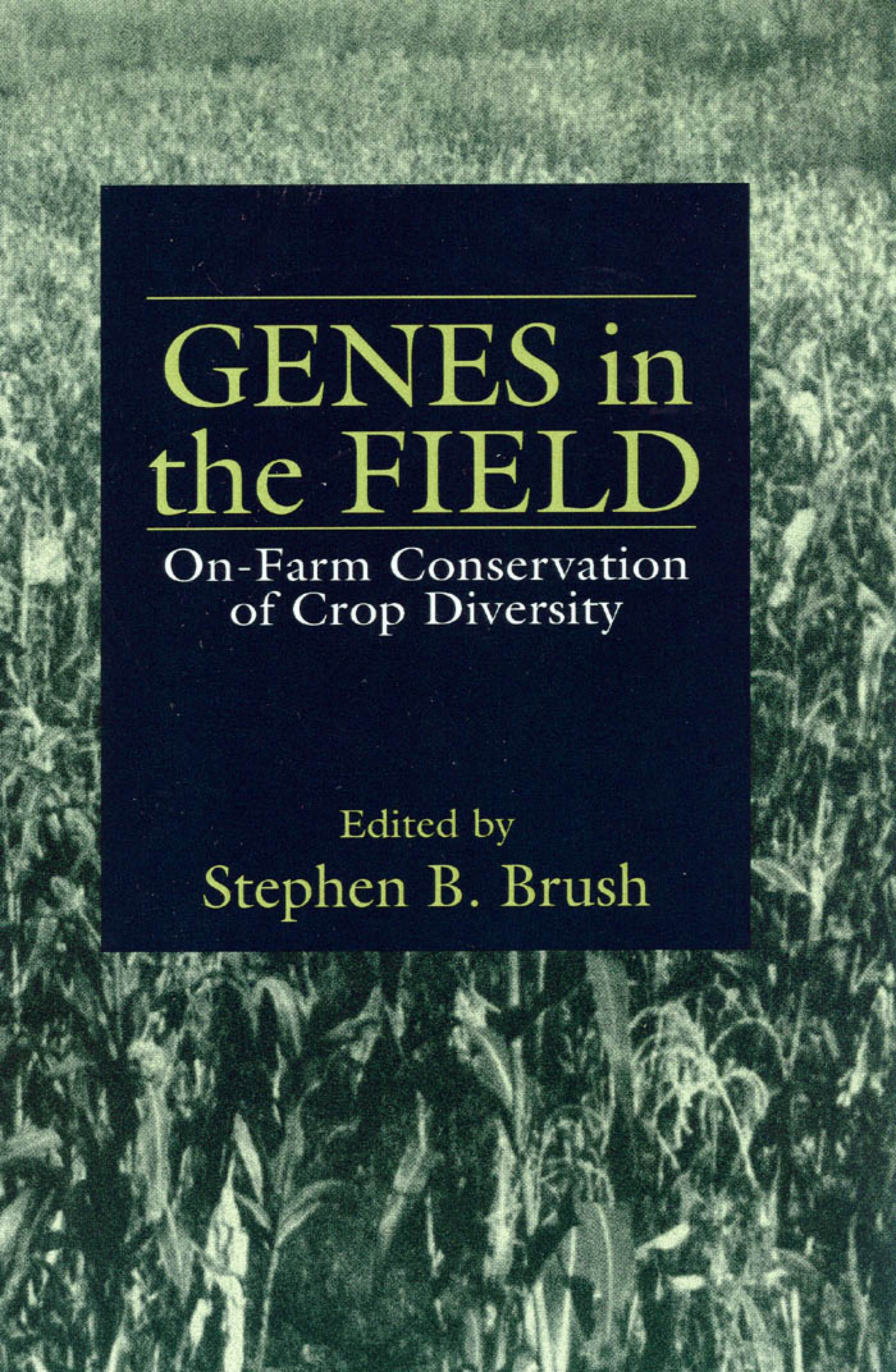

GENES in the FIELD

On-Farm Conservation of Crop Diversity

Edited by
Stephen B. Brush

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Edited by

Stephen B. Brush, Ph.D.

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Traditional management of seed and genetic diversity: what is a landrace?

Dominique Louette

Introduction

Increasing concern about the loss of genetic resources over the past 20 years has led to a heightened concentration on methods for conservation of genetic resources in gene banks (*ex situ* conservation) (Bommer 1991). Conservation of the genetic resources in the agrosystem in which they have evolved (*in situ* conservation) is now being more widely considered as complementary to *ex situ* strategies for conserving genetic diversity (Altieri and Merrick 1987; Cohen et al. 1991; Cooper et al. 1992; FAO 1989; Keystone Centre 1991; Merrick 1990; Montecinos and Altieri 1991; Oldfield and Alcorn 1987). *In situ,* or on-farm, conservation has been proposed essentially for wild relatives of cultivated plants or for plants with recalcitrant seeds. When considered for other cultivated species, this alternative (on-farm conservation) continues to be highly polemic, considered unfeasible from a socioeconomic perspective. The model also raises numerous questions about how policies aimed at fostering economic development relate to those designed to conserve plant genetic resources and whether conservation can coexist with the integration of communities into commercial markets (Cohen et al. 1991; Cooper et al. 1992; Montecinos and Altieri 1991).

