In Situ Conservation of Landraces in Centers of Crop Diversity

Stephen B. Brush*

ABSTRACT

The importance of crop germplasm found in landraces is well established, and a comprehensive international program exists to conserve this resource ex situ in gene banks and botanical gardens. Landraces are still cultivated in regions of crop domestication and diversity. In situ maintenance has been neglected by genetic resource conservation programs in part because of misconceptions about farming systems that produce landraces. This paper presents three cases of on-going maintenance of landraces by farmers who have also adopted high-input technology, including high yielding crop cultivars. These cases are potatoes (Solanum spp.) in the Andes of Peru, maize (Zea mays L.) in southern Mexico, and wheat (Triticum spp.) in western Turkey. These cases suggest that on-farm conservation of landraces can be decoupled from traditional farming practices. Factors that promote in situ conservation are the fragmentation of land holdings. marginal agricultural conditions associated with hill lands and heterogeneous soils, economic isolation, and cultural values and preference for diversity. Landraces are likely to persist in patches and islands of farming systems in regions of crop domestication and diversity, and these patches provide potential sites for conservation programs. In situ conservation may be a valuable complement to ex situ methods because it can preserve the biological and social processes of crop evolution. Research is needed on the biogeography and conservation biology of remaining landrace populations in order to plan in situ conservation.

NETWORK OF INTERNATIONAL CENTERS to conserve A crop genetic resources was organized nearly 25 yr ago (Plucknett et al., 1987). The Consultative Group for International Agriculture Research (CGIAR) system built on earlier efforts in individual countries and was an important achievement and of great value to the primary users of crop genetic resources in private, national, and international crop improvement programs. Nevertheless, a sense of dissatisfaction and ferment on the periphery of the system is found (e.g., Krattiger et al., 1994). The ferment concerns the long-term prospects for conservation and participation by nations and farm groups which originally supplied the germplasm to international gene banks. Ex situ conservation does not maintain evolutionary processes that created crop germplasm (Hamilton, 1994; Harris, 1989). The concentration of stored genetic resources in industrial countries and international centers and the lack of recognition of the contribution of less developed countries and their farmers are politically troublesome to some (Fowler and Mooney, 1990). In situ conservation of crop genetic resources is a means to address these concerns (Altieri and Merrick, 1987; Friis-Hansen, 1994; Jana, 1993; Shands, 1991).

The United Nations Convention on Biological Diver-

Published in Crop Sci. 35:346-354 (1995).

sity defines in situ conservation as "the conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties" (Reid et al., 1993, p. 305).

In situ conservation of landraces means maintenance in farmers' fields and orchards where they originated. In situ conservation is the preferred method for wild species, and it was briefly considered for landraces (e.g., Frankel, 1970) but never implemented in the international crop germplasm system. In situ conservation is now, however, perceived as a possible complement to ex situ conservation for landraces (e.g., IRRI, 1994; Shands, 1991; Swaminathan and Hoon, 1994).

A NEGLECTED CONSERVATION STRATEGY

A primary reason for neglecting in situ conservation was concern over genetic erosion in traditional farming systems (Harlan and Martini, 1936) and the belief that replacement of landraces by modern cultivars is inevitable (Hawkes, 1983). If genetic erosion is novel, inevitable, and inexorable, then the only means of preserving crop germplasm would be in gene banks. Little is known about the actual crop populations in question, and even less about the farming cultures that produce them. With this uncertainty, the safest choice is to assume the worst, that genetic erosion would shortly eliminate landraces.

Frankel (1970) observed that no "steady state" is possible in the population of primitive cultivars because of technological change in the farming systems that once produced them. This observation errs in two ways. First, it suggests that some type of steady state existed before the advent of fertilizers, mechanization, irrigation, pest control, and crop improvement programs. Second, it assumes that landraces are mutually exclusive with new cultivars and fertilizers. Frankel was voicing popular wisdom about agricultural change; he was not expressing conclusions drawn from careful observation of the actual farming systems and crop populations undergoing technological change. Frankel's conclusion that "farms cannot simply be conserved" (1970) laid the foundation for the dismissal of in situ conservation (e.g., Ford-Lloyd and Jackson, 1986).

The idea that some type of steady state has been upset by modern technology is pervasive, but not well supported. Landraces are grown today under low-input as well as high-input agricultural technology, in subsistence-oriented and commercialized economies (e.g., Bellon and Taylor, 1993; Brush et al., 1992, Dennis, 1987). Human communities simply do not achieve a homeostatic or climactic stage. Change, in the form of population growth and technological innovation, occurs at different rates among communities, but it never ceases. Agricul-

Applied Behavioral Sciences, Univ. of California, Davis, CA 95616. Paper originally presented at the Symposium on Global Implications of Germplasm Conservation and Utilization at the 85th Annual Meetings of the American Society of Agronomy, Cincinnati, OH, 8 Nov. 1993. Received 7 Feb. 1994. *Corresponding author (sbbrush@ucdavis.edu).

tural communities everywhere undergo the constant adjustment to new environmental conditions, environmental perturbations, technological innovations, contact with other groups, and demographic change. Agricultural evolution of Europe and North America is fairly well described (Slicher van Bath, 1963; Loomis, 1984), and innovation is accepted as a normal characteristic of these regions' farming systems. Unfortunately, historical data for agricultural evolution are less complete for other parts of the world, especially for regions where crop genetic resources are found; but there is no basis to suggest that a steady state existed there. The flux of genetic, human, biotic, and physical systems and their interaction make a steady state impossible to achieve or maintain. Rather, change in this evolutionary context is continuous, and homeostasis is illusory. An extensive literature review on the human ecology of non-Western societies documents the steady change therein (e.g., Turner and Brush, 1987). Most of the farming systems that provide crop genetic resources are part of agricultural societies where agricultural intensification is thousands of years old and predates European intensification (e.g., Bray, 1986).

