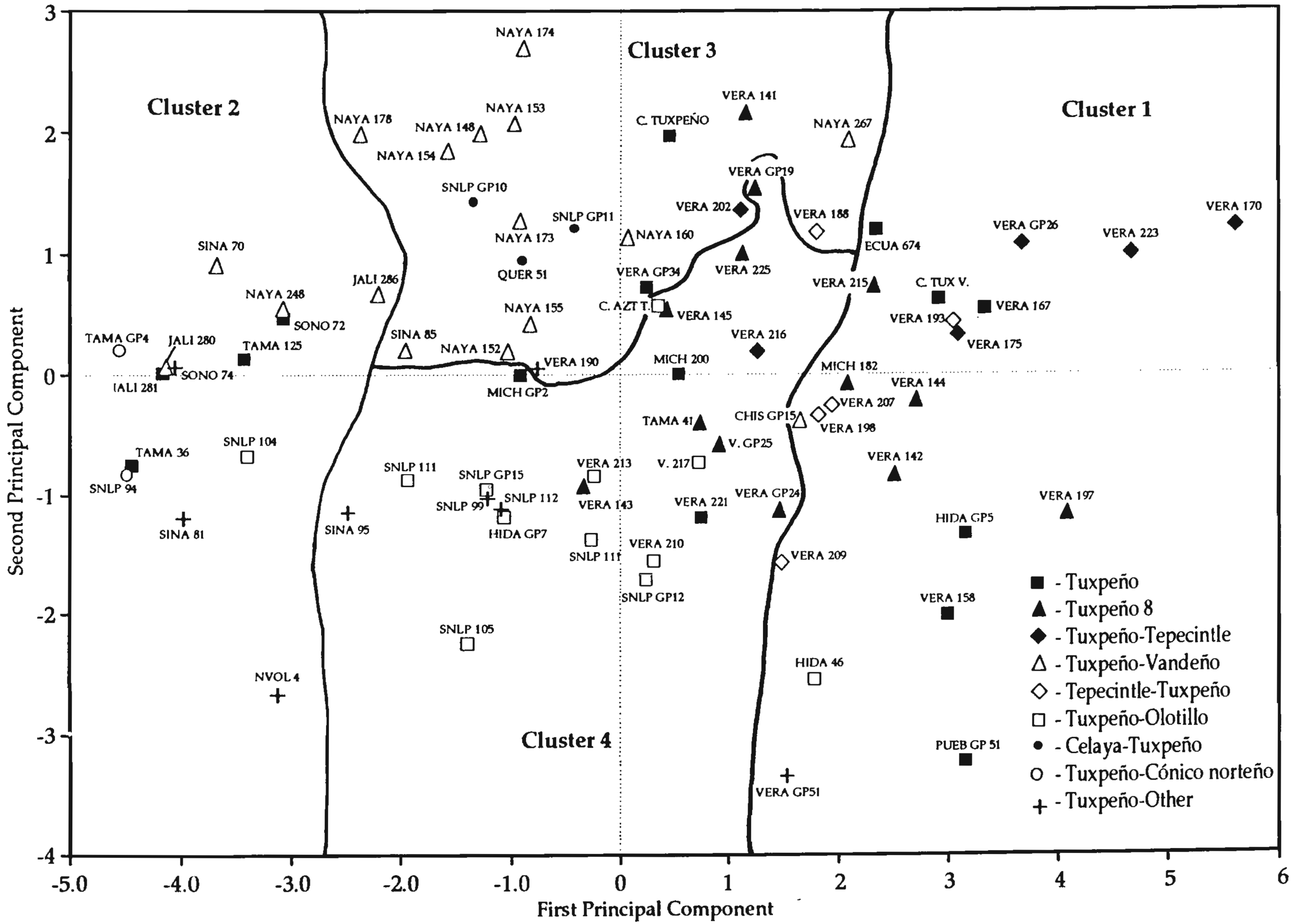

**Figure 1.** Principal component analysis (PCA) of diversity for an 80-accessions of the Tuxpeño maize race complex, using the means of trial data from two sites for eleven morphological/agronomic traits. The accessions are identified with the collection numbers or names to show collection sites and with the symbols for race classifications. Solid lines delimit the four main clusters.

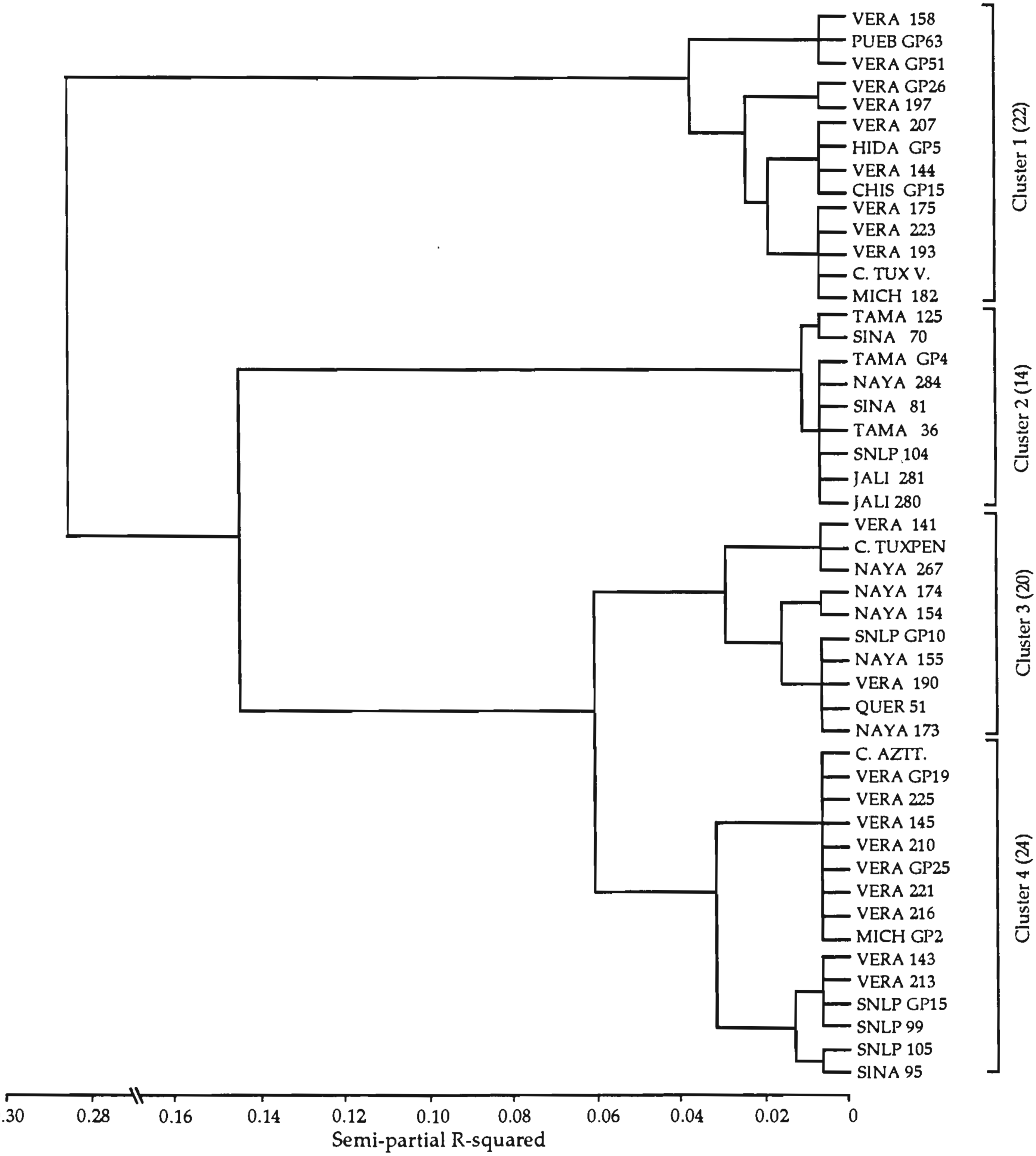

**Figure 2. Dendogram of an 80-accession subset of the Tuxpeño maize race complex. The number of accessions per cluster is given in parentheses. The accessions representing each cluster are listed.**

### *Chapter 3*

# Teosinte: Geographic Variations and Conservation

*S. Taba*

## Introduction

Teosinte is a wild relative of maize that thrives in wild or cultivated fields by dispersing seed or, in the case of perennial forms, through rhizomes. Teosinte is adapted to mid- and high-elevation regions in Mexico and Central America that are seasonally dry with summer rains (Wilkes 1967). Archeological specimens of teosinte are scarce in Mexico, but the varied local names for the plant suggest a long association between man and teosinte in the maize-oriented cultures of Mesoamerica. Despite this, it is only in the last hundred years or so that teosinte has become widely known to the rest of the world.

Teosinte was first classified as *Euchlaena mexicana,* a botanical grass, by Schrader in 1832, based on a sample of seed sent from Mexico to Germany by a mine engineer. The common name teosinte derives from the Nahuatl[1] *teocintle* associated with the annual population (*Zea luxurians,* race Guatemala) that grows wild in southeastern Guatemala (Wilkes 1967). Seed of this population was sent to France in 1869, whence it was distributed worldwide as a potential fodder crop in the late 19th century. The teosinte later increased in tropical Florida, USA, and distributed widely as "Florida teosinte" was descended from the sample sent to France.