Discussions on *in situ* genetic resources conservation generally consider the "biological reserve model" proposed by Iltis (1974). This model is based on the belief that the best means for *in situ* preservation of the diversity found in genetic material is to "freeze" the genetic landscape by isolating it in space and time, maintaining intact the technical, social, and cultural context in which it occurs (Iltis 1974; Benz 1988). Cultivation of local varieties would be encouraged and introduction of foreign cultivars and of new techniques would be discouraged. In this on-farm conservation model, local varieties or landraces are identified as the conservation units. A local variety is well defined in space and as the result of local management. It is also genetically defined as there is concern about geneflow or contamination from other varieties in the case of open-pollinated plants. This chapter adopts a different approach to on-farm conservation. The dynamic nature of agricultural systems precludes "freezing" local varieties into a static system, since local varieties exist as part of a dynamic system that extends beyond a single place.

In the indigenous community of Cuzalapa in western Mexico (within the region of origin for maize), traditional maize variety management is not conducted in accordance with the preconceptions of freezing genetic landscapes or focusing on localness. This study examines the structure of genetic diversity in maize and analyzes the effect of farmers' seed management strategies on this structure. Its objective is to determine what farmers conserve of the varieties they cultivate and to specify the mechanisms responsible for the structure and dynamic of diversity in traditional agroecosystems. Two specific questions are examined in this chapter. First, to what extent can the genetic diversity in the maize varieties of Cuzalapa be attributed to the management of materials of strictly local origin? Second, how well defined, genetically, is a local variety of an open pollinated plant?

Data on seed sources illustrate the important role played by seed acquired from other farmers in and outside of the region relative to seed that local farmers obtain from their own harvests. Analyses of phenotypic and phenological characteristics combined with data on the origin of seed demonstrate the effect of introduced varieties on the diversity of maize cultivated in the Cuzalapa community. The amount of seeds used to reproduce the variety, the management of those seeds in space and time, and the traditional selection of seed call into question the genetic definition of a land race.

The Valley of Cuzalapa and the Sierra de Manantlán Biosphere Reserve

The indigenous community of Cuzalapa is located in a valley in the southern section of the buffer zone of the Sierra de Manantlán Biosphere Reserve (SMBR), in the municipality of Cuautitlán, in the state of Jalisco, on the Pacific Coast of Mexico (Figure 5.1). As the Biosphere Reserve is situated on the Pacific slope of Mexico, most likely one of the zones where the genus *Zea* originated (Benz and Iltis 1992), it is considered an important zone for on-farm conservation of the maize genetic diversity (Jardel 1992). In the reserve and nearby, various species of teosinte, wild relatives of maize (*Zea mays* spp. *parviglumis* Iltis, Doebley; Zea *diploperennis* Iltis, Doebley, Guzman; and *Zea perennis* Hitchc. Reeves, Mangelsdorf) are found growing alongside

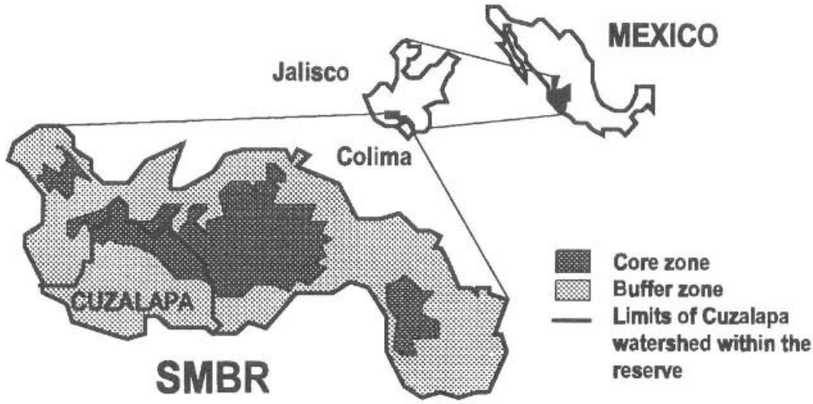

Figure 5.1 Sierra de Manantlán Biosphere Reserve (SMBR) and Cuzalapa Watershed Location within the Reserve.

pre-colonial races of maize such as Tabloncillo and Reventador (Benz 1988; Benz n.d.; Benz et al. 1990; Wellhausen et al. 1952).

The Cuzalapa watershed covers nearly 24,000 ha (most of which lies within the boundary of the Biosphere Reserve) of mountainous land of extremely irregular topography, ranging from an elevation of 550 to 2660 m. The agricultural zone is located at an elevation of 600 m and is characterized by a hot subhumid climate, with a mean annual temperature of 22°C and mean annual precipitation of 1,500 mm, concentrated from June to October (Martinez et al. 1991). Fields are generally located near rivers on alluvial soils of moderate fertility (Martínez and Sandoval 1993).

Each year, about 1,000 ha are sown in Cuzalapa, 600 ha of which are irrigated (Martinez and Sandoval 1993). Maize *(Zea mays* spp. *mays)* is the dominant crop in the valley. Nearly half of the survey farmers cultivate maize in association with squash *(Cucurbita* spp.) on an average of 2 ha per farmer during the rainy season, from June to November. Maize is also planted under irrigation in the dry season, which extends from December to May, intercropped with beans *(Phasealus vulgaris* cv. bayo and bayo berrendo) for the majority of the survey farmers, on an average of 2 to 3 ha per farmer. During this season, a green tomato *(tomatillo* or *Physalis philadelphicum)* grows spontaneously in the fields. Irrigation and intercropping have been common features of agriculture in Cuzalapa since pre-colonial times (Laitner and Benz 1994). Cultural practices have evolved in Cuzalapa but continue to be relatively traditional when compared to those found outside the Sierra de Manantlán. Farmers generally till arable soils with horse-drawn plows in the rainy season. Tractors are used more frequently during the dry season because at this time, the economic returns to maize production are greater and more reliable, and the irrigated soils contain fewer rocks. Weeds are usually controlled by horse-drawn cultivator before sowing and 1 month after. Sowing, fertilization, and harvesting are always manual operations.