Frankel (1970) observed that "modern agriculture is a great leveler," but modern agriculture may be no more powerful than other levelers in the past that have not eradicated local farming cultures and their biological resources. The beginning of crop exploration and research on crop biogeography occurred long after the tremendous biological impact of the European expansion into Africa, Asia, and the Americas. Both the prehistoric and historic records are replete with evidence of continued change at every place and time: demographic change, the rise and fall of states and empires, the invention and diffusion of technology (e.g., Sanders et al., 1979). European expansion into the Americas is known to have triggered human population collapse, the widespread diffusion of exotic crops and animals, and the economic reorganization of society at all levels (Cook, 1981). Certainly, genetic erosion resulted from this expansion, yet the crop evolutionary system of the Americas appears to have been resilient and durable (Gade, 1992). If native American farming cultures maintained local crop cultivars during the catastrophe of European expansion, it is likely that they will maintain them during technological change such as the diffusion of nitrogenous fertilizer. While genetic erosion undoubtedly occurs with the replacement of landraces by modern cultivars, heterogeneity and resilience of farming systems in areas of crop diversity may allow for the maintenance of crop genetic resources, and not as an alternative to agricultural modernization or intensification.

CASE STUDIES

Andean Potato Agriculture

The origin and diversity of potatoes (*Solanum* spp.) in the central Andes are well established (Hawkes, 1990). Several thousand potato morphotypes and four polyploid

groups are grown by Andean farmers. Farms in a single community may have 50 morphotypes representing all four ploidy groups. Andean potatoes are also subject to genetic erosion because improved cultivars have been available since the early 1950s, and these have diffused into virtually every potato growing village and farm (Horton, 1984). Nitrogenous fertilizer, fungicides, nematicides, and insecticides are also widely used by potato farmers throughout the Andean region. Moreover, virtually all households sell some of their potato crop, even if they can be classified as subsistence farmers (Mayer and Glave, 1992). These changes have impressed many seasoned observers of Andean agriculture and led to predictions of genetic erosion of potato genetic resources (Ochoa, 1975).

As an outcrossing species, cultivated potatoes might be expected to be diverse, but diversity within cultivated stocks may be limited by clonal propagation. Introgression of germplasm from wild species into cultivated stocks is possible (Rabinowitz et al., 1990), but cultural practices tend to restrict introgression. The montane environment of the Andes might be expected to promote diversity; yet the customary method of managing potato inventories as populations may diminish the likelihood of adaptation by different clones to specific field conditions. Andean farmers rotate diverse collections of potato landraces among fields and exercise very limited selection of specific clones for distinct fields, soils or microenvironments (Brush, 1992). The rugged environment encourages isolation, but isolation is broken down by exchange among households, villages, and regions. Diversity in the Andean potato crop is partly a function of human selection for environmental fit, but the agronomic advantage of diversity is difficult to ascertain (Brush, 1992; Zimmerer, 1991). Diploids, especially S. phureja and S. stenotomum, are more prominent at the lower altitudes (2000-3000 m). Tetraploids, S. tuberosum subs. andigena, predominate in the mid-altitudes (2000-3900 m). Bitter, frost-resistant species, the triploid S. \times juzepczukii Buk. and the pentaploid S. \times curtilobum Juz. et Buk., are grown above 3900 m (Brush et al., 1981).

Andean potato diversity, however, is greatest within species, especially the andigena group that accounts for as much as 70% of all morphotypes (Hawkes, 1990). Farmer management of the andigena group would seem to minimize specific adaptive fit of single morphotypes to highly local (field) conditions. Farm households in Andean villages practice a system of field rotation in which the entire inventory of potatoes for broad altitudinal zones is moved each year to a different field within the zone (Brush, 1992; Zimmerer, 1991). A few morphotypes are selected, usually because of yield and commercial demand, but these are not assigned to specific fields or microenvironments. Most of the potato diversity is maintained in fields that are purposefully planted with mixed collections of local morphotypes. Diversity is an object of selection for cultural reasons, taste, gifts, and local identity, and for potential future markets (Brush, 1992). Mixed collections of morphotypes are meant primarily for home consumption, although these are also

Table 1. Characteristics of farming systems in Tulumayo and Paucartambo, Peru.

	Tulumayo	Paucartambo	
Average farm size (cultivated area, hectares)	1.63	2.18	
Average number cultivated plots	11.0	11.8	
Intensity index [†]	62.7	55.3	
Fragmentation index [‡]	12.7	8.4	
Household size (persons)	6.4	5.8	
Percent households with off-farm employment	67	26	

† Intensity Index = number cultivated plots/number total plots.

‡ Fragmentation Index = number cultivated plots/cultivated area.

sold at premium prices. New morphotypes make their appearance in the inventories of these mixed collections through exchange between farms and villages and through the results of sexual reproduction. The latter mechanism is discouraged by the frequent rotation of fields, the slow process of seed multiplication, and the fact that many farmers are oblivious to sexually-produced seed (Brush et al., 1981).

The impact of technology adoption on the biological diversity of potatoes kept on small-scale farms was examined in Peru using case studies (Brush et al., 1992; Mayer and Glave, 1992). Due to the lack of baseline and time-series social and biological data, a cross sectional approach was used where factors, such as adoption of high yielding cultivars, can be measured by comparing households and villages. Research was conducted in two valleys in eastern Peru that were environmentally similar, alike in their distance from major markets, and known for potato diversity. The major differences between valleys could be traced to the length of time that improved potatoes had been cultivated, the degree of commercialization, and the inhabitants' ethnicity. The Paucartambo Valley in the Cusco region of southern Peru is the more traditional, with a higher percent of monolingual Quechua speakers, less intensive agriculture, and less frequent off-farm employment (Table 1). The Tulumayo Valley in central Peru is more modern, with more commercial intensive production.

Comparison among Paucartambo farms shows how adopting improved potato cultivars has decreased the diversity of local potatoes. At Paucartambo, a significant decrease in the number of landraces at the farm level occurred as the area in improved cultivars increased (Brush et al., 1992). At Tulumayo, where modern cultivars have been present longer, no significant correlation was found between increased area in improved cultivars and loss of biological diversity (Brush et al., 1992). Ironically, Tulumayo had a higher average number of potato landraces per household, even though improved cultivars had been grown longer and to a greater extent than in Paucartambo (Table 2). The loss of biological diversity from modern cultivar adoption may follow an asymptotic trajectory after an initial period of genetic erosion. This plateau in the loss of diversity is described in Fig. 1. Farmers in Tulumayo have fully adopted improved cultivars, yet they retain local landraces on a small percent (11%) of their land. Landraces are grown mainly for home consumption, and less chemical amendments are applied than to commercial fields of improved varieties (Mayer and Glave, 1992).