Though the closest relative of maize -- as evidenced by its ability to cross fertilize with that crop -- teosinte is morphologically and genetically distinct from maize. It has solitary female spikelets (compared with paired ones in maize) that are two-ranked (versus many-ranked in maize), a shattering rachis (i.e., the cob breaks into pieces, whereas in maize it does not), and fruitcase-enclosed kernels (maize kernels have no hard covering) (Galinat 1992). Numerous studies on teosinte's taxonomy (Bird 1978; Iltis et al. 1979; Iltis and Doebley 1980; Doebley and Iltis 1980; Doebley 1990ab); cytology (Kato Y. 1984; Kato Y. and Lopez R. 1990; Sanchez G. et al. 1995); genetics (Galinat 1992, 1985, 1988, 1995; Doebley 1984; Beadle 1980; Mangelsdorf 1986; Allen et al. 1989; Kermicle and Allen 1990; Mazzoti and Velasquez 1962); ecology,

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[1] Language of the Aztec Indians.

geography, and taxonomy (Wilkes 1967, 1977, 1986, 1988, 1993; Sanchez G. et al. 1995; Benz 1988; Benz et al. 1990; Orozco and Cervantes S. 1986); as well as molecular analyses (Doebley 1990ab; Smith et al. 1984, 1985; Doebley et al. 1987a, 1987b) and recent reviews (Goodman 1988; Wilkes 1986; Benz 1987; Iltis 1987; Galinat 1992) have contributed much to knowledge on the possible role of teosinte in the domestication and evolution of maize and on the natural diversity of teosinte.

Perhaps the most significant use of teosinte to date has been in research on the evolution of maize, but teosinte could also prove a source of traits for improving maize. Allelic variations in isoenzyme loci indicate great diversity within teosinte that is not found in maize. However, except for use in forage crop development,[2] researchers have largely been unable to capitalize on its promise as a genetic resource. Maize and teosinte have many alleles in common, but there are significant differences in allelic frequencies and in some alleles unique to each (Smith et al. 1985). Information that has come to light in recent years on its natural variation and plant characteristics should help researchers use teosinte more effectively as a source of genetic diversity to improve maize.

## Geographic Distribution

A general map of teosinte distribution was published by Wellhausen et al. (1952). Wilkes (1967) reported in detail on the distribution of annual teosinte in Mexico and Central America. The discovery of the perennial diploid teosinte *Zea diploperennis* in 1978 (Iltis et al. 1979), as well as the rediscovery of the perennial tetraploid teosinte *Zea perennis* by Guzman (1978), spurred much research and additional exploration and collection of teosinte in Mexico. Later Sanchez G. and Ordaz S. (1987) provided new descriptions of teosinte's distribution in Mexico and Sanchez G. et al. (1995) updated that information and characterized Mexican teosinte populations using morpho-agronomic and chromosome knob data. Wilkes (1988, 1993) and CIMMYT (1986) added a report on the status of populations in situ. A new taxonomic classification of teosinte which integrated it and maize in the genera *Zea* was summarized by Doebley (1990ab). For the purposes of conservation and utilization, natural variations in teosinte can be characterized either through descriptions of ecogeographic races of populations in situ (Wilkes 1967) or taxonomic classifications (Doebley 1990ab) (Table 1).

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[2] Around the turn of the century, teosinte was distributed to Europe, Asia, Africa, and the Caribbean Islands as well as to Australia and the United States as a potential fodder crop.

Collections of teosinte populations have been made at more than 100 sites in Mexico by genetic resource experts of the Mexican National Institute of Forestry, Agriculture, and Livestock Research (INIFAP) and other collaborators in Mexico. Sanchez G. (personal communication) estimates that 20% more uncollected populations might exist in Mexico. New teosinte sites have been discovered by scientists acting on information from local agronomists who had sighted what they thought to be teosinte. Figure 1 depicts the geographic distribution of races of teosinte as identified in Table 1. Teosinte in Honduras is considered extinct in the wild (Wilkes 1967). A teosinte collection of *Zea luxurians* from Rancho Apacunca, Department of Chinandega, Nicaragua (collection number: Iltis, Medina and Castrillo 30919 from the University of Wisconsin) in 1991 has been increased at CIMMYT. Given its use there as a fodder crop, however, it may have been introduced from southeastern Guatemala to the collection site in recent times, in response to the local need for such a crop.

## Teosinte Races in Mexico and Guatemala

### Race Guatemala

This race has been distributed worldwide as fodder crop. It is known as *teocintle* or *milpa silvestre* and is found in small, isolated populations in broad valleys and hills at 900-1,200 meters above sea level (masl) in the Departments of Jutiapa, Jalapa, and Chiquimula, southeastern Guatemala. Teosinte was encountered at El Progresso (Ranch of Cecilio Hernandez), Jutiapa, and at Mojarritas (Ranch of Carlos Pinto), Monjas, Jalapa, in addition to the vicinity around those sites, during a monitoring visit by staff of the maize germplasm banks of the Guatemalan Institute of Science and Agricultural Technology (ICTA) and CIMMYT, along with Dr. Garrison Wilkes, in 1991. La Laguna Retana, Jutiapa, had been reported to lie in a sea of teosinte in the 1930s, but showed no plant extant during this monitoring visit. Local inhabitants, though, recognized the plant by name and accurately described its morphology. In general, Wilkes (1993) reported a roughly three-quarter reduction in teosinte sites, number of populations, and population sizes from 1962-63 to 1991. Finally, as mentioned above, there is also a Florida collection of race Guatemala.

Race Guatemala has trapezoidal rachis segments (seeds). At higher latitudes it produces abundant tillers, which parallels the tillering pattern in *Tripsacum* (Wilkes 1988). Male tassel branches are few (1-10), and extend from the short central branching axis; they are stiff, straight, and erect, and the central spike has the same morphology as the lateral branches (Doebley and Iltis 1980; Wilkes 1967). The large terminal chromosome knobs are more numerous than for any other teosinte and bespeak a distant relation to the annual Mexican teosintes (Kato Y. 1976, 1984; Kato Y. and

Lopez R. 1990; Smith et al. 1984). Race Guatemala requires an artificially shortened daylength to flower in temperate environments.

**Race Huehuetenango**

This race grows at 500-1,650 masl in northwestern Guatemala, bordering on Mexico, where it is known as *salic* or *milpa de rayo*. The 1991 monitoring expedition visited Santa Ana Huista, Buxhap, San Antonio Huista, and Jacaltenango, sites where teosinte populations had been previously reported, and observed teosinte at all except San Antonio Huista. Again, teosinte is no longer as abundant as it once was in the region. Wilkes (1993) reported population sizes that were only about 10% of those observed in 1963.

Huehuetenango teosinte flowers from December to January, making it the latest-maturing wild teosinte. Rachis segments are curvo-triangular, with a broad-to-blunt apex. It has a tassel morphology typical of the section *Zea*, with many lax, lateral branches. The central spike is somewhat stiffer and stronger than that in section *Zea* and more densely-set with spikelets than lateral spikes (Wilkes 1967; Doebley and Iltis 1980). The chromosome knob pattern is similar to that of *Zea diploperennis;* the presence of many terminal knobs (Kato Y. and Lopez R. 1990) seems to indicate a close relationship with races of the section *Luxuriantes*. The isozyme diversity of Huehuetenango is intermediate between *Zea* and *Luxuriantes*. However, tassel morphology, data on cytoplasmic cpDNA, and plant and seed morphology support its placement in the phylogenetic/taxonomic section *Zea* as ssp. *huehuetenangensis* (Doebley 1990ab).

**Race Balsas and its Variations**

This race grows in the seasonally dry, thorn-scrub vegetation of the mountains of the Balsas River basin, south-central Mexico. Balsas teosinte is known as *maíz de pajaro* or *maíz de huiscatote* in the Balsas area and *atzitzinte* in the Chilpancingo area of Guerrero State. The habitat is larger and more xeric than other collection areas, with varied altitude and latitude.

Its rachis segments are curvo-triangular, with a blunt apex. The seed is smaller than that of any other race. The tassel morphology is typical of section *Zea*, with many lateral branches, including tertiary branches, and a small central branch. The Balsas race hybridizes less with maize in the field than do other teosinte races and exhibits sub-racial variations from collection site to collection site. Between 17 and 18° N at 500-1,200 masl in the states of Guerrero, Michoacán, and Mexico, teosinte populations are characterized by very late maturity, slow seedling growth, narrow and shorter leaves, very small seeds, increased tassel ramification with a shorter central spike, and tillering when grown in the state of Mexico. The variation in this sub-race is represented by collections from Mazatlán, a site south of Chilpancingo in central Guerrero State (Wilkes 1967, 1977; Sanchez G. et al. 1995; Orozco and Cervantes S. 1986; Iltis 1987; Doebley 1984). Collections from Mazatlán possess a trait, resulting from farming practices in the area, which allows its seed to lie dormant for as long as a year (Wilkes 1977). A few collections from sites at 19° N in Jalisco State are also classified in the same group.

Another distinct group comes from elevations of 1,200-1,700 masl within 18-19° N in the states of Guerrero, Oaxaca (at the recently collected site of San Cristobal Honduras), Mexico, and Michoacán, bordering the Rio Balsas basin. Teloloapán, Arcelia, Huetamo, and Valle de Bravo are the representative sites for this central Balsas teosinte. According to Sanchez G. et al. (1995), it differs slightly in maturity and plant type from teosinte of central Guerrero, and also differs clearly from race Central Plateau. Another ecotype separated from the above two groups in Jalisco has earlier maturity, relatively large seed, and some tolerance to leaf rust (*Puccinia sorghi* Schw.). Still other Balsas-type teosintes grow in Nayarit State at 20° N and about 900 masl and at Amatlán, near Tepoztlán, Morelos.