The irrigation system is gravity powered. With these techniques, the survey farmers have obtained mean maize yields of 2.8 tons per hectare (unshelled) during the rainy season and 2.1 tons per hectare (unshelled) in the dry season (under irrigation). Beans are produced exclusively for home consumption. Part of the annual maize crop and almost all of the tomatillo crop of Cuzalapa are sold outside the valley, yet generally the Cuzalapa community is poorly integrated into commercial markets. Extensive cattle raising is now emerging as a commercial activity.

Because of the use of the land by indigenous peoples since pre-colonial periods, the region was officially recognized as a *comunidad indigena* (indigenous community) under the Agrarian Reform of 1950. The valley of Cuzalapa has approximately the same number of inhabitants today (1,500) as it did in 1540 (Laitner and Benz 1994). Now, however, a large proportion of the inhabitants are *mestizos* (of both European and indigenous ancestry). Although it is one of the largest communities of the Biosphere Region, Cuzalapa is also located in one of the most marginalized municipalities of the region, based on quality of housing and level of education (Rosales and Graf 1995). At the time of this study (1989-1991), these localities were all remote from major roads and urban areas. Based on its farming and socioeconomic characteristics, Cuzalapa is representative of many indigenous, poor, and isolated rural areas in Mexico. Cuzalapa is one of the many traditional communities in Mexico which are being drawn slowly into commercial marketing systems while maintaining features of indigenous society.

Varieties and seed lots: flow and diversity

"Seed lot" and "variety" defined

The terms and concepts used in this work are based on farmers' own practices and concepts. In this context, the term "seed lot" refers to the set kernels of a specific type of maize selected by one farmer and sown during one cropping season to reproduce that particular maize type. A "variety" or "cultivar" is defined as the set of farmers' seed lots that bear the same name and are considered to form a homogeneous set. A seed lot, therefore, refers to a physical unit of kernels associated with the farmer who sows it; a variety is associated with a name.

A maize variety is defined as "local" when seed from that variety has been planted in the region for at least one farmer generation (that is, for more than 30 years, or if farmers maintain that "my father used to sow it"). This definition implies that a "local" variety has been cultivated continuously among survey farmers in Cuzalapa for many years. By contrast, an "exotic" variety is characterized either by the recent introduction of its seed lots or by episodic planting in the valley. Exotic varieties may include landraces (farmers' varieties which have not been improved by a formal breeding program) from other regions and commercial improved varieties recently or repeatedly reproduced by farmers using traditional methods.

Seed exchange

Documenting the exchange of seed lots and varieties

To document which maize varieties are cultivated and to record the exchange of seeds and varieties in the community and between the valley of Cuzalapa and other regions, 39 farmers (one fifth of Cuzalapa farmers) were surveyed during six cropping seasons spanning three calendar years (the 1989, 1990, and 1991 rainy and dry seasons). For each farmer and cropping season, data were collected on varieties cultivated and seed source. Cultivars included those grown on the farmer's own fields, on rented fields, and on fields in association with other farmers. Each variety was registered with the name given by the farmer. When the seed introduced from another region shared the same name as a local variety but was not considered, by the farmer growing it, to be the local variety, a second label was noted in brackets (e.g., Negro [Exotic]).

The seed source was classified in three ways: (1) as own seed (seed selected by the farmer from his own harvest); (2) as seed acquired in Cuzalapa (seed obtained in the valley of Cuzalapa from another farmer); and (3) as an introduction (seed acquired outside of the Cuzalapa watershed). The origin of a seed lot is defined independently of the origin of the previous generation of seed. A seed lot is considered "own seed" if the ears from which the kernels were selected were harvested by the farmer in his field in Cuzalapa, even though the seed that produced those ears (i.e., the previous generation of seed) may have originated in another region. The data, therefore, are representative of the extent of seed exchange, but they understate the importance of exotic seed in Cuzalapa.

Regular introduction of exotic varieties

During the six seasons included in the survey, survey farmers grew a total of 26 varieties (Table 5.1). Each farmer grew between one and seven maize varieties during each season and, on average, more than two varieties *per season*. Most of these cultivars are white-grained dents and are primarily used for making tortillas, the starchy staple of the Mexican diet. Three flinty popcorn varieties (Guino Rosquero, Negro [Guino], and Guino Gordo) were also identified, as well as three purple-grained varieties (Negro, Negro [Exotic], Negro [Guino]) and three yellow-grained varieties (Amarillo Ancho, Amarillo, Amarillo [Tequesquitlán]). The taste of the purple varieties is considered sweeter and the ears of these varieties are generally consumed roasted at the milky stage, while yellow varieties are used essentially as feed for poultry and horses.

Contrary to the general perception of traditional rural societies in relation to cultivated varieties, this community does not function as an isolated area. On the contrary, exotic varieties are regularly introduced for on-farm testing. From the 26 varieties identified, only the cultivars Blanco, Amarillo Ancho, Negro, Tabloncillo, Perla, and Chianquiahuitl are local and all related

Table 5.1 Importance of Varieties Cultivated in Cuzalapa

Varieties	% Maize Area	% Farmers	Grain Color	Cycle Length
6 Local				
Blanco	51%	59%	White	Short
Chianquiahuitl	12%	23%	White	Long
Tabloncillo	5%	6%	White	Short
Perla	0.4%	0.02%	White	Short
Amarillo Ancho	8%	23%	Yellow	Short
Negro	3%	34%	Purple	Short
20 Foreign				
3 most cultivated				
Argentino	5%	10%	White	Long
Enano	3%	12%	White	Long
Amarillo	3%	11%	Yellow	Long
17 minor varieties	<3% per variety	<4% per variety	Mainly white	Mainly long

to the Tabloncillo race (Table 5.1). In other words, only these six varieties had been grown continuously for at least one farmer generation in the valley of Cuzalapa. Only the introduction date of the Chianquiahuitl can be traced to 40 years ago. Four of the six local varieties are cultivated by a large percentage of farmers. Since two of these varieties have white grains (Blanco and Chianquiahuitl), one has yellow grains (Amarillo Ancho), and the fourth has purple grains (Negro), all four varieties provide for the different household uses of maize in Cuzalapa. Although reduced in number, the local varieties cover more than 80% of the area. The two principal white varieties alone occupy an estimated 63% of the area planted to maize.