Table 2. Potato production systems of Tulumayo and Paucartambo, Peru.

	Tulumayo	Paucartambo
Percent cultivated area in potatoes	54	47
Percent potato area in landraces	11	61
Percent improved cultivar crop sold	80	64
Percent potato landrace crop sold	45	25
Percent farmers using purchased		
inputs on landraces	6	43
Investment/ha in potatoes (US\$)†	1,368	712
Average potato yield (metric tons/	-,	
hectare)†	16.89	8.96
Percent farmers who have planted		0.70
improved cultivars	96	79
Average years using improved		
cultivars	13.9	7.8
Average number landraces per farm	12.8	9.6

† Mayer and Glave, 1992.

Farmers who adopt higher yielding cultivars in both Tulumayo and Paucartambo had several reasons for also cultivating landraces (Brush, 1992; Mayer and Glave, 1992). Landraces are regarded in these regions as superior in flavor. They are believed to store better for home consumption due a higher percent of dry matter. Landraces are prized as gifts and as special payment for exchange labor. Finally, landraces are marketed at higher prices, and landrace mixtures are kept as an inventory for possible multiplication to meet new commercial demand.

An asymptote of genetic erosion in Andean potatoes hypothesized in Fig. 1. This contradicts the genetic erosion hypothesis in two ways. First, the original hypothesis does not suggest that the proportion of acreage devoted to improved cultivars might reach a peak and then plateau. Second, it does not suggest that diversity might be concentrated into a small area and maintained by conscious selection and management. Because farmers who adopt high yielding potato cultivars, other high-input technologies and commercial production strategies also choose to keep local potato landraces, the occurrence of genetic erosion should be reevaluated.

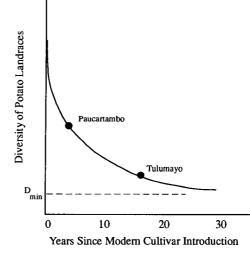


Fig. 1. Hypothesized relationship between adoption of modern cultivars and diversity of landraces on Peruvian potato farms. $D_{min} =$ diversity asymptote following adoption of modern cultivars.

Maize in Southern Mexico

Mexico is the center of origin for several New World crops including maize (Z. mays L.) (Doebley et al., 1985). Numerous races and local landraces of maize are indigenous to Mexico (Wellhausen et al., 1952; Sanchez and Goodman, 1992). Maize's outcrossing breeding system may help conserve genetic diversity. Hybridization with the close wild relative teosinte [Zea mexicana (Schrad) Kuntze] may be another cause of diversity. Mexicos rugged terrain and cultural diversity have tended to define and isolate maize growing regions (Hernández X., 1985). Yet, agricultural development in Mexico may threaten its maize diversity. Mexico has had an ambitious agricultural development program for more than 50 yr. with maize production as a principal target (Austin and Esteva, 1987). Maize improvement has occurred through modern scientific breeding methods and the introduction of short-stature cultivars. State and private seed multiplication and distribution offices are located throughout the country. A broad program of credit, input supply, agricultural extension, and purchasing through a state commodity company complements Mexico's national maize improvement program. Short-stature maize is now widely diffused in areas of commercial maize production (Bellon and Brush, 1994; Winkelmann, 1976). Equally important is the trend of national unification because of increasing urbanization, educational development, economic integration of different regions into a national economy, and the decline of local languages and indigenous cultural groups (Collier et al., 1994). The diffusion of improved maize cultivars, other agricultural technology, and national unification might be expected to cause genetic erosion in maize. The limited use of hybrids and maize's outcrossing tendency might act as buffers against genetic erosion. In a study conducted in the early 1970s, Ortega-Packza (1973) found that maize diversity in the southern state of Chiapas had actually increased over that reported by Wellhausen (1952) and others in the 1940s.

To examine further the dynamics of genetic erosion and in situ conservation, a study was conducted in central Chiapas in 1989 (Bellon, 1990, 1991). Bellon's research focused on the town of Vicente Guerrero in the central region and on farmers who had adopted improved agricultural technology, including improved maize cultivars. Chiapas has three distinct maize growing regions: (i) the Mayan highlands where local landraces predominate. (ii) the central region of the Grijalva River watershed where mixed commercial and subsistence agriculture is practiced, and (iii) the low Pacific coastal plain where improved maize is cultivated. Vicente Guerrero is located in the central region. Farmers there grow 15 different types of maize. Thirteen of these are sown in fields, and two were found only in kitchen gardens. These locally named maize landraces represent six of the maize races occurring in Mexico (Sanchez and Goodman, 1992). Several of the local landraces in Vicente Guerrero are actually a mixture of two races. Some are advanced generations of cultivars introduced several decades ago. but which have now been thoroughly mixed with local

landraces and are managed as landraces (Bellon and Brush, 1994).

Two maize production systems occur in Vicente Guerrero: (i) plow and (ii) slash and burn (hoe) agriculture (Bellon, 1991). Plow agriculture is practiced on the flat bottom land, using tractors or oxen and relying on fertilizer. Sixty-eight percent of the town's total cultivated area is in plow agriculture (Bellon, 1990). The most common maize cultivar here is the high yielding, short stature V-524 known locally as 'Tuxpeño' and planted on 51% of the plowed area (Bellon, 1991). Seed is purchased from the state seed company, but a common practice is to reuse seed until the short-stature characteristic is lost, typically after 3 yr (Bellon, 1991).

Slash and burn agriculture is practiced on the hillsides, which represents 32% of the cultivated area (Bellon, 1990). This system is much more typical of *traditional* Mexican agriculture, with various combinations of intercropping of maize, beans (*Phaseolus* spp.), and squash (*Cucurbita* spp.) on half of the fields (Bellon, 1990). No single maize cultivar predominates in the slash and burn system as V-524 does in plow agriculture. The most common maize cultivar on hillsides is advanced generations of Híbrido Amarillo that are managed as a landrace (Bellon and Brush, 1994).