Morpho-agronomic and chromosome knob variations (Sanchez G. et al. 1995; Orozco and Servantes S. 1986) seem to coincide largely with isozyme variations (Doebley et al. 1984; Smith et al. 1985) within race Balsas. Balsas teosinte, especially accessions from Valle de Bravo, state of Mexico, and central Michoacán, has the greatest similarity to maize of any teosinte. Doebley (1990ab) suggested *Zea may* ssp. *parviglumis* should be divided into races Jalisco, Central Balsas, and Central Guerrero, based on numerical analysis of isozyme variations. However, much more variation appears to exist even within these subdivisions (Razo L. 1989; Sanchez G. et al. 1995; Orozco and Cervantes S. 1986). Maize chloroplast DNA patterns were similar to those of Balsas and Huehuetenango teosinte (Timothy et al. 1979; Doebley et al. 1987b; Doebley 1990ab). Good compatibility between race Balsas and maize has been reported (Kermicle and Allen 1990; Goodman et al. 1983) and Iltis (1987) and Doebley (1990b) have even suggested that maize was domesticated in the Balsas basin.

**Race Central Plateau**

Collection sites range from around 1,700 to 2,150 masl in the states of Michoacán, Guanajuato, and Jalisco. The common name is *maíz de coyote* in Michoacán and Guanajuato. The southernmost sites are in Michoacan at 19° N, extending to 20° N in Guanajuato. One population is located at 21° N, 1,950 masl in Jalisco (Sanchez G. et al. 1995). Populations of Opopeo at 2,320 masl and Ciudad Hidalgo at 2,040 masl in Michoacán are considered very similar to race Chalco, based on cluster analysis using morpho-agronomic traits (Sanchez G. et al. 1995) -- despite the fact that these collection sites are in the general distribution area of race Central Plateau. In the same study, chromosome knob frequencies used for the cluster analysis separated race Central Plateau very well from the other races studied. The population of Degollado, Jalisco, 1,650 masl, was classified as race Balsas by Sanchez G. and Ordaz S. (1987), but isozymic and morphological analyses (Doebley et al. 1984) suggest that it belongs to race Central Plateau. Modern agriculture is apparently taking its toll on the distribution of Central Plateau teosinte. Teosinte was disappearing at Copandaro, Michoacán, in 1993.

The seed of this race is triangular and large; in some cases, as large as that of race Chalco. The tassel is rather robust and open with lesser branches, a non-prominent central spike, and no tertiaries. The plant is green, dilute sun red or sun red, and has a wider leaf than race Balsas. It has early maturity and moderate resistance to leaf rust. One of its two forms is adapted to cultivated maize fields (weedy form) and the other is found on limestone outcroppings along the field margins (wild form). Both plant and seed of the weedy form are larger than those of the wild form, when grown together in a uniform field, and closer to race Chalco in plant and seed type (Wilkes 1967, 1977).

### Race Durango

This race is closely associated with race Central Plateau in many characteristics. Locally known as *maicillo*, it has fewer leaves, more pronounced tillers, smaller seeds, and much fewer lateral tassel branches than Central Plateau. It is found at 24° N, 1,900-1,950 masl, in the valley of Guadiana some 8-20 km east and northeast of Durango city. There are three known sites from which collections were made along a river bank and irrigation canals: Francisco Villa, Puente Dalila-Hacienda de Dolores, and Puente Gavilan (Sanchez G. et al. 1995). First sighted early this century, Durango teosinte subsequently remained hidden from the view of teosinte hunters until fairly recently, and was recognized as a separate race after its rediscovery (CIMMYT 1986, Sanchez R. et al. 1995). It is vulnerable to loss from local agricultural practices such as maize and sorghum farming, and could disappear at any time. Nonetheless, it has been able to hold its own under similar conditions for the last fifty years (Wilkes, personal communication).

### Race Chalco

Known by the local name of *acece* in Chalco, valley of Mexico, this race also grows in Toluca, state of Mexico, (Wilkes and Taba 1993) and at Ciudad Serdán, in the San Juan Atenco municipality, and Tlachichuca, in the San Salvador El Seco municipality, both of Puebla State (Sanchez G., personal communication). It is normally found as a weed in maize fields and alongside roads and field margins at 2,200 to 2,800 masl. Chalco mimics maize in cultivated fields, often exhibiting a sun-red color and hairy leaf sheath similar to those of adjacent maize plants. Thus, although farmers consider them weeds, they cannot easily single them out for weeding prior to flowering. Like maize production in the area, Chalco teosinte is seriously affected by the rapid expansion of nearby Mexico City (Listman 1994).

Together with the weedy form of race Central Plateau, Chalco teosinte has the largest seeds of the teosinte races. They are triangular and enclosed in rachis-segments, thus endosperm color and texture are not visible. The latter characteristics vary in Chalco between hard and soft, white and yellow endosperms, aleurone colorless or sometimes colored, and brown or brownish pericarps. The tassel has a prominent central spike. Chalco is resistant to leaf rust (Wilkes 1967; Doebley 1984; Sanchez G. et al. 1995). It has a cross incompatibility factor which functions like Ga1-s from popcorn against normal dent maize with ga1, designated as Ga1-s:Chalco, and which has stronger expression in heterozygotes than Ga1-s (Kermicle and Allen 1990). This factor possibly acts as an isolating mechanism between maize and teosinte; even so, $F_1$ hybrids are frequent (Wilkes, personal communication).

### Race Nobogame

This is the northernmost site for teosinte in Mexico. Nobogame is adapted to a valley in the Sierra Madre Occidental at 26° N, 1,750-1,920 masl. It is earlier maturing than any other teosinte. Seeds are intermediate-to-small but larger than those of race Balsas, and curvo-triangular with a sharp apex. The tassel has a few, short lateral branches that are widely spaced on main axis, with a central spike and tassel glumes as large as those of races Central Plateau and Chalco (Wilkes 1967; Iltis and Doebley 1980; Sanchez G. et al 1995). Race Nobogame crosses freely with dent maize (Kermicle and Allen 1990).

### Perennial Teosintes

There are two forms: a tetraploid (*Zea perennis;* 2n = 40) and a diploid (*Zea diploperennis;* 2n = 20) which has the same number of chromosomes as the annual teosintes described above. Both perennial teosintes are late maturing with slow seedling growth, wide and short leaves, large tassel glumes very much like those of race Guatemala, and tolerance to leaf rust (Sanchez et al. 1995). As classified in the section *Luxuriantes,* both forms have trapezoidal seeds but differ from annual teosintes of race Guatemala in having rhizomes. According to Doebley and Iltis (1980), *Z. diploperennis* has a robust plant type and rhizomes with internodes shorter than *Z. perennis,* often forming tuber-like short shoots. *Z. perennis* plants are more slender. Norton et al. (1985) reported that *Zea diploperennis* supported the fewest *Pratylenchus scribner* and *Helicotylenchus pseudorosbustus* nematodes in field tests among teosinte and maize geneotypes. The tetraploid was first reported early this century at Ciudad Guzmán, Jalisco (Collin

1921), and was rediscovered by Guzmán in 1978 at Los Depósitos (1,650 masl) and at Piedra Ancha (2,100 masl) in Ciudad Guzmán on the northern slope of the Nevado de Colima at 19 °N, Jalisco. Z. *diploperennis* was first discovered at the east end of the Sierra de Manantlán, Jalisco, at La Ventana, head of the San Miguel valley, 19 °31' N, 2,250 masl, and subsequently at Las Joyas (1,800 masl) and Manantlán, 1,350 masl (Iltis et al. 1979). Population San Miguel is grown in rotation with maize for use as a forage crop. Population Las Joyas grows in an area where slash-and-burn farming is practiced and grazing occurs. Teosinte was apparently introduced at the Manantlán sites in recent times (Benz et al. 1990). The Sierra de Manantlán Biosphere Reserve was created in 1987 for in-situ conservation of perennial teosinte and other endemic species (Sanchez-Velasquez 1991). Isozymic variations (Doebley et al. 1984; Doebley 1990ab) and chloroplast cpDNA restriction site analysis (Doebley 1990ab) differentiated diploid and tetraploid perennial teosintes in a hierarchical classification system, although Z. *perennis* is considered an autotetraploid derived from Z. *diploperennis* (Galinat and Pasupuleti 1982).

Eubanks (1995) has obtained fertile hybrid plants with paired kernel rows from crosses between *Tripsacum dactyloides* and Z. *diploperennis*, and suggests that such a cross may have played a role in the origin and evolution of maize.

## Conservation and Utilization

Staff of the INIFAP maize germplasm bank, Mexico, have been active in collecting and preserving teosinte (Sanchez G. and Ordaz 1987). In the mid-1980s, CIMMYT, INIFAP, and ICTA began coordinating efforts to monitor teosinte populations in situ (CIMMYT 1986; Wilkes 1993; Sanchez G. et al. 1995). Monitoring visits have been made in recent times to the following sites:

- The regions of Jutiapa, Jalapa, and Huehuetenango[3]
- Central Guerrero, central Balsas, and San Cristobal Honduras in San Pedro Juchatengo Province, Oaxaca
- Uriangato-Moroleón in southern Guanajuato and Copandaro-Penjamillo-Cuitzeo in north central Michoacán
- Francisco Villa and Puente Gavilán in the valley of Guadiana, in Durango
- Guadalupe y Calvo, Nabogame, in Chihuahua
- Chalco, Los Reyes, and Texcoco in the valley of Mexico
- Toluca in the valley of Toluca

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[3] These locations are in Guatemala; the rest are in Mexico.