The remaining 20 of the 26 varieties that Cuzalapa farmers grew during the survey period are classified as exotic. Each exotic variety covered less than 5% of the maize area planted in each season, and most were cultivated by only a few farmers at a time. The composition of this group of varieties changed from season to season. Only three of these varieties (Argentino, Enano, and Amarillo) had been regularly cultivated over the preceding 4 or 5 years by a significant percentage of farmers (10 to 12%). Most had been used for the first time recently or during the survey period and had been planted again once or twice.

The origin of the exotic varieties is often difficult to ascertain. Farmers are able to indicate in which community they acquired a variety, but not its true source. Even the original name of the variety can disappear or take on a different meaning when farmers exchange seed. Based on the information collected, exotic varieties can be classified into three groups: farmers' varieties (landraces) (15); farmers' advanced generations of improved varieties (4); and recent generation of an improved variety (1). The group of exotic varieties is morphologically diverse, including white-, yellow-, and purple-grained materials, and representatives of different races. Most cultivars were introduced from communities of southwestern Jalisco, less than 100 km from Cuzalapa, although the Guino [U.S.] variety cultivated by one farmer originated in the U.S. In general, the data indicate that maize cultivation in Cuzalapa depends notably on local materials but also on a changing and diverse group of exotic varieties introduced through farmer-to-farmer exchanges.

Seed lot exchange

By detailing the geographic origin of each farmers' seed lots, for each variety, in each planting cycle, one can determine and characterize the frequency of seed exchange among farmers and the pattern of variety diffusion. During the study period, the survey farmers sowed 484 seed lots for the total 26 varieties they cultivated, on 442 ha. Many of these seed lots came from other farmers or regions (Figure 5.2). On average, for all cropping seasons, survey farmers selected slightly over half (53%) of their seed lots from their own harvest. About 36% of the seed lots were obtained from another farmer in Cuzalapa, and 11% were introduced from other regions. Calculated in terms of area planted, seed from farmers' own harvests represented 45% of the maize area in the study zone, whereas 40% was planted to seed from other Cuzalapa farmers and 15% was planted to exotic introductions. Seed exchange — whether between farmers inside the valley or with farmers outside the valley — is clearly very important.

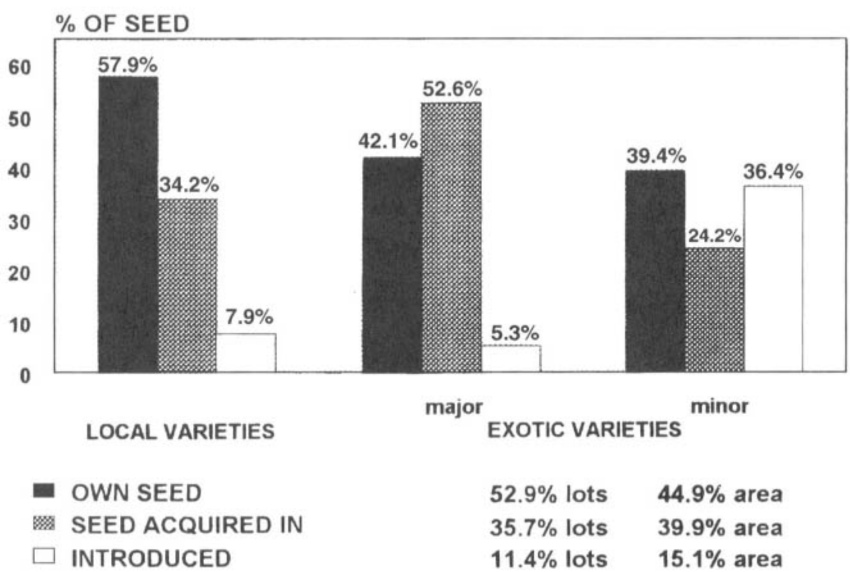

Figure 5.2 Origin of seed planted in Cuzalapa by origin of variety (39 farmers during six growing cycles).

The pattern of varietal diffusion

Both local and exotic varieties were planted from farmers' own seed lots, from seed lots acquired in Cuzalapa, and from introduced seed lots, but in different proportions. Significant differences in origin were associated with the dominance of the variety in terms of planted area (Figure 5.2). Three different groups of varieties were considered: local varieties (6 varieties); most important exotic varieties (3 varieties, Argentino, Amarillo, and Enano); and minor exotic varieties (17 varieties). Seed of the most widely grown varieties, noted in the text as "major varieties" — including the local varieties and the three most important exotic varieties — is less likely to have been obtained from farmers outside of Cuzalapa than seed of the more minor exotic cultivars (7.9% of local varieties and 5.3% of important exotic varieties seed lots were introduced, compared to 36% of minor exotic varieties seed lots). Nevertheless, it is difficult to establish a pattern for the minor exotic varieties because each variety appears to be a special case defined by the time of its introduction and the number of farmers planting it.