Farmers in Vicente Guerrero cite six factors as being important in maize cultivar choice: (i) suitability to soil type, (ii) drought tolerance, (iii) wind resistance, (iv) input responsiveness, (v) sensitivity to scheduling of weeding and fertilizer application, and (vi) yield (Bellon and Taylor, 1993). No single cultivar scores high on all five of these factors (Bellon and Taylor, 1993), with the result that most farms plant more than one cultivar, with a mean of three cultivars per farmer. No farmer plants all of the different maize cultivars or races, nor do these occupy equal areas. Data in Fig. 2 show that four cultivars dominate the maize area in Vicente Guerrero: V-524, Híbrido Amarillo, Olotillo, and Olotillo Blanco (Bellon and Brush, 1994). The first is a high yielding cultivar, the second an advanced generation improved cultivar

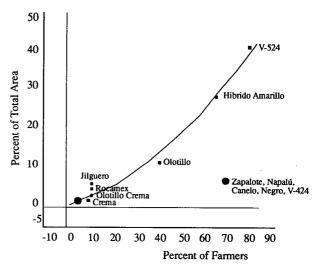


Fig. 2. Relative importance of maize cultivars by area and farmers in Vicente Guerrero, Mexico (Bellon and Brush, 1994).

that is managed as a landrace, and the third and fourth are landraces. These four cultivars account for 82% of the maize area of the town (Bellon, 1990). Seventy-seven percent of the farmers plant the improved cultivar (V-524), 66% planted Híbrido Amarillo, and 35% planted Olotillo (Bellon, 1990). Soil quality, especially pH and percent of organic matter, clay and sand, plays an important role in cultivar choice. The landrace Olotillo is preferred for soils with high pH (7.3) and low organic matter (1.7%) (Bellon and Taylor, 1993).

In contrast to Peru, in situ conservation in Vicente Guerrero is more of a response to agronomic factors than cultural or economic factors. While genetic erosion has probably occurred in areas where improved cultivars have replaced maize landraces in Vicente Guerrero, this threat is mitigated by the fact that landraces are kept for specific agroclimatic conditions (hillsides, hoe agriculture, and problem soils). Genetic erosion may also be lessened by the pattern of managing improved cultivars as landraces and by the hybridization between improved cultivars and landraces. By cultivating landraces and creole cultivars, the farmers of Vicente Guerrero appear to maintain the processes of maize evolution that existed before the advent of nitrogenous fertilizers, mechanization, state marketing and high yielding maize cultivars.

Wheat in Turkey

Unlike potatoes and maize, wheat (Triticum spp.) is self-pollinating, a trait leading to a different pattern of genetic diversity. Seed management of potato and maize cultivars plays a very large role in controlling diversity in those outcrossing crops. While wheat's selfing trait does not limit genetic diversity (Hamrick and Godt, 1990), diversity between populations is possibly more important. Thus, wheat diversity at the farm level is likely to be lower than for potatoes or maize. Zohary and Hopf (1988) observe that self-pollination results in the wheat gene-pool being comprised of a variety of genetically distinct homozygous lines. In contrast to the two crops previously discussed, cultivated wheat is more genetically isolated from its wild and weedy relatives. Nevertheless, the diversity of wheat landraces also appears to be large, as farmers have identified, multiplied and preserved them for millennia in regions of wheat domestication. Assessing the diversity of wheat at different spatial levels is difficult because of the large number of inbred lines from different locations and environments.

Turkey lies within the broad region of domestication of wheat (Zohary and Hopf, 1988). The Turkish Plant Genetic Resources Research Institute maintains a collection of 3216 accessions of cultivated *Triticum* species (IBPGR, 1990). In 1948 to 1949, J. Harlan collected 2128 wheat accessions from each province in Turkey (Harlan, 1950). In 1990, C. Qualset and the author initiated research in Turkey to assess the extent of wheat genetic diversity at the farm, village and regional level and the impact of changing social and agricultural conditions on wheat diversity. Because of the preservation of Harlan's collections, they could be compared with germplasm collected 45 yr later. However, differences in conditions and methods between Harlan's collections and contemporary collections necessitate cross-sectional analysis of contemporary collections and farm data.

Research was conducted in the Western Transitional Zone of Turkey in order to study a farming system that has undergone many of the changes thought to cause genetic erosion. The transitional zone appears to have retained traditional farming methods to a higher degree than the intensively cultivated (irrigated) coastal zone or on the Anatolian plateau (Aresvik, 1975). Research was conducted along a transect in the western Taurus Mountains, in three provinces located between the Aegean and Central Anatolian regions. Surveys were conducted in some villages representative of farming conditions of modern wheat production in central Anatolia, but also where local and more traditional technology predominates. The area studied is within the most economically advantaged part of Turkey. The farm population is fully integrated into the national economy and culture of Turkey. Agricultural development programs have been present for several decades, making extension, credit, subsidized input supply, and state commodity purchasing available to every community in the study region. An important part of these development programs has been providing improved wheat seed through the national seed corporation, so that high vielding, short-stature cultivars of wheat are known among all farmers surveyed.

Turkish wheat scientists estimate that by 1984, about 50% of Turkey's wheat area was planted in high yielding wheat cultivars (Dalrymple, 1986). Even before the advent of the semi-dwarf Mexican cultivars, the Turkish national wheat program had embarked on a program of breeding, selecting high quality farmer cultivars, importing improved cultivars, and seed multiplication, distribution and cleaning. These efforts began as early as the 1930s, soon after the establishment of the Turkish Republic (Aresvik, 1975). In 1989, the national seed multiplication program produced 273 355 t of wheat seed (Turkey, 1989). Within the study region, eight improved cultivars are currently recommended by the Ministry of Agriculture. The national seed company produced 119 630 t of seed of these eight cultivars in 1989 (Turkey, 1989). Farmers throughout the region studied knew about improved wheat cultivars, and at least some farmers in all study sites had cultivated the new wheat cultivars. In a survey of 280 farms, we found improved cultivars on 160.