Monitoring trips serve to 1) collect a representative sampling with sufficient seed for both preservation and utilization, and 2) determine the current status of the population. Future monitoring trips in Mexico will cover additional sites in the states of Jalisco, Puebla, where a new collection was recently made (Sanchez G. personal communication), and Chiapas, where a teosinte population is reported to exist near Villa Flores in the Freylesca region. Most teosintes except Balsas are considered "vulnerable," according to the terms of the Species Survival Commission of the International Union for Conservation of Nature and Natural Resources (IUCN) in Switzerland (Wilkes 1988, CIMMYT 1986). Grazing often affects populations of races Guatemala, Huehuetenango, part of Balsas and Central Plateau, and Nobogame. The races Nobogame and Durango are considered rare, as they are scarce enough that they can be eliminated easily. However, with recent collections in Toluca, state of Mexico, and in Puebla State, race Chalco can be considered stable, despite such cases as the Chalco population at Los Reyes that survives in a single field on the urban outskirts of Mexico City (Listman 1994). Monitoring trips have confirmed no immediate threat of extinction for other populations, despite occasionally significant reductions in their size (races Guatemala and Huehuetenango, for example, have shrunk to 25% and 10% of their size in 1963 and are considered endangered). However, in-situ monitoring should be intensified, with the possibility of organizing in-situ conservation of the endangered Guatemalan populations (Wilkes 1993). Races Central Plateau and Durango are in modern agricultural regions where land use and cropping patterns will greatly affect their survival.

It is problematic for maize germplasm banks to conduct regular seed increase programs for teosinte, given its ability to contaminate experimental plots of maize and to outcross with maize or other teosinte accessions. Seed increase must be done in isolation, using open pollination among more than 100 plants, if possible. Each year a few accessions are regenerated at CIMMYT in isolation from experimental maize plots. Ideally, a permanent seed increase plot for teosinte managed by germplasm bank personnel is needed. The CIMMYT Maize Germplasm Bank preserves samples collected in the 1960s and some recently collected during the monitoring trips, but needs additional samples from currently known locations in Mexico and Guatemala. Teosinte accessions are preserved in medium- and long-term storage, once seed has been cleaned and dried to RH 23-25%.

Teosinte has been used as a fodder crop and for studies on maize evolution. Teosinte has so far been of little use for maize improvement or hybrid development (Goodman 1988). However, results of experiments using teosinte germplasm to increase yield in maize hybrid combinations were encouraging (Cohen and Galinat 1984). Viral resistances were reported in perennial teosintes (Nault et al. 1982), but their use in maize improvement has been limited, because maize lines were found that confer similar resistance (Louie et al. 1990). Some teosinte races show cross incompatibility with normal maize genotypes, making it difficult to introgress their germplasm into maize. *Zea diploperennis* seems to have a barrier to fertilization with maize (Sanchez G., personal communication). On the other hand, such races as Balsas and Nobogame cross quite easily with maize. Maize races Camelia Vicuña and Arrocillo Amarillo were cross-compatible with Guerrero teosinte (Castro G. 1970). Kermicle and Allen (1990) reported that race Central Plateau has a dominant barrier complex on chromosome 4 different from the incompatibility factor in race Chalco. In the same study, races Nobogame (*Zea mays* ssp *mexicana*) and Balsas (*Zea may* ssp *parviglumis*) accepted pollen from dent maize and set seeds, but *Zea luxurians* only partially set seeds and ssp *huehuetenangensis* was incompatible through the first backcross generation. Allen et al. (1989) developed cytolines having different teosinte cytoplasm and the maize genome of inbred W23. They found a teosinte-cytoplasm-associated miniature trait (TCM) expressed by section *Luxuriantes* and which is countervailed by a dominant nuclear gene, denoted Rcm1 (rectifier), present in many maize inbreds. Balsas teosinte may have the greatest genetic diversity of any teosinte, making it a logical candidate for use in introgressive hybridization with maize. Teosinte may contribute to maize improvement in the future in the same manner as maize landraces have: by increasing genetic diversity in the crop.

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**Table 1: Taxonomy of *Zea*.**

| Wilkes (1967) revised | Iltis and Doebley (1980); Doebley (1990ab) revised |
|---|---|
| **Section *Euchlaena*** (Schrader) Kuntze | **Section *Luxuriantes*** Doebley and Iltis |
| - | *Zea diploperennis* Iltis, Doebley and Guzman |
| *Zea perennis* (Hitchc.) Reeves and Mangelsdorf | *Zea perennis* (Hitchc.) Reeves and Mangelsdorf |
| *Zea mexicana* (Schrader) Kuntze | *Zea luxurians* (Durieu) Bird |
| Race Guatemala | |
| | **Section *Zea*** |
| | *Zea mays* L. ssp. *mexicana* (Schrader) Iltis |
| Race Chalco | Race Chalco |
| Race Central Plateau | Race Central Plateau |
| Race Nobogame | Race Nobogame |
| Race Durango* | Race Durango* |
| Race Balsas | ssp. *parviglumis* Iltis and Doebley |
| | Within race variations** |
| Race Huehuetenango | ssp. *huehuetenangensis* (Iltis and Doebley) Doebley |
| **Section *Zea*** | |
| *Zea mays* L. | ssp. *mays (L.)Iltis* |

* Race Durango was included previously in race Central Plateau (Wilkes 1967). After recollection of the population it was recognized as race Durango (CIMMYT 1986; Sanchez G.et al. 1995).

** Within-race variations have been shown in race Balsas (Doebley 1990ab; Razo L. 1989; Sanchez G. et al. 1995) to form possible ecogeographic races or groups (see the text below).

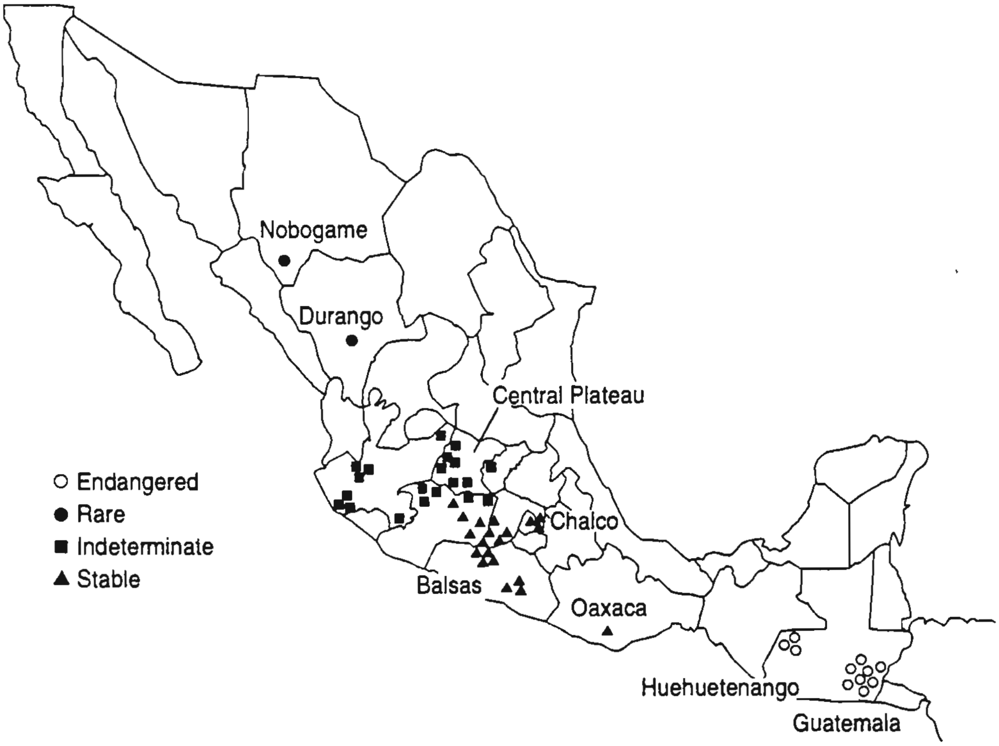

**Figure 1. Current status of teosinte populations in Mexico and Guatemala.**

### *Chapter 4*

# *Tripsacum:*
# Diversity and Conservation

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Although they are very different morphologically, the genus *Tripsacum* (L.) L. is genetically related to the genus *Zea* L., and hybrids have been produced from crosses between plants of the two (Mangelsdorf and Reeves, 1931; Harlan and de Wet, 1977; Leblanc et al. 1995). Maize can be recovered from maize x *Tripsacum* hybrids through a series of backcrosses, suggesting the feasibility of gene exchange between the two genera. Galinat (1977) showed that introgression between maize and *Tripsacum* is possible. Still, attempts to use *Tripsacum* as a genetic resource for maize breeding remain limited, both because of the difficulties involved and because there is sufficient diversity in maize for most traits of interest. The efficiency of transferring genes from *Tripsacum* to maize could be enhanced by a better understanding of what can be transferred and made to express in maize. A team of ORSTOM researchers at CIMMYT is well along in a project to transfer apomixis (vegetative propagation through seeds) from *Tripsacum* to maize.

*Tripsacum* species are widely distributed in America and most numerous in Mexico (de Wet et al 1983; personal observations in herbaria). Mexico and Guatemala are the center of diversity for the genus. During 1989-92, we conducted a detailed survey of *Tripsacum* populations in Mexico, taking extensive samples to establish a living collection that would represent an important part of the genus' diversity. We then performed careful morphological studies on this field genebank.

The taxonomy in this chapter is based on Cutler and Anderson (1941), Randolph (1970), and de Wet et al. (1976, 1981, 1982, 1983) (Table 1). We will use the following species names and corresponding abbreviations.