Among local varieties, farmers manage the seed for Chianquiahuitl and Negro the most conservatively. More than 70% of the seed for these varieties is selected from farmers' own maize harvests. In fact, farmers plant such a small area to the variety Negro that, on average, seed equivalent to only 27 ears is required per farmer (Louette 1994). This amount of seed, in good condition, is carried over easily from one cycle to the next, and farmers do not need to seek out seed from another farmer. Chianquiahuitl is a variety of unknown origin that is believed to be no longer widely cultivated outside the study zone. Thus, of necessity, farmers in the Cuzalapa Valley must rely on their own stocks.

The case of Blanco, the most important local variety, contrasts with that of Chianquiahuitl. Of all the local varieties, Blanco has the highest proportion of seed obtained from farmers outside the study zone (15%). This result reflects the importance of Blanco in terms of area cultivated in Cuzalapa and nearby regions. Because Blanco is important for household subsistence, an insufficient number of ears suitable for seed may remain at planting time, compelling farmers to search for seed from other farmers in and outside the community.

Both important and minor exotic varieties are also sown from a significant percentage of own seed lots (42.1% and 39.4%, respectively). Farmers reproduce the more important exotic varieties as they do with local varieties. Recently introduced minor varieties are reproduced from farmers' own seed and tested over several seasons. Important and minor exotic varieties can be distinguished by their pattern of diffusion. The percentage of seed brought from other regions is small for the most widely grown exotic varieties (5.3%), while for some of the minor varieties introduced late in the survey period all seed lots were introduced (average 36.4%). Farmers in the valley exchange seed of the important exotic varieties (52.6%) much more frequently than seed of the minor exotic varieties (24.2%). This is explained by the fact that important exotic varieties were introduced some 10 years ago, and because they have demonstrated characteristics of value, their seed is redistributed to other farmers in Cuzalapa. In contrast, survey farmers who did not plant the minor varieties during the study period are presumably not yet convinced of their advantages and do not look for seed.

In summary, there is a moderate level of diffusion of local varieties inside the watershed and little infusion from other regions. Recently introduced exotic varieties are infused from outside the valley. Older exotic varieties that have attained a moderate level of acceptance are also diffused inside the watershed. The pattern of varietal diffusion is therefore linked essentially to the local acceptance of the variety, the time it has been sown in the region, and the availability of seed inside and outside the region. What is important to note is that seed lots introduced from outside the valley can be considered as part of the local varieties. A "local" variety is therefore not constituted by seed lots of exclusively local origin. This finding is important for the concept of a local variety and will be discussed later in this chapter.

Farmer type

The general patterns of maize seed exchange described above nevertheless conceal major differences among survey farmers. Three major farmer groups can be identified. At one extreme are farmers who select seed almost exclusively from their own maize harvests. They sow the same varieties regularly and only modify the proportion of maize area planted to each variety in each cropping season. These farmers are considered suppliers of seed of local cultivars ("they always have seed").

Other farmers use their own seed lots in addition to seed acquired in the community or introduced from other regions, and the proportions of each type of seed vary from season to season depending on each farmers' objectives and constraints. These farmers are generally regarded as suppliers of introduced seed, and some are known in the community for their curiosity about new varieties. At the other end of the spectrum are farmers who have never used their own seed. Throughout the study period, these farmers acquired seed both within and outside of Cuzalapa. This group of farmers includes those who do not have rights to land and cannot plant maize each season and those who farm small areas on which they cannot harvest enough maize for both family consumption and seed. Farmers in this group are obliged to look for seed from other farmers when they want to plant maize.

A relationship exists between the number of varieties (different seed lots) sown by each farmer in each cycle and farmer type or proportion of the farmers' seed stocks originating from his own harvest (correlation coefficient of 0.5). In general, farmers who have more recourse to seed produced by other farmers appear to plant fewer varieties per cycle. For example, the group of farmers who sow more than 90% of their crop with seed from their own harvests planted an average of 2.6 varieties per cycle, while those who used no seed from their own harvests planted an average of only 1.3 varieties per cycle. This finding may reflect either a greater reliance on diverse maize types by more conservative farmers, or it may reflect the fact that searching for seed from other farmers requires more effort and is therefore associated with fewer varieties sown.

Factors explaining seed exchange

Several factors induce farmers to exchange seed. The first is the traditional method of seed storage. Maize (for seed and for food) is stored in bulk in a room of the house. Ears are often attacked by weevils and other insects when the grain is stored for longer than 6 months (from one dry season to another dry season, for example). If a farmer sows a particular variety in only one season per year and has not sown that variety in the previous year, or if the cropping calendar obliges him to plant before harvest, he will search for seed from ears that have been harvested more recently by other farmers. The dry season is better for providing seed because more area is cultivated. Either as a percentage of area planted or as a percentage of total seed stocks, the interchange of seed is more evident at the end of the rainy season. For example, farmers' own maize harvests provide 32 and 57% of the seed for Blanco and Chianquiahuitl grown in the dry season and 69 and 81% of the seed for these varieties during the rainy season.

A second important factor affecting the importance of farmers' seed sources in planting decisions is the socioeconomic status of the household, as represented by farm size, land use rights, and access to the market for renting land. As noted above, many farmers do not cultivate an area large enough to meet their annual food consumption needs, whereas others own no land and must rent a field to cultivate maize. These farm households often consume all of one season's production before planting and are obliged to search for seed each season.