The study area includes three agroclimatic zones: valley bottom land, hillsides above the valleys, and mountainous regions. The farmers surveyed consider valley bottom land to be superior, especially because it is amenable to irrigation. Mountainous regions are the most marginal. Preliminary analysis of our survey data suggest that in situ conservation of wheat landraces occurs in the Western Transitional Zone of Turkey. Data in Table 3 show the same pattern of partial adoption of high yielding crop cultivars as found in Peru and Mexico, with emphasis on either modern or local cultivars in different subsystems. While high yielding cultivars predominate, local landraces are still cultivated in all three production zones. In Turkey, villages tend to specialize

Table 3. Wheat landrace production in western transitional zone, Turkey.

	Eskisehir	Kutahya	Usak
Percent total area in wheat	72	68	33
Percent wheat area irrigated	56	14	3
Percent wheat area in modern cultivars	85	25	20
Percent wheat area in landraces	15	75	80
Percent modern wheat plots irrigated	61	35	9
Percent wheat landrace plots irrigated	36	7	1
Average number plots per household Average number wheat cultivars per	13	20	8
household	1.8	1.9	1.1

in either high yielding cultivars or landraces. Modern wheat is concentrated on irrigated and valley bottom land, although farmers sometimes grow both modern and local wheat cultivars. In Kutahya province, 30% of the farms reported growing both landraces and improved wheat cultivars. Farmers throughout our study area had tested the high yielding cultivars on their land. Testing was followed by complete adoption in few cases. Agronomic factors, particularly drought tolerance, are critical in choosing wheat cultivars, but farmers also referred to wheat quality as important.

Data in Fig. 3 show the distribution of local and improved wheat cultivars among farms within the study region that planted both types in 1991. While the distribution in Fig. 3 is similar to maize in our Mexican sample (Fig. 2), one cultivar does not dominate in Turkey. The wheat case reports on 24 villages and the maize case on one village. Not only are several distinct landraces found within the study region, but diversity is evident within individual landraces (C. Qualset, 1993, personal communication).

IN SITU CONSERVATION

The three case studies demonstrated that farmers in regions of crop diversity maintain genetic resources while also adopting modern agricultural technology. The notion that in situ conservation of landraces requires preserving primitive agricultural conditions is erroneous, since landraces are kept by *modern* farmers in our study areas. For instance, landraces are grown with purchased inputs (fertilizers and pesticides) and are produced for market.

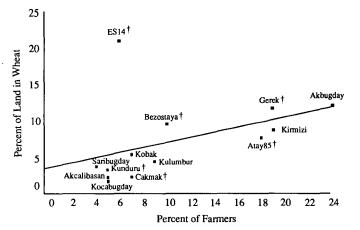


Fig. 3. Relative importance of wheat cultivars by area and farmers in western transitional zone, Turkey (†indicates modern cultivars).

Thus, conservation of traditional germplasm may be decoupled from traditional farming practices. This agrees with the fact that agricultural modernization in less developed countries rarely occurs through the adoption of entire packages of improved technology (Feder et al., 1985). Four factors emerge from these case studies as causes for the practice of in situ conservation of traditional crops. First, fragmentation of land holdings allows farmers to manage several fields and to cultivate landraces in at least one field. Second, marginal agronomic conditions, especially steep slopes and heterogeneous soils of mountain agriculture, make landraces competitive with improved cultivars, at least in that part of the agroecosystem. Third, economic isolation creates market imperfections and lessens the competitive commercial advantage of improved cultivars. Fourth, cultural identity and preference for diversity cause farmers to maintain landraces. These four factors are neither fixed nor immutable, but their appearance in the three different cases suggests their prominence.

Whether in situ conservation is an effective method for long-term preservation of crop germplasm depends on two general issues. First, will farmers continue to maintain local crop populations in the extant field *patches* and *islands*? Or, are these islands merely remnants of earlier systems that will soon fade and disappear? Second, how will the reduction of diverse crop populations to small and fragmented islands affect crop evolution? Like most conservation questions, these cannot be answered definitively, but posing them may facilitate designing a program of in situ conservation.

Much of the evidence for genetic erosion is based on the analogy to the U. S. and northern Europe, where local cultivars were rapidly replaced by improved ones. Environmental, economic, and cultural conditions in regions of crop domestication differ in important ways from the conditions of the USA and northern Europe. The ecological, cultural, and economic heterogeneity of regions of domestication is likely to encourage farmers there to keep landraces for the foreseeable future.

The evolution of crops might be directed toward a particular ideotype, as both natural and conscious selection may favor certain phenotypes in the short term (Donald and Hamblin, 1984; Fischbeck, 1991). Yet, diversity persists because of the heterogeneity of natural and conscious selection. The great amount of genetic diversity that has arisen after the genetic bottleneck of domestication suggests that diversity is as strong as crop ideotype (e.g., Jana and Pietrzak, 1988). Diversity is a product of selection in many different natural and human environments, but it may also reflect a deep-seeded human preference (e.g., Boster, 1985). This preference may give way to technological transformation, as in the U. S. corn belt, but the instances of such transformation may be exceptional and unlikely to be repeated in regions of crop domestication.

The specific nature of the evolutionary process depends, of course, on the crop in question. An outcrossing crop such as maize will be greatly affected by hybridization. Cultural practices and socio-economic conditions are also likely to affect crop evolution. Conscious selec-

tion is likely to be more important where seed and plant are individually managed (maize and potatoes). Conscious selection may be less important where seed is harvested in bulk and broadcast in planting (wheat). Conscious selection is often assumed to emphasize agronomic characteristics (Donald and Hamblin, 1984), although non-agronomic attributes may be equally or more important (Boster, 1985; Brush, 1992). Competition between genotypes may be inversely related to within-field diversity (Donald and Hamblin, 1984), itself a function of seed management and conscious selection. Crop diversity is promoted by physical and economic isolation, dependence on local inputs, production for local consumption rather than for market, and the persistence of local knowledge systems (Friis-Hansen, 1994). Germplasm exchange among farms is predicated on the existence of distinct local crop populations and human knowledge of those populations.