TAD = *T. andersonii* Gray
TAA = *T. australe* var *australe* Cutler and Anderson
TAH = *T. australe* var *hirsutum* de Wet and Timothy

TBV = *T. bravum* Gray
TCD = *T. cundinamarce* de Wet and Timothy
TDD = *T. dactyloides* (L. ) L.
TDH = *T. dactyloides* var. *hispidum*(Hitchc. ) de Wet and Harlan
TDM = *T. dactyloides* var. *mexicanum* de Wet and Harlan
TMR = *T. dactyloides* var. *meridionale* de Wet and Timothy
TFL = *T. floridanum* Porter ex Vasey
TIT = *T. intermedium* de Wet and Harlan
TJL = *T. jalapense* de Wet and Brink
TLC = *T. lanceolatum* Ruprecht ex Fournier
TLT = *T. latifolium* Hitchc.
TLX = *T. laxum* Nash
TMZ = *T. maizar* Hernandez and Randolph
TMN = *T. manisuroides* de Wet and Harlan
TPR = *T. peruvianum* de Wet and Timothy
TPL = *T. pilosum* Scribner and Merrill
TZP = *T. zopilotense* Hernandez and Randolph

## Taxonomy

*Tripsacum* plants are perennial. *Tripsacum* and *Zea* belong to the subtribe Tripsacinae of the Andropogonae of the Poaceae family. Male and female spikelets of *Tripsacum* are born on different parts of the same inflorescence (monoecy). Male spikelets are found in pairs. The grain is enclosed in a cupulate fruit case formed from a rachis internode and the outer glume. Two sections, *Tripsacum* and *Fasciculata,* are distinguished, the main distinctive traits being the presence (*Fasciculata)* or absence *(Tripsacum)* of a pedicel on a male spikelet of the pair. This trait correlates with the stiffness of the inflorescences and the number of branches in the inflorescence.

The basic chromosome number is x = 18, whereas in *Zea* x = 10. Several ploidy levels have been observed in this genus and we discovered ploidy levels not reported in the literature (Table 1).

## Key Factors for Determining Species

It is sometimes difficult to place a given sample of *Tripsacum* under a species name, because variation for many characters does not allow a clear-cut determination. A key for species from Mexico was developed based on observations of materials in our field genebank. The values proposed for the number of racemes on a terminal (RAC1) and secondary inflorescences (RAC2) are the average of observed values. Actual determination of species should allow for variation around these values.

- *TBV.* Vegetative traits: basal sheaths in a fan-like position; strong brace roots; pilosity on basal sheaths (mostly on mid-rib). Inflorescences: RAC1 = 4, RAC2 = 3; flowering mostly synchronous on terminal and secondary inflorescences; erect or slightly bended rachis; sessile paired spikelets.
- *TDH.* Vegetative traits: basal sheaths with variable pilosity, often hairs near the ligule; sheaths not fan-like. Inflorescences: RAC1 = 3, RAC2 = 1; infrequent ramifications on secondary inflorescences; erect rachis; sessile paired spikelets.
- *TDM.* Vegetative traits: strong stems; basal sheaths pilose to glabrous; sheaths not fan-like. Inflorescences: RAC1 = 12, RAC2 = 5; rachis erect to pendulous, often bent; one spikelet sessile, the other sessile or on a short pedicel.
- *TIT.* Vegetative traits: almost no hairs on basal sheaths; intense tillering, sometime from the main stems. Inflorescences: RAC1 = 4, RAC2 = 2; erect, becoming pendulous over the flowering period; one sessile and one shortly-pedicellate spikelet.
- *TJL.* Vegetative traits: almost no hairs on basal sheaths; high stems. Inflorescences: RAC1 = 8, RAC2 = 3; pendulous; long male glumes; one sessile and one shortly-pedicellate spikelet.
- *TLC.* Vegetative traits: basal sheaths with hairs; leaves very often blue. Inflorescences: RAC1 = 6, RAC2 = 3; erect to pendulous; paired spikelets, often one sessile and one pedicellate.
- *TLT.* Vegetative traits: strong decumbent stems of indeterminate growth; no hairs on basal sheaths; not all stems produce inflorescences during flowering. Inflorescences: RAC1 = RAC2 = 4; erect rachis for the diploid form and almost pendulous for the triploid; short, purple male glumes; sessile spikelets for the diploid form and sessile and pedicellate paired spikelets for the triploid.
- *TLX and TMZ.* Vegetative traits: basal sheaths with long stinging hairs; a few strong stems per plant; large leaves. Inflorescences: RAC1 = 27, RAC2 = 13; pendulous.
- *TMN.* Vegetative traits: comparable to TIT, no hairs on sheaths, small plant. Inflorescences: RAC1 = RAC2 = 1; sessile paired spikelets.
- *TPL.* Vegetative traits: basal sheaths with long, non-stinging hairs, also often hairs on terminal sheaths. Inflorescences: RAC1 = 15, RAC2 = 8; bent-to-pendulous; short-to-long pedicel of spikelet.
- *TZP.* Vegetative traits: Small plant, glabrous basal sheaths, very thin stems. Flexuous leaves, curly and reddish-brown when old. Inflorescences: RAC1 = RAC2 = 1. Erect inflorescences, sessile paired spikelets.

No key is proposed for the South American species, as the morphological variation is minimal, at least for the samples established in our field genebank.

## Ecogeographic Distribution

In South America, *Tripsacum* species have been collected at 250 to 650 meters above sea level (masl) for TAA and TAH, 500 to 1,700 masl for TMR, and 600 to 1400 masl for TCD. *Tripsacum* in Central America is found from sea level to 2,600 masl. TDH is found from 100 to 2,600 masl, and the TDH population at the highest elevation is a diploid.

The general distribution of *Tripsacum* species appears to be structured more in relation to climate than to altitude. TLX (and TMZ) and TLT are clearly adapted to the humid tropics. It is also difficult to find any relationship between altitude and ploidy level. For example, near Tuxtla Gutierrez, Chiapas, in southeast Mexico, at altitudes ranging from 750 to 1,200 masl, it is possible to find TIT (tetraploid and pentaploid), TJL (tetraploid), TLX (diploid), and TMN (diploid). In the northern state of Sinaloa, Mexico, diploid, triploid and tetraploid forms of TPL grow together in the same population or as neighboring populations. This lack of relationship between altitude and ploidy level could be best explained by the existence of polyploid series in most *Tripsacum* species.

*Tripsacum* species extend from longitude 42 °N to 24 °S. The published information on general distribution is not always accurate. TBV was first described as endemic in Valle de Bravo, state of Mexico (de Wet et al. 1976), but in fact is as widespread as TDH. By the same token, TZP was reported as coming from Cañón del Zopilote, Guerrero, and other parts of Mexico (Randolph, 1970), but is actually limited to the Cañón; the specimens reported from other locations, though resembling this species, belong to TDH. Finally, TLT was reported from only Belize, Guatemala, Costa Rica, and Honduras (de Wet et al. 1982; Pohl 1980), but we collected samples from wild diploid and triploid TLT populations in Mexico.

The various *Tripsacum* species in Mexico can be placed in three groups based on distribution, although these groups do not present clearcut boundaries:

1. *Northwestern group.* This group comprises various forms of TLC found in the Durango region and Sierra Madre Occidental. TLC has been encountered in these mountains and in the USA in the state of Arizona. All plants checked for chromosome number are tetraploid (2n=72).

2. *Southern group.* This includes TIT, TJL, TLT, TLX, TMZ, and TMN. According to de Wet et al. (1982), TJL, TLT and TLX are found in Guatemala. There are also specimens of TLT in Belize and Honduras. This group covers not only southern Mexico from Guerrero to Oaxaca, Veracruz, and Chiapas, but also Central America. It involves species with ploidy levels from diploid to pentaploid. However TMN and TLX have only diploid specimens; TLT, diploid and triploid.
3. *Central group.* This group includes TBV, TDM, TPL, TZP and some forms of TLX, TMZ. These species are found from Jalisco to Guerrero, Michoacán, and Mexico states. One species (TDH, related to the TDD found in the eastern USA) extends to the northeast through the Sierra Madre Oriental. The group is very diverse, comprising species such as TZP, which are endemic in specific locations, and broadly distributed species, such as TBV and TDH. Except for TDM, species of this group exhibit a range of ploidy levels (see description of polyploid series, below).

These groups were formed using the geographical origins of *Tripsacum*, but also illustrate the history of *Tripsacum* species. Species from the southern group would be more related to the South American group, which are diploid, with the exception of TPR (de Wet et al. 1981). South American species are distributed from Venezuela to the South of Brazil. Samples in the CIMMYT collection come from Venezuela, Columbia and Peru.

## Cytology and Reproduction

### Polyploid series

Considering each species/ploidy/population combination as a unit, in the CIMMYT collection 16.6% of the plants are diploid, 8% are triploid, 71.5% tetraploid, and 3.8% are pentaploid and hexaploid. Most *Tripsacum* species exhibit a polyploid series (Table 1) from diploid to tetraploid and in some cases pentaploid and hexaploid. The series do not exhibit drastic morphological variations, suggesting that polyploidization is occuring within the species and not only through interspecific hybridization between a diploid and a polyploid species. Our observations and those of Leblanc et al. (1995) found that polyploid plants from 48 populations tested were apomictic. *Tripsacum* is then a genus with the same reproductive organization as other agamic complexes: diploid plants reproduce sexually while polyploids rely on apomixis.

### Origin of triploid plants and natural hybridization

Observations on triploids have shown these plants to be apomictic, and male and female fertile (Moreno 1994). They could act as genetic bridges between diploid and tetraploid forms. Analyses of diversity using molecular markers (Barre et al., unpublished data) showed geneflow across species and ploidy levels to be quite free.

Apomixis has occasionally been described as an evolutionary dead-end. From analyses of *Tripsacum*, though, it can be considered as favoring hybridization and geneflow, through the fixation and propagation of hybrid forms.