Another factor influencing the seed sources used by farmers is the custom in the Cuzalapa region of producing maize under sharecropping arrangements. Under these arrangements, the partner (or *mediero)* generally supplies labor while the field owner (or *patron*) supplies the inputs, in particular, maize seed. Generally the *mediero* does not choose which varieties to plant and at harvest time acquires seed from the *patron*. Seed is also loaned, under the proviso that double the quantity of seed loaned must be returned at harvest. In either case, the farmer obtains maize seed of a variety that another farmer has chosen to grow and that is derived from another farmer's harvest.

Another finding from the survey is that few farmers expressed any particular preference for or allegiance to their own maize as a source of seed. Seed of a given variety selected from their own maize harvest or acquired from other farmers was considered equivalent. In other words, another farmer's method of seed management was not a cause for concern. Furthermore, if a farmer does not grow a particular variety for several successive seasons, this does not signal that the farmer has ceased cultivating it altogether, as long as the seed for that cultivar can still be obtained from other farmers if necessary. Farmers also generally consider that they must change seed regularly to maintain the productivity of the variety ("sow the same maize type but from new seed"). The frequency of seed renewal varies from several cycles to several years. It appears unlikely that any farmer in Cuzalapa sows seed derived from a stock bequeathed directly from his parents.

Finally, farmers appeared to be very curious and open-minded, in general, about testing new cultivars. After visiting a relative or friend, or after harvesting a maize field as a laborer, a farmer often returns with maize ears so that he can test a variety the ear characteristics of which he admires. The introduced seed lots acquired from other farmers are almost never bought as seed. They are gifts from friends or family members living outside the zone or are selected from maize ears bought for consumption.

Phenotypic diversity of varieties

The patterns of maize production and seed management described above are characterized by continual introductions of varieties and, within varieties, considerable exchange of seed among farmers. These findings raise questions about the structure of maize diversity in the Cuzalapa watershed. For example, how can an introduced seed lot be integrated into a local variety? Do exotic varieties compete with local varieties or are they complementary? Analyses of the phenotypic diversity of maize grown in Cuzalapa provide a way to examine some of these questions.

Measuring morphological diversity

The structure of phenotypic diversity was studied both within a variety (among seed lots of a variety) and across varieties (among sets of seed lots bearing different names). Fourteen of the 26 cultivars identified by farmers (all six local varieties and eight exotic varieties) were selected for analysis based on their origin and seed availability. The number of seed lots per cultivar (one to six) varied according to the importance of the cultivar in terms of planted area.

Morphological descriptors were measured in a controlled experiment of maize grown in pure stand in three complete blocks. The experiment was established in a farmer's field during the 1991 dry season. Each elementary plot (one seed lot) contained six rows, 5 m in length and separated by 0.75 m, which conforms to the spacing most commonly used by farmers in the study region. To obtain a sample representative of the diversity of each seed lot, seed for each plot was taken from 100 ears (two grains per ear) selected by the owner. Descriptors were measured using a sample of 20 plants and 15 ears per elementary plot, and refer to characteristics of the vegetative parts, tassel, and ear (see Table 5.2).

Factorial Discriminant Analysis (FDA) and Hierarchical Cluster Analysis (HCA) (STATITCF program) were used to analyze diversity among the seed lots within and across varieties. Factorial Discriminant Analysis distinguishes seed lots (or varieties) based on the variables for which the ratio of the sum of squared differences within a lot (or a variety) to the

Table 5.2 Vegetative and Ear Descriptors Measured

	Vegetative descriptors
HPL	Plant height
HEA	Ear height
DIA	Stalk diameter
LLE	Length of the leaf of the superior ear node
WLE	Width of the leaf of the superior ear node
NLE	Number of leaves above the superior ear, including the leaf of the superior ear node
	Tassel descriptors
LTA	Tassel length
PED	Peduncule length
LBR	Length of branched part of the tassel
BR	Total number of branches
	Ear descriptors
LEA	Ear length
WEA	Ear weight
DEA	Ear diameter
WCO	Cob weight
DCO	Cob diameter
ROW	Number of rows of grain
HGR	Grain height (3 grains mean)
WGR	Grain width (10 grains mean)
TGR	Grain thickness (10 grains mean)
WIG	1-grain weight (mean of 3 samples of 100 grains)

sum of squared differences among lots (or among varieties) is the greatest. Hierarchical Cluster Analysis ranks lots (or varieties) based on the mean of the weighted Euclidean distances among their center of gravity coordinates on the first five axes identified by the results of the FDA analysis. All variables were used in the FDA-HCA analyses except flowering date, grain color, and I-grain weight obtained at the sample level (not at the plant level).

Phenotypic characteristics and varietal identification

With the exception of the B1 lot of the Blanco variety, the HCA analysis of seed lots for five of the more widely grown varieties (four locals and one exotic) demonstrates that seed lots bearing the same name cluster together based on their morphological characteristics (Figure 5.3). The results support the hypothesis that a farmer's concept of a variety corresponds closely to that of a phenotype. A farmer variety is a set of seed lots having the same name; these seed lots produce maize with similar plant, tassel, and ear characteristics.