Two modern conditions threaten the processes of crop evolution: (i) human population growth and (ii) spatial integration of production systems. High yielding crop cultivars and fertilizers are responses to increased demand for food, decreasing land area for farming, declining percentage of farmers, and improved means of distribution over larger areas. The ability of population growth and spatial integration to transform farming systems is evident in the rapid diffusion of modern cultivars (e.g., Dalrymple, 1986). Although the forces of population growth and spatial integration are not autonomous, they will probably not abate in the foreseeable future, and the future of crop evolution may be determined by these pressures. But, will these forces so distort crop evolution as to effectively end it?

The case studies of potatoes, maize, and wheat reported herein may shed some light on this question. Population growth and spatial integration unmistakably occur in each of the described farming systems. Moreover, these factors have been present for over a generation. Current population growth in the three regions extends trends that are traceable for over 100 yr. Rural population growth may have stabilized because of urban migration, but overall population growth affects all rural communities. Spatial integration also dates back more than 50 yr in the three regions, and is marked by agrarian reform, rural development programs, road building, education development, and new communication technology. National agricultural research and extension to improve staple crop production has existed in all three regions for nearly 50 yr.

Thus, agriculture in Peru, Mexico, and Turkey has been exposed for several decades to the pressures thought to provoke genetic erosion (Hawkes, 1983). Adoption of new crop cultivars, nitrogenous fertilizer, and increasing commercialization in agriculture have reduced the area of local crop production in all three countries. Indigenous farming cultures have maintained local crop populations, because local conditions are heterogeneous, agricultural research capacity is small, and the means and benefits of acquiring new technology are limited. Agricultural research in these three countries has yielded superior genotypes, but these are adapted to only a portion of the agroecosystems. Landraces are grown in some areas of each country because, according to farmer criteria, they outperform introduced cultivars there. Both local environments and farmer criteria may be too variable for any crop breeding program to overwhelm. Moreover, local crop populations are kept for reasons other than simply yield: cultural and aesthetic preference for diverse crop landraces with local identity may be important.

The case studies in Peru, Mexico, and Turkey suggest that human population increase and spatial integration have had three effects on the cultivation of local crop populations. First, the area devoted to cultivating landraces has been greatly reduced, to as low as 10% of the crop area as in the Tulumayo Valley, Peru. Second, the areas of cultivation of landraces have become fragmented into islands interspersed among larger areas of improved crop cultivars. Third, landraces have disappeared from certain portions of the farming system. Landraces that were adapted to optimal conditions are particularly vulnerable. Farmers keep local landraces in fields that are relatively marginal, and characterized by poorer soils, steeper slopes and higher altitudes. The impact of these three changes on the overall amount of genetic diversity and on evolutionary processes of crops is not known.

Biogeography theory (MacArthur and Wilson, 1967) predicts that a decrease in area and increasing fragmentation of a particular ecosystem should depress its biological diversity. Yet, three features of crop ecology may limit this prediction's utility for crop populations that experience decreased area and fragmentation. First, biogeography theory generally deals with species diversity, whereas crop evolution concerns infraspecific diversity. Second, biogeography theory is not suited for assessing conscious selection and management's effect on diversity. Third, population genetic issues, such as minimum viable population and inbreeding depression, may not be relevant for crops that are self-pollinated or maintained as clones. Menges (1991) finds that many aspects of biogeographic theory, such as genetic stochasticity, demographic stochasticity, and minimum island size, are not particularly pertinent to in situ conservation of wild plants. They are likely to be even less important for cultivated plants. Twenty years after the genetic erosion alarm was raised (Frankel, 1970), neither the extent of genetic erosion nor the efficacy of the existing farmerbased conservation have been measured quantitatively. The conservation biology of crop populations has not yet addressed such issues as minimum viable population, the effect of fragmented crop populations, or the effects of relatively small and isolated crop populations connected by means of exchange. The conservation biology of crops must still resolve such fundamental issues as the desirable level of allele content to be conserved and how population size and distribution affect allele frequency. The sociological rudiments of crop conservation are poorly understood. Nevertheless, the work outlined above suggests that in situ conservation does occur because of the social, economic, and physical heterogeneity of farming systems.

The current status of in situ conservation policy is

best characterized as benign neglect, and this characterization is mirrored in the science of crop conservation. Virtually all public resources for crop conservation are directed to ex situ methods. Although in situ conservation might be acknowledged as possible and perhaps necessary (Jana, 1993; Shands, 1991), there are few efforts to plan or implement in situ conservation. This benign neglect

or implement in situ conservation. This benign neglect approach appears, however, to be changing because of the interest of governments and non-governmental organizations in regions of genetic diversity. The recently formulated United Nations Convention on Biological Diversity (Reid et al., 1993) is strong evidence of the shift of political winds to greater participation in conservation.

Landraces have persisted in situ because of the nature of farming systems in regions of crop domestication, but its future is unknown. It may persist indefinitely or it may succumb to the pressures of population increase and spatial integration. A concerted public and international effort to support in situ conservation might guarantee its persistence. Two questions might be asked as the first step to designing a viable in situ conservation program for landraces: (i) How much genetic diversity is preserved on the portion of farms that is dedicated to landraces, and (ii) what incentives exist for farmers to maintain landraces? An interdisciplinary program of research in biogeography, population biology and social science (ethnobotany and agricultural economics) is needed to answer these questions. This research program is an essential component of any in situ conservation program. In situ conservation seeks to preserve the processes of crop evolution, defined by hybridization within and between populations of wild, weedy and cultivated plants, competition among genotypes, natural and conscious selection at the local level, and exchange of different genotypes among farms (Donald and Hamblin, 1984; Hawkes, 1991; Horovitz and Feldman, 1991; Jana, 1993; Oldfield and Alcorn, 1987).

Support for in situ conservation would help to satisfy the need for broader participation effort by recognizing farmers who have heretofore been overlooked. Support for in situ conservation may be hampered by the fact that this strategy does not directly make crop germplasm available to breeders. Rather than directly providing genes for crop improvement, in situ conservation should be seen as satisfying four other needs. First, it preserves evolutionary processes that generate new germplasm under conditions of natural selection (Hamilton, 1994). Second, in situ conservation will maintain important field laboratories for crop biology and biogeography (Hawkes, 1991; Horovitz and Feldman, 1991). Third, it provides a continuing source of germplasm for ex situ collections. Finally, it provides a means for wider participation in conservation, allowing for a larger role for nations with abundant crop germplasm resources.