### Origin of *T. andersonii*

*Tripsacum andersonii*, guatemala grass, has 64 chromosomes (Levings et al. 1976). As of this writing, the species is thought to be the result of a hybridization event between *Zea* (10 chr) and *Tripsacum* (54 chr = 3x). Based on morphological similarities between the two species, de Wet et al. (1983) proposed *T. latifolium* (2n = 36) as the putative *Tripsacum* parent. Studies by Talbert et al. (1990) have shown that the *Zea* genome is from *Zea luxurians* and the *Tripsacum* genome is not *T. latifolium* (2x), but could be *T. maizar* or *T. laxum*. By analysing at CIMMYT the diversity of the material surveyed in Mexico, two types were found in Mexican *T. latifolium* accessions, both with the same gross morphology but one diploid (as is normal in the species) with paired sessile spikelets, and the other triploid with paired spikelets, one sessile and one shortly-pedicellate. We therefore propose that the triploid *T. latifolium* is a hybrid between a diploid *T. latifolium* and another *Tripsacum* species of the *Fasciculata* section (to explain the pedicellate spikelets). Results of molecular marker analysis at CIMMYT suggest that TLT (3x) originated in the hybridization event:

*T. latifolium* (2x) x *T. maizar* (2x) => *T. latifolium* (3x = 54chr), with an unreduced gamete from one of the parents.

A second hybridization event led to the creation of *T. andersonii*:

*T. latifolium* (3x = 54) x *Zea luxurians* (2n = 20) => *T. andersonii* (54 + 10 chr)

The first event must have occurred several times, as fingerprinting (isozymes) indicates that the two triploid *T. latifolium* populations are different. The second event was probably unique, as the more than 20 different accessions of *T. andersonii* from several South American countries show exactly the same morphology, isozyme pattern, and DNA fingerprint. *T. andersonii* is the only example of a natural *Zea* x *Tripsacum* hybrid.

### Genetic structure of wild populations

RFLP fingerprinting shows that polyploid plants are vegetatively propagated by apomixis in wild populations, but that apomixis does not limit genotypic diversity (Table 2). Still, some clones are represented by more plants than others. Populations comprising several species and ploidy levels have been found in the wild, but many have few (10-100) plants representing only a few clones.

## Conservation and Utilization

### In situ conservation

Despite its widespread distribution in the Americas, *Tripsacum* is not a very common plant. Populations of various size exist, but their colonizing ability is inferior to that of plants such as *Panicum maximum*. Our surveys in Mexico have shown that *Tripsacum* species are also widely distributed, and we have located more than 150 different populations. Some plants have been transferred to the field bank, but these populations continue to exist *in situ*, permitting normal geneflow and the processes that led to the current natural diversity. *Tripsacum* populations are very sensitive to grazing. Land tenure modifications that change cattle raising practices could endanger certain populations, but *Tripsacum* species should at most be considered vulnerable, not endangered.

### Ex situ conservation

During 1989-92, we collected samples from 158 *Tripsacum* populations in Mexico, the center of diversity for this genus. We obtained 2,500 accessions as cuttings, some 1,000 of which have been established in a field collection on the CIMMYT experiment station at Tlaltizapán, state of Morelos, Mexico (940 m, 18 °N latitude).

In the case of *Tripsacum*, it appears necessary to establish a living collection in an environment (in this case, subtropical) appropriate for most of the species to be preserved. Studying genotypic diversity through RFLP fingerprinting and ploidy levels through chromosome counts allowed us to identify duplicate accessions. We verified the fact that, in wild populations of *Tripsacum*, apomictic plants are always polyploid, an important step toward propagating the collection through seeds, both for conservation and distribution.

### Propagation and exchanges

One option is vegetative propagation (cuttings), which was the method used to establish our base collection. However, the disadavantages of using cuttings for distribution are well known, so we would consider apomictic propagation a feasible alternative; especially since apomixis exists in most populations of our base collection.

Diploid plants do not exhibit apomixis; thus, all diploid plants are different from one another, being reproduced through recombination and open pollination (a fact confirmed by molecular marker studies). Depending on the pollen sources, seed from diploid plants may be diploid or triploid, and distribution of germplasm identical to that collected is only possible through vegetative propagation or time-consuming controlled pollinations within populations. If some genetic variation is permissible, then seeds constitute a viable means of distribution, but progenies must be checked to cull morphological and cytological off-types.

For *Tripsacum,* the most common off-types are produced as 2n+n seedlings (i.e., an unreduced female gamete fertilized by a normal male gamete). This "ploidy building" mechanism was observed in most progenies from the live collection and also in progenies from seeds collected directly in the wild. Observed frequencies of these off-types vary from 3 to 35%, depending on the genotypes.

Before conserving seeds as accessions, one should assess their viability through germination tests. It should also be noted, though, that dormancy is a common phenomenon in *Tripsacum* seeds. We eliminated the dormancy problem through embryo rescue and culture on an N6 medium. The process is as follows:

1. Carefully remove the seed from the fruit case, using pliers. It is essential to avoid any damage to the seed, as this could cause abnormal germination and deformation in the plant.
2. Sterilize the seeds with commercial chlorine bleach (6% active Cl) at 1:4 dilution for 1 h using a magnetic stirrer.
3. Rinse the seeds several times with sterile water under aseptic conditions.
4. Place the disinfected seeds in vials with sterile water. After 2-3 d, they can be germinated. Germinate the seeds in tubes (16 x 100 mm) with 4-5 ml of culture medium (N6), embryo-up. Seeds are kept in the dark at 27-30°C until germination. Place the seedlings under light when the coleoptiles reach 3-4 cm.
5. The seedlings should remain in tubes for 7-10 d, until they are 3-to-4-leaf plantlets. Uncap the tubes then and fill them with water. Transplant the plantlets to soil 5-7 d later.

To summerize, a vegetatively established, living collection of *Tripsacum* is necessary, along with analyses of its genotypic diversity and seed production, before a seed collection can be kept for long-term storage. Apomixis is mostly obligate in our

*Tripsacum* populations. A high percentage of plants are identical to the mother plant but off-types are produced. Seeds are a good vehicle for distributing germplasm. However, their use introduces some variation that can be controlled by chromosome counts (to detect 2n+n seeds) and isozyme checks (only if it matters to detect the true sexual seeds, n+n).

**Direct utilisation**

*T. dactyloides* is cultivated in some places in the USA and forms part of forage breeding programs at the USDA research station, Woodward, Oklahoma, and at Iowa State University. *T. andersonii* is also used as a forage plant. The spread of this crop is related to its use as a fodder for Guinea pigs by indigenous people in South America (Hernandez X. 1970). As a large collection of wild *Tripsacum* populations is now available, it may be worthwhile to find new opportunities for *Tripsacum* as a forage crop in the tropics.

**Gene transfer to maize**

The introgression route has been reviewed by Harlan and de Wet (1977). A transfer program for apomixis is currently underway at CIMMYT, applying new molecular tools. In addition to the potential benefits for farmers in developing countries, the transfer of apomixis from *Tripsacum* to maize constitutes an interesting case study that show the way for tranferring other useful genes. As one example, scientists at the International Institute of Tropical Agriculture (IITA; D. Berner, personal communication) and the University of Bristol, U.K., (A. Lane, personal communication) have identified *Tripsacum* plants that possess resistance to *Striga hermonthica*, a parasitic flowering plant which causes significant economic damage to maize in sub-Saharan Africa and to which no known source of resistance exists in maize.

## Conclusion

Interest in *Tripsacum* as a genetic resource has been limited, outside certain academic circles. Now that we have at our disposal a comprehensive field genebank of *Tripsacum* and tools for efficient gene transfer, it is the right time for more research on unique traits available in *Tripsacum* and for large-scale gene transfer projects.

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**Table 1. Distribution of ploidy levels in *Tripsacum* species collected from wild populations in Mexico, 1989-92.**

| Species or hybrids | # pop | # pop with | # pop with | # pop with | # pop with |
|---|---|---|---|---|---|
| | | 2x | 3x | 4x | 5-6x |
| BV | 36 | 1 | 1[a] | 35 | |
| BVLC | 2 | | | 2 | |
| DH | 32 | 4[a] | 1[a] | 29 | 2[a] |
| DHBV | 2 | | | 2 | |
| DHIT | 8 | | | 8 | |
| DM | 20 | | 1[a] | 20 | 2[a] |
| DMBV | 2 | | | 2 | |
| DMLT | 1 | | | 1 | |
| DMPL | 2 | | | 2 | |
| IT | 13 | | 2[a] | 10 | 2[a] |
| JL | 2 | | | 2 | |
| LC | 9 | | | 9 | |
| LCPL | 1 | | | 1 | |
| LT | 9 | 7 | 2[a] | 0[b] | |
| LX | 4 | 4 | | | |
| MN | 1 | 1 | | | |
| MZ | 13 | 5 | 4[a] | 5 | |
| MZPL | 2 | | | 2 | |
| PL | 10 | 4[a] | 3[a] | 5 | 1[a] |
| ZP | 5 | 5 | 1[a] | 1[a] | |
| **Total** | **174** | **31** | **15** | **136** | **7** |
| % | | 16.4[c] | 7.9 | 72 | 3.7 |

[a] New ploidy levels compared with literature.

[b] Ploidy level found in Randolph (1970), but the specimen had mistakenly been described as atypical *T. latifolium*.

[c] Percentages are taken from the total population/species/ploidy combinations. In some populations there are several ploidy levels and sum of % greater than 100.