The implication of these findings is that when farmers in Cuzalapa classify seed as that of a given variety, they use morphological and

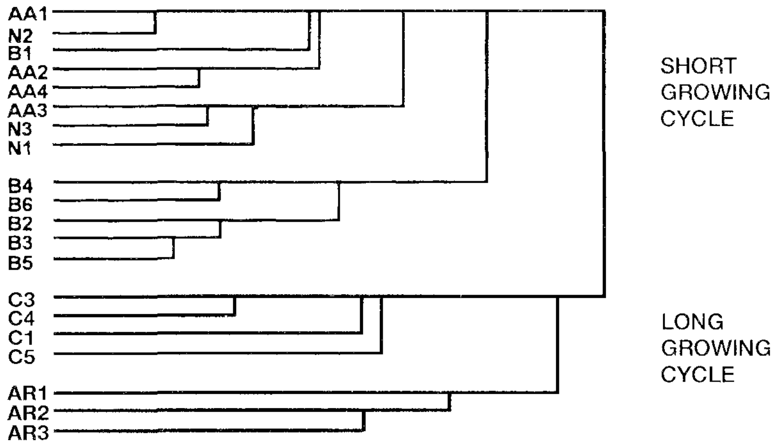

Figure 5.3 Hierarchical cluster analysis of seed lots of five varieties, by phenotypic characteristics (B = Blanco, AA = Amarillo Ancho, N = Negro, C = Chianquiahuitl, AR = Argentino).

phenological criteria rather than criteria such as geographic origin, adaptation to some limiting factor, or ritual function. A seed lot that resembles seed of a "local" landrace is classified as such by the farmer, even though its origin may be exotic or unknown. As a consequence, some seed lots of "local" landraces are in fact introduced from other regions.

Phenotypic variation between varieties

The phenotypic characteristics of the six local varieties and eight exotic cultivars (including the three most widely cultivated) were studied with the methods described above. The data reveal a large amount of phenotypic diversity with respect to several characters (Table 5.3). For example, the sum of degree days from sowing to tasseling varied from 1,130°C for the earliest maturing variety, Blanco, to 1,550°C for the latest maturing variety, Argentino. Mean height of the ear varied between varieties from 129 to 195 cm, the number of rows of grain varied from 8.7 to 12.7, the grain width from 0.85 to 1.13 cm, the cob diameter from 1.8 to 2.7 cm, and the ear weight from 104 to 181 g.

For the varieties studied, 78% of the variability in phenotypic characteristics was explained by the first two axes of the FDA (Figure 5.4). The first axis is essentially defined by row number (-ROW), grain width (+WGR), plant height (-HPL), and ear height (-HEA). The second axis is determined by ear development, including the weight and diameter of the cob (+WCO, +DCO) and weight and diameter of the ear (+WEA, +DEA). A test comparing farmers' methods for identifying varieties and these two axes indicated that both the statistical analysis and farmers classify maize varieties in a similar way (Louette 1994).

Table 5.3 Principal Characteristics of the 14 Varieties under Study (Descriptors in Table 5.2)

Varieties	MF day	HEA cm	HPL cm	NLE	LLE cm	RM	ROW	WGR cm	TGR cm	WCO g	DCO cm	PEA g	DEA cm	W1G g
Short cycle														
Blanco B	77.3	129	219	5.9	7.9	16.1	8.7	1.13	0.40	19.7	2.1	140	4.0	0.42
Perla P	82	144	235	6.1	8.1	16.9	8.7	1.08	0.39	18.7	2.2	128	3.9	0.38
Amarillo Ancho AA	82	146	231	6.1	7.9	19.3	9.8	1.00	0.39	19.8	2.2	126	3.9	0.33
Amarillo de Teq. AT	82	160	242	6.2	7.8	20.8	9.6	0.99	0.38	17.5	2.1	123	3.9	0.35
Negro N	83.2	156	232	6.3	7.9	19.8	10.0	0.97	0.37	18.1	2.2	123	3.9	0.31
Tabloncillo T	85	145	230	6.2	7.7	19.2	9.3	0.95	0.33	12.0	1.8	104	3.6	0.29
Long cycle														
HT47 HC	89.5	130	193	6.4	8.9	13.2	15.0	0.82	0.40	30.8	3.0	137	4.5	0.27
Negro (exot) NX	91.5	171	232	6.1	8.2	20.5	10.2	1.00	0.38	23.1	2.4	126	4.0	0.31
Híbrido H	92	179	254	6.3	8.1	20.4	11.9	0.91	0.37	22.0	2.3	141	4.2	0.30
Amarillo A	92	185	261	6.6	8.1	19.8	11.3	0.99	0.38	27.3	2.6	164	4.4	0.36
Enano E	92.5	161	231	6.8	8.5	23.2	13.4	0.89	0.40	29.7	2.7	160	4.5	0.31
Guino G	92.5	174	249	6.5	8.6	20.0	12.7	0.94	0.36	30.1	2.7	181	4.6	0.34
Chianquiahuitl C	93.2	188	260	6.2	7.8	21.5	11.7	0.85	0.34	17.6	2.1	126	3.9	0.27
Enano Gigante EG	93.5	185	261	6.6	8.4	20.5	12.4	0.93	0.36	26.2	2.6	158	4.4	0.32
Argentino AR	96	195	273	6.5	8.4	22.8	12.6	0.92	0.36	26.2	2.5	158	4.4	0.32

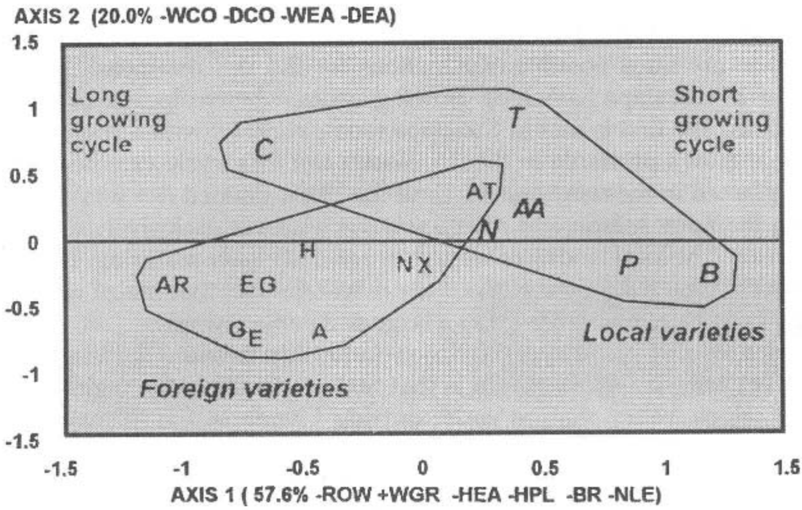

Figure 5.4 Phenotypic diversity in Cuzalapa maize (Factorial Discriminant Analysis).