Strategies that might be pursued for in situ conservation of landraces include developing markets for landraces, elevating their prestige with agricultural fairs and expositions, encouraging seed savers networks, and undertaking research on the population biology and ecology of landraces (Brush, 1991). A quarter century ago, we embarked on a program to save crop resources in gene banks. Ex situ conservation was given priority and remains valid because pockets of in situ conservation are at risk and relatively inaccessible for use by breeders and geneticists. Nevertheless, in situ maintenance is now being examined more critically as a complementary conservation method. The time is now right to identify key areas and methods whereby both crop resources and evolutionary processes can be preserved. The future of the conservation effort will be more positive when this step is taken.

ACKNOWLEDGMENTS

This research was supported by funds from the National Science Foundation (BNS 8416724, BNS-8815002 and DBS-8923008), USAID grant DPE-10680G-SS-8003, and the University of California, Davis. Fieldwork in Peru was conducted in collaboration with Enrique Mayer and Cesar Fonseca. Edward Taylor at Davis provided Fig. 1. Fieldwork in Mexico was carried out by Mauricio Bellon. Fieldwork in Turkey was carried out in collaboration with Calvin Qualset of UC-Davis and Emin Isikli of the Aegean University in Bornova. Erika Meng provided Fig. 3. M. Brush prepared the final versions of Fig. 1 through 3. I am grateful to Fred Bliss, Calvin Qualset, anonymous reviewers for *Crop Science*, and Ronny Duncan for comments on an earlier draft of this paper.

REFERENCES

- Altieri, M.A., and L.C. Merrick. 1987. In situ conservation of crop genetic resources through maintenance of traditional farming systems. Econ. Bot. 41:86-96.
- Aresvik, O. 1975. The agricultural development of Turkey. Praeger Publ., New York.
- Austin, J.E., and G. Esteva (ed.). 1987. Food policy in Mexico: the search for self-sufficiency. Cornell University Press, Ithaca, NY.
- Bellon, M.R. 1990. The Ethnoecology of maize production under technological change. Unpublished Ph. D. dissertation, Univ. California, Davis. UMI no. 9102056. Univ. Microfilms Internat. Ann Arbor, MI.
- Bellon, M.R. 1991. The ethnoecology of maize variety management: A case study from México. Human Ecol. 19:389-418.
- Bellon, M.R., and S.B. Brush. 1994. Keepers of maize in Chiapas, Mexico. Econ. Bot. 48:196-209.
- Bellon, M.R., and J.E. Taylor. 1993. Farmer soil taxonomy and technology adoption. Econ. Dev. Cult. Change 41:764-786.
- Boster, J.S. 1985. Selection for perceptual distinctiveness: evidence from Aguaruna cultivars. Econ. Bot. 39:310-325.
- Bray, F. 1986. The rice economies of Asia: technology and development in Asian societies. University of California Press, Berkelev.
- Brush, S.B. 1991. A farmer-based approach to conserving crop germplasm. Econ. Bot. 45:153–165.
- Brush, S.B. 1992. Ethnoecology, biodiversity, and modernization in Andean potato agriculture. J. Ethnobiol. 12:161-185.
- Brush, S.B., J.E. Taylor, and M.R. Bellon. 1992. Biological diversity and technology adoption in Andean potato agriculture. J. Dev. Econ. 39:365–387.
- Brush, S.B., H. Carney, and Z. Huanán. 1981. Dynamics of Andean potato agriculture. Econ. Bot. 35:70–88.
- Collier, G.A., D.C. Mountjoy, and R.B. Nigh. 1994. Peasant agriculture and global change. BioScience 44:398–407.
- Cook, N.D. 1981. Demographic collapse, Indian Peru, 1520-1620. Cambridge University Press, New York.
- Dalrymple, D. 1986. Development and spread of high-yielding wheat varieties in developing countries. USAID, Washington, DC.
- Dennis, J.V. 1987. Farmer management of rice variety diversity in northern Thailand. Unpublished Ph.D. dissertation, Cornell University. UMI no. 8725764. Univ. Microfilms Internat., Ann Arbor, MI.
- Doebley, J.F., M.M. Goodman, and C.W. Stuber. 1985. Isozyme

variation in the races of maize from Mexico. Am. J. Bot. 72:629-639.