**Table 2. Distribution of *Tripsacum* genotypes in the wild population "La Toma".**

| Species and types | Number of chromosomes | Number of plants | Species and types | Number of chromosomes | Number of plants |
|---|---|---|---|---|---|
| BV1 | 72 | 33 | DM12 | 54 | 1 |
| BV2 | 72 | 3 | DM13 | 54 | 2 |
| DM1 | 72 | 4 | DM14 | 72 | 1 |
| DM2 | 72 | 2 | DM15 | 72 | 1 |
| DM3 | 72 | 2 | DM16 | 72 | 1 |
| DM4 | 72 | 27 | DM17 | 54 | 1 |
| DM5 | 54 | 5 | DM18 | 54 | 1 |
| DM6 | 90 | 1 | DM19 | 54 | 1 |
| DM7 | 108 | 1 | DM20 | 72 | 1 |
| DM8 | 72 | 1 | DM21 | 72 | 1 |
| DM9 | 72 | 1 | DM22 | 72 | 1 |
| DM10 | 72 | 1 | DM23 | 72 | 1 |

## *Chapter 5*

# Transferring Apomixis from *Tripsacum* to Maize: Progress and Challenges

*Y. Savidan, D. Grimanelli, and O. Leblanc*

Cooperative *Tripsacum* Project, the French National Research Institute for Development Cooperation (ORSTOM) and CIMMYT

As described in the previous chapter, the first phase of the ORSTOM-CIMMYT *Tripsacum* Project (1989-94) centered on collecting and studying *Tripsacum* diversity in Mexico. A series of collection trips led to the establishment of ca. 1,200 accessions, representing 158 populations, on CIMMYT's experiment station at Tlaltizapán, Morelos. Cytological, morphological and biochemical analyses were carried out, with detailed analyses on a few of the more polymorphic populations. Among other things, this work will result in several publications on the *Tripsacum* taxonomy and the structure of diversity in the overall collection, as well as a core collection (ca. 150 accessions) to be kept at Tlaltizapán.

This chapter outlines progress in the second part of the project (1994-97), which focuses on gene transfers from *Tripsacum* to maize, with emphasis on apomixis. The presentation will be divided in four parts:

- Understanding apomixis
- Transferring apomixis via wide crosses
- Molecular mapping and tagging of apomixis
- Perspectives

## Understanding Apomixis

Our ability to manipulate apomixis through a series of backcrosses or biotechnology depends on our understanding of the developmental and genetic systems involved. Before we started, diplospory -- apomictic development from a reproductive cell which fails to undergo meiosis -- was thought the most difficult type to work with, due to difficulties in detecting this kind of apomixis. Embryological analyses by Leblanc and Savidan (1994) and Leblanc et al. (1995a) show that, far from being difficult to detect, diplospory presents at least two major advantages over apospory (the type of apomixis in which the maternal progeny originate from a somatic nucellar cell instead of the reproductive cell):

1. Diplospory directly affects meiosis, meaning that it can be detected through clearing using interference-contrast microscopy at early developmental stages: diplosporous meiocytes and young (2-nucleate) embryo-sacs are easily characterized morphologically. The tetrad stage of meiosis, quite long in sexual individuals, is omitted, allowing screening at this stage as well.
2. Reproductive cells are surrounded by callose until the tetrad degeneration stage, whereas diplosporous meiocytes are not, making it easy to detect diplospory using sucrose clearing and aniline fluorescence.

Like aposporous grasses, diplosporous *Tripsacum* shows precocious development of embryo sacs. The desynchronisation between the development of organs such as the pistils and integuments on one hand, and the ovule and the megagametophyte on the other, may be the cause of the failure of both meiosis and fertilization. In *Arabidopsis,* the sin1 mutant illustrates the requirement for coordinated development of the ovule and the gametophyte: late development of integuments is associated with an aberrant meiosis and the absence of tetrads. In the ovm3 mutant, integument formation is aberrant and gametophyte development is arrested during meiosis. Apomixis genes in aposporous and diplosporous grasses are likely to be of the same family of mutants, which regulate these interactions between gametophyte, ovule, and pistil. Both fertilization and meiosis depend on coordinated growth and development in these tissues. It is likely as well that the failure of fertilization in apomicts results from discharge of the pollen tube after the embryo sac has passed the stage of maturity and receptivity.

## Transferring Apomixis via Wide Crosses

Widecrosses are characterized by sterility in early hybrid generations. The problem is complicated when the target trait is one like apomixis, which affects reproduction (Fig. 1). Male-sterile F1s and BC1s have to be used as females, but since we select them for apomixis, the progeny of the backcross is predominantly maternal, the rate of useful off-types being about the same as in the parental *Tripsacum* (2-3%). This rate decreases sharply at the BC3 (Table 1).

Genetic structure in the BC4 appears unbalanced: a full haploid set of *Tripsacum* chromosomes (n=18) is far less deleterious for the hybrid than the uncomplete set. Only

0.4% of these off-types reach the seedling stage (when DNA content can be evaluated using flow-cytometry) and most produce weak and highly sterile plants. For the most part, only BC4s with as few as one-to-three alien chromosomes can be grown to full maturity, these plants being largely maize-like. To sidestep these problems, we have adopted two approaches:

- To increase the BC3 population and develop our capacity to screen larger numbers of progenies. An estimated 20,000 progenies will have been screened by late 1995.
- To start alternative procedures using molecular tools.

## Molecular Mapping and Tagging of Apomixis

Three alternative methods to the widecross transfer are being tested by the different labs working on apomixis. The first one relates to mapping, the second to transposon tagging, and the third to differential screening of cDNA libraries.

### Mapping apomixis in *Tripsacum*

Using addition forms with an average six *Tripsacum* chromosomes from a sexual 2n=38=20M+18Tr) BC2 hybrid, we have identified RFLPs specific to each of the *Tripsacum* chromosomes. Eleven markers have been found for the *Tripsacum* chromosome carrying the apomixis control, four through a bulk segregant analysis (Leblanc et al., 1995b). The closest is at 15cM from the apomixis gene. These four markers are mapped on the long arm of maize chromosome 6 (Fig. 2). In addition, although they are distributed in the same order (with differences in distance) on the maize and the diploid *Tripsacum* maps, they appear totally linked in apomictic plants. This absence of recombination shows the limits of classical genetic analyses of apomixis: simple segregations between apomictic and sexual hybrids can result from one dominant gene as well as from a cluster of genes on a chromosome sector where recombination is prevented.

Work continues to locate seven additional markers which belong to maize chromosome 3. Loci on long arm of chromosomes 6 and 3 are duplicated on chromosome 8. Thus markers mapped on this chromosome also have to be tested before undertaking the fine mapping of the *Tripsacum* segment involved in apomixis control. The identification of markers specific to this chromosome will allow us to identify potentially apomictic BC4s before flowering. So far a handful have been tested, with only one showing the chromosome; but the plant turned out to be 2n=32 and was sterile.

### Transposon tagging of apomixis

Linkage desequilibrium, such as that observed in apomictic materials for four RFLP markers, suggests that apomixis may be controlled by a cluster of genes. Elucidating the nature of genetic control -- i.e. one dominant gene vs. a cluster of genes -- may be possible using transposon tagging. Maize lines have been introduced from the University of California-Berkeley (courtesy of Dr. Michael Freeling), which are rich in mutator elements (Mu) and mutator activators. Assuming Mu-elements can move from maize chromosomes to insert on *Tripsacum* chromosomes, our plan is to introduce such Mu-elements in our BC3 hybrids and search for Mu-insertions on the apomixis gene(s). If apomixis is controlled by one major gene, the insertion should result in a reversion towards sexuality (Fig. 3), whereas if apomixis is controlled by a cluster of genes, insertion on one of the genes involved would produce off-types but not sexual plants. An experiment has been designed which uses apomictic 2n=28 BC2s. Crosses are being made, and the first results should be obtained in 1996. The transposon experiment on maize-*Tripsacum* BC3 hybrid derivatives also has the advantage of not contaminating neighbouring maize fields, since the BC3 plants are 100% male-sterile.

The third approach, differential screening of cDNA libraries, is being discussed with Texas A&M University, where such an approach is being used on apomictic and sexual *Cenchrus ciliaris* (buffelgrass). It may be started at CIMMYT during the coming year (see below).

### Perspectives

In 1995 the Leverhulme Trust (London, UK) gave the project a two-year grant for a post-doctoral position and support staff salaries. This will allow the addition of a molecular biologist/geneticist to the group to focus on alternative approaches such as transposon tagging and differential screening. At the same time, an additional effort will be put on the "conventional" widecross approach, through the screening of more progenies using flow-cytometry and RFLPs.

The ORSTOM-CIMMYT agreement ends in mid-1997. Continuation of the current project towards gene isolation and plant (e.g. rice) transformation is being discussed with other laboratories that possess extensive experience in the techniques required. Apomictic hybrid rice is one priority of the International Rice Research Institute (IRRI). Since there is no apomictic relative to cultivated rice, introduction of apomixis in this crop will only be possible once apomixis genes have been isolated from an unrelated apomictic material. The status of apomixis projects elsewhere and the specific advantages of maize suggest this is likely to be achieved from the maize-*Tripsacum* hybrids generated at CIMMYT.