- Donald, C.M., and J. Hamblin. 1984. The convergent evolution of annual seed crops in agriculture. Adv. Agron. 26:97-143.
- Feder, G., R.E. Just, and D. Zilberman. 1985. Adoption of agricultural innovations in developing countries: a survey. Econ. Dev. Cult. Change 33:255-298.
- Fischbeck, G. 1991. The evolution of cereal crops. p. 31-54. *In* L.G. Firbank et al. (ed.) The Ecology of temperate cereal fields. Blackwell Scientific Publications, Oxford, England.
- Ford-Lloyd, B., and M. Jackson. 1986. Plant genetic resources: an introduction to their conservation and use. Edward Arnold, London.
- Fowler, C., and P. Mooney. 1990. Shattering: food, politics and the loss of genetic diversity. University of Arizona Press, Tucson.
- Frankel, O.H. 1970. Genetic conservation in perspective. p. 469-488. In O.H. Frankel and E. Bennett. (ed.) Genetic resources in plants-their exploration and conservation. IBP Handbook 11. Blackwell Scientific Publishing, Oxford, England.
- Friis-Hansen, E. 1994. Conceptualizing in situ conservation of landraces. p. 263-276. In A.F. Krattiger et al. (ed.) Widening perspectives on biodiversity. IUCN, Gland, Switzerland and Internat. Acad. of the Environ., Geneva.
- Gade, D.W. 1992. Landscape, system and identity in the post-conquest Andes. Ann. Assoc. Am. Geogr. 82:460–477.
- Hamilton, M.B. 1994. Ex situ conservation of wild plant species: time to reassess the genetic assumptions and implications of seed banks. Conserv. Bio. 8:39–49.
- Hamrick, J.L., and M.J. Godt. 1990. Allozyme diversity in plant species. p. 64-82. In A.H.D. Brown et al. (ed.) Plant population genetics, breeding, and genetic resources. Sinauer Associates Inc. Sunderland, MA.
- Harlan, H.V., and M.L. Martini. 1936. Problems and results in barley breeding. p. 303-346. *In* USDA yearbook of agriculture. U.S. Gov. Print. Office, Washington, DC.
- Harlan, J.R. 1950. Collection of crop plants in Turkey, 1948. Agron. J. 42:258-259.
- Harris, D.R. 1989. An evolutionary continuum of people-plant interaction. p. 11-26. *In* D.R. Harris and G.C. Hillman. (ed.) Foraging and farming: The evolution of plant exploration. Unwin-Hyman, London.
- Hawkes, J.G. 1983. The diversity of crop plants. Harvard University Press, Cambridge, MA.
- Hawkes, J.G. 1990. The potato: evolution, biodiversity and genetic resources. Smithsonian Inst. Press, Washington, DC.
- Hawkes, J.G. 1991. International workshop on dynamic *in situ* conservation of wild relatives of major cultivated plants: summary of final discussion and recommendations. Israel J. of Bot. 40:529-536.
- Hernández X., E. 1985. Maize and the greater Southwest. Econ. Bot. 39:416-430.
- Horovitz, A., and M. Feldman. 1991. Evaluation of the wild-wheat study at Ammiad. Israel J. of Bot. 40:501-508.
- Horton, D. 1984. Social scientists in agricultural research: lessons from the Mantaro Valley project, Peru. Internat. Devel. Res. Corp (IDRC), Ottawa.
- IRRI (Internat. Rice Res. Inst.). 1994. Safeguarding and preservation of the biodiversity of the rice genepool. Report of a Discussion Workshop on On-farm Conservation of Crop Genetic Resources. IRRI, Los Baños, Philippines.
- Jana, S. 1993 Utilization of biodiversity from *in situ* reserves, with special reference to wild wheat and barley. p. 311-324. *In* A.B. Damania. (ed.) Biodiversity and wheat improvement. John Wiley & Sons, Chichester, UK.
- Jana, S., and L.N. Pietrzak. 1988. Comparative assessment of genetic diversity in wild and primitive cultivated barley in a center of diversity. Genetics: 119:981-990.

- Krattiger, A.F., J.A. McNeely, W.H. Lesser, K.R. Miller, Y. St. Hill, and R. Senanayake (ed.). 1994. Widening perspectives on biodiversity. IUCN, Gland, Switzerland and Internat. Acad. of the Environ., Geneva.
- Loomis, R.S. 1984. Traditional agriculture in America. Annu. Rev. Ecol. Syst. 15:449-478.
- MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.
- Mayer, E., and M. Glave. 1992. Rentabilidad en la producción campesina de papas. p. 29-214. *In* E. Mayer. (ed.) La chacra de papa: economía y ecología. Centro Peruano de Estudios Sociales, Lima, Peru.
- Menges, E.S. 1991. The application of minimum viable population theory to plants. p. 45–61. *In* D.A. Falk and K.E. Holsinger (ed.) Genetics and conservation of rare plants. Oxford University Press, New York.
- Ochoa, C. 1975. Potato collecting expeditions in Chile, Bolivia and Peru, and the genetic erosion of indigenous cultivars. p. 167-173. In O.H. Frankel and J.G. Hawkes (ed.) Crop genetic resources for today and tomorrow. IBP Vol. 2. Cambridge University Press, Cambridge, England.
- Oldfield, M., and J. Alcorn. 1987. Conservation of traditional agroecosystems. BioScience 37:199-208.
- Ortega-Paczka, R. 1973. Variación en maíz y cambios socioeconómicos en Chiapas, México 1946-1971. Unpublished M.S. Thesis. Colegio de Postgraduados, ENA, Chapingo, México.
- Plucknett, D.L., N.J.H. Smith, J.T. Williams, and N.M. Anishetty. 1987. Gene banks and the world's food. Princeton University Press, Princeton, NJ.
- Rabinowitz, D., C.R. Linder, R. Ortega, D. Begazo, H. Murguia, D.S. Douches, and C.F. Quiros. 1990. High levels of interspecific hybridization between *Solanum Sparsipilum* and *S. Stenotomum* in experimental plots in the Andes. Am. Potato J. 67:73-81.
- Reid, W.V., S. Laird, C. Meyer, R. Gámez, A. Sittenfeld, D. Janzen, M. Gollin, and C. Juma. 1993. Biodiversity prospecting: using resources for sustainable development. World Resources Institute, Washington, DC.
- Sanchez, J.J., and M.M. Goodman. 1992. Relationships among Mexican races of maize. Econ, Bot. 46:72-85.
- Sanders, W.T., J.R. Parsons, and R.S. Santley. 1979. The basin of Mexico: ecological processes in the evolution of a civilization. Academic Press, New York.
- Shands, H.L. 1991. Complementarity of *in-situ* and *ex-situ* germplasm conservation from the standpoint of the future user. Israel J. of Bot. 40:521-528.
- Slicher van Bath, B.H. 1963. The agrarian history of western Europe A. D. 500-1850. Edward Arnold Publishers, LTD, London.
- Swaminathan, M. S., and V. Hoon. 1994. Methodologies for recognizing the role of informal innovation in the conservation and utilization of plant genetic resources. Proceedings 9. Centre for Res. on Sustainable Agric. and Rural Devel. Madras, India.
- Turkey, Republic of. 1989. Bugday ve arpa tohumlugu dagitim sistemi. Tarim Orman ve Koyisleri Bakanligi, Ankara.
- Turner, B.L., II, and S.B. Brush (ed.). 1987. Comparative farming systems. Guilford Press, New York.
- Wellhausen, E., J. Roberts, L.M. Roberts, and E. Hernández X. 1952. Races of maize in México: their origin, characteristics, and distribution. The Bussey Institution, Harvard Univ., Cambridge, MA.
- Winkelmann, D. 1976. The adoption of new maize technology in Plan Puebla, Mexico. Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico City.
- Zimmerer, K.S. 1991. The regional biogeography of native potato cultivars in highland Peru. J. Biogeogr. 18:165-178.
- Zohary, D., and M. Hopf. 1988. Domestication of plants in the old world. Clarendon Press, Oxford, England.