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**Table 1. Progeny analyses at the BC1 and BC3 levels.**

| Progeny | Maternal | Off-types | | | Total |
|---|---|---|---|---|---|
| of | 2n+0 | 2n+n | **n+n** | others | screened |
| BC1s | 5,006 | 1,024 | **218** | 152 | 6,400 |
| BC3s | 7,787 | 728 | **37** | 58 | 8,610 |

**Step 1:** maize (2n=20M) x apomictic *Tripsacum* dactyloides (2n=72Tr)
F1s: 2n=46=10M+36Tr
segregate 1:1 for mode of reproduction (31APO:30SEX)

**Step 2:** apomictic F1 (2n=46) x maize (20M)
BC1s: 2n=56=20M+36Tr
all apomictic

**Step 3:** apomictic BC1 (2n=56) x maize (20M)
apomictic BC2s: 2n=28=10M+18Tr
polyhaploids of BC1s

**Step 4:** apomictic BC2s (2n=28) x maize (20M)
BC3s: 2n=38=20M+18Tr
all apomictic

**Step 5:** apomictic BC3s (2n=38) x maize (20M)
BC4s: 2n=21-34=20M+1-14Tr
production and screening in progress

**Figure 1. Pathway of apomixis transfer, as of July 1995.**

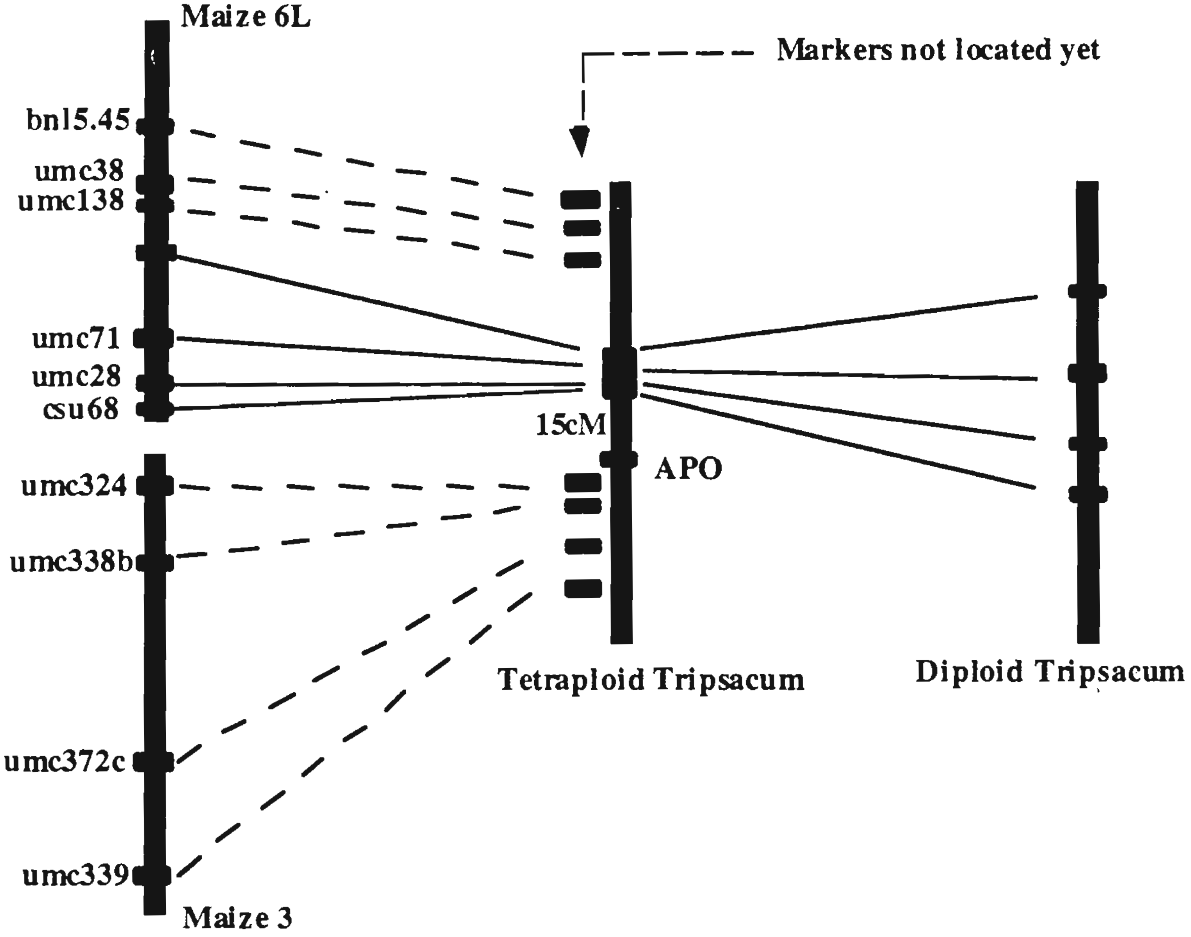

Figure 2. Current status of apomixis mapping.

**Hypotheses:**

1. APO is one dominant gene

———APO——— is apomictic ———APO-Mu——— is sexual

2. APO is a cluster of genes

——ABCDEF—— is apomictic ——ABMuCDEF—— is aberrant

**Experiment design:**

**Step 1:** apomictic BC2s (2n=28) x maize Mu-lines (20M-Mu)
15% BC3s: 2n=38=10M+10M-Mu+18Tr
all apomictic

**Step 2:** multiplication (through apomictic seeds) of BC3s

**Step 3:** screening of 10-40,000 BC3s
Progeny-testing on one-plant progenies (flow-cytometry):
(a) the plant is 38 (maternal): apomixis not affected
(b) the plant is 20+ (off-type):
    b.1. a second seedling is 38: apomixis not affected
        (the 20+ belongs to the 0.4% of BC4 off-types)
    b.2. a second seedling is also 20+: Mu-insertion on APO
        (confirmation on the one gene hypothesis)
(c) the plant has a different chromsome number and second and third seedling show the same: cluster broken (confirmation of the cluster hypothesis)

**Figure 3. Transposon experiment on maize-*Tripsacum* hybrids.**

### *Chapter 6*

# Regenerating Latin American Maize Landraces: Progress in the USAID/USDA-NSSL Collaborative Project

*S. Taba*

## Background

As of late 1991, 14 national seed banks in Latin America and the Caribbean have been cooperating to regenerate endangered holdings of maize landraces in their collections. Coordinated by CIMMYT and financed by USAID and the US National Seed Storage Laboratory (NSSL-USDA), the rescue effort has restored seed of more than 3,000 endangered accessions and partially regenerated nearly 3,000 more.

The project was proposed in March, 1991, when leaders of the region's banks gathered at CIMMYT to assess maize germplasm conservation in the Americas. They concluded that thousands of landrace accessions were in immediate need of regeneration and that many collections, some unique, had already been lost, mainly as a result of the region's chronic economic instability.

The seedbank leaders thus drew up a proposal to salvage maize holdings in Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Mexico, Paraguay, Peru, and Venezuela. CIMMYT took the proposal to USAID and a grant document was signed in November, 1991. Each participating bank is planting, harvesting, and processing its own endangered holdings. The banks are keeping the collections they renew. As an added safety net against catastrophic loss, back-up samples are shipped for storage at CIMMYT and NSSL.

In addition to providing back-up seed, participating national banks are sending CIMMYT information obtained during regeneration plantings. The banks have also received copies of CIMMYT's "accession editor" software, for updating with basic information about their accessions and return to the Center, where the data will be compiled and made available to all participants.

### Seed Shipment and Data Compilation: Accessions Regenerated though 1994

Progress during the initial year was slow. In several cases, much time went into finalizing agreements with participants. Nearly all cooperators had performed or begun regenerations by the second year, although few were able to ship seed of the accessions they had regenerated.

During 1993, I visited participating national banks in South America to inspect regeneration plantings and provide advice, where needed. Major problems encountered included poor germination and adaptation, resulting in unsuccessful regeneration (i.e., fewer than the 100 ears were obtained). Researchers in Peru required several planting cycles to regenerate some highland materials. Paraguayan specialists cited poor germination, with some accessions failing to germinate at all. Participants in Cuba reported the loss of some accessions. Cooperators in Chile were unable to regenerate accessions from northern parts of the country, and sent them to Bolivian cooperators for regeneration. Mexican researchers reported difficulties with plant height limiting the number of pollinations.

Discussing these problems, cooperators and I agreed that, barring special cases, they should perform at most two regeneration plantings using the original seed of the accession, rather than continuing plantings until they obtained the originally stipulated minimum of 100 ears (the ideal needed to conserve a sampling of rare alleles in a given gene pool). This decision, which stemmed in part from urgency to regenerate accessions which were loosing viability, encouraged cooperators to plant more accessions at a time. By late 1994, most cooperators had sent seed and data for a number of regenerated accessions to CIMMYT and NSSL (Table 1).

### Mid-term Project Review

Review meetings involving all principal investigators and a technical advisory committee of internationally recognized experts in crop genetic resources were held at CIMMYT in April 1994. An entire day was spent visiting the regeneration field of an experiment station operated by the Mexican National Institute of Forestry, Agriculture, and Livestock Research (INIFAP). The advisory committee praised the work of the project and recommended an unfunded extension. Regeneration was supposed to be completed in September, 1994, for more than 7,000 accessions. However, due to the above problems and the lag between the project's fiscal schedule and southern hemisphere growing seasons, only half the projected growing cycles were planted by that time. Since funds are disbursed for work completed, the review panel recommended that regeneration continue through 1996, drawing on yet unused reserves to plant the remaining cycles. Other major suggestions included:

- Organizing future meetings among cooperators to review progress and strengthen the network.
- Offering short, practical courses on seed handling at CIMMYT for regeneration cooperators.
- Forming core subsets of major race complexes in cooperating banks.

Another review meeting is scheduled for spring, 1996.

## Donation of Seed Dryers

A special amendment in 1993 allocated US$62,000 for seed drying facilities for certain national germplasm banks. A dehumidifier and a walk-in cooler with a thermostat and humidistat were installed at INIFAP, Mexico, and a similar unit was ordered for the germplasm bank of Argentina. Smaller, portable seed dryers were given to the banks of Guatemala, Venezuela, and Colombia. Other cooperating banks (except that of Brazil) have requested new seed drying facilities, and many countries require improved containers and seed vaults.

**Table 1. Seed and data sent to CIMMYT as part of the USAID/USDA-NSSL collaborative project to regenerate Latin American maize landrace accessions, through 1994.**

| Country | No. of accessions shipped | | Data compilation Passport | Regeneration |
|---|---|---|---|---|
| Argentina | 57 | | yes | yes |
| Brazil | 99 | | yes | yes |
| Bolivia | 336 | | yes | yes |
| Chile | 235 | | yes | yes |
| Colombia | 378 | | no | partial |
| Ecuador | 90 | | yes | yes |
| Guatemala | 177 | (due to NSSL) | partial | no |
| Mexico | 1,579 | | yes | partial |
| Peru | 122 | | yes | no |
| Venezuela | 78 | | yes | yes |
| CIMMYT | 1,998 | | yes | partial |
| Total* | 5,149 | | | |

* Includes duplicate shipments, in some cases.