The descriptors listed above facilitated the differentiation of varieties in two ways: by duration (length of growing cycle) and by origin or race. These characteristics could not be included as variables in the analysis because they were not collected at the level of the plant or ear, but at that of the seed lot. Nevertheless, they characterize well the different groups that appear in the FDA as they are closely related to some descriptors that define the first two axes of the FDA. Length of growing cycle is highly correlated with descriptors for the first axis ($|r| > 0.80$ between male flowering date and HEA, NLE, WGR, ROW). A long-duration variety is characteristically a taller plant that has more leaves and smaller grains arranged in more rows.

The origin of a variety (local or exotic) also relates to differences in phenotypic characteristics. The only exception to this general rule is the variety Amarillo [Tequesquitlán] (AT), which is phenotypically associated with the local varieties even though it was introduced from a community located some 20 km from Cuzalapa. The local varieties are characterized by narrower, lighter ears and less vegetative development than the exotic varieties (Table 5.3). Local varieties and Amarillo [Tequesquitlán] are related to the Tabloncillo race, which originated on the Pacific Coast of Mexico (Wellhausen et al. 1952). The exotic varieties included in the trial (except Amarillo [Tequesquitlán]) are linked to other races. Origin is therefore related to variation in race.

Origin and length of growing cycle are also interrelated. Most of the varieties with long growing cycles are exotic, with the exception of Chianquiahuitl. In Cuzalapa, therefore, local and exotic varieties appear to be complementary from a morphophenological point of view. Most local varieties have a short growing cycle, reduced vegetative development, few rows, and large kernels, whereas introduced varieties have a long growing cycle, taller plants, and small kernels.

There are three possible explanations for the fact that nearly all exotic varieties in Cuzalapa have long growing cycles, whereas local varieties have short ones. The first is that in Cuzalapa today, varieties with a short growing cycle are grown primarily in the dry season and long-cycle varieties are generally planted in the rainy season. Until the 1970s, flooded rice was cultivated during the rainy season and maize was sown almost exclusively during the dry season. The local landraces were then generally early maturing. The longer growing cycles of exotic varieties may reflect the fact that maize cultivation during the rainy season began on a large scale only recently.

Another explanation for the close relationship between the length of the growing cycle and exotic origin is that few landraces in the region around the Cuzalapa Valley mature early; outside Cuzalapa, the major cropping cycle for maize is the rainy season as most irrigated fields are sown with sugar cane. Few early maturing improved varieties have been developed for the lowland tropical zones where most maize is produced in developing countries (CIMMYT 1993).

Finally, the complementary characteristics of local and exotic varieties may be interpreted in yet a different way. When a lot of seed introduced from another community has the same phenotypic characteristics as seed of a local variety, farmers may consider it as seed of a local variety. The new seed would be identified by the name of the local variety and would no longer be distinguishable from it. For example, all introduced seed of maize with short, thick stalks is named Enano ("dwarf") after the first exotic variety that had such a stalk. Farmers do not use different names for these different varieties as the characteristic uses for classification refers to the height and diameter of stalk which are very similar among the different varieties. Farmers appear to use different names only for seed lots with particular characteristics of interest to them. Therefore, no introduced seed lot that is morphologically similar to a local variety would be distinguished, so no exotic variety with characteristics similar to those of local varieties would be recognized as a distinct cultivar.

Genetic definition of a landrace

Geneflow between seed lots

Monitoring gene flow

Maize is an open pollinated crop. If geneflow between local and exotic material is not controlled, the introduction of foreign varieties can have an important effect over the genetic structure of local ones. To evaluate the risk of geneflow between different varieties, we have studied over three seasons, on a 10-ha area, the sowing organization of seed lots in space (localization of the different seed lots) and in time (sowing date and flowering date). This area corresponded to seven fields separated from each other by less than 200 m. As this is the minimum distance for reproductive isolation in maize breeding (Hainzelin 1988), geneflow can take place between all seed lots planted on this area.

In six farmers' fields, we evaluated the level of geneflow between seed lots sown on contiguous areas; using the xenia effect of the grain, and in particular the dominant character of the Negro color, an ovule with alleles that give white or yellow color to the grain, fecundated by a pollen with alleles that confer a purple or black color to the grain will give a purple or Negro grain at harvest time. The level of geneflow was then determined by the proportion of purple or Negro grains per furrow in the white or yellow varieties sown on contiguous areas to a Negro variety with a similar growing cycle. As the Negro variety is not homozygous for grain color, geneflow is probably greater than the one measured with the number of purple or Negro grains in the white or yellow variety.

Continual genetic exchange

The survey and the observation of the sowing pattern on an area of 10 ha during three cultivation seasons indicate that traditional management of seed lots does not aim to prevent the sowing in contiguous areas of different varieties (Figure 5.5). A farmer sows an average 2.5 varieties per cycle in the same field, independently of those sown on the contiguous fields. There is no physical isolation between local and exotic varieties and between locally reproduced seed lots and seed lots planted in other areas. For example, during the 1991 dry season, 15 seed lots, 3 of which were introduced from other regions, of six different varieties were sown in the area surveyed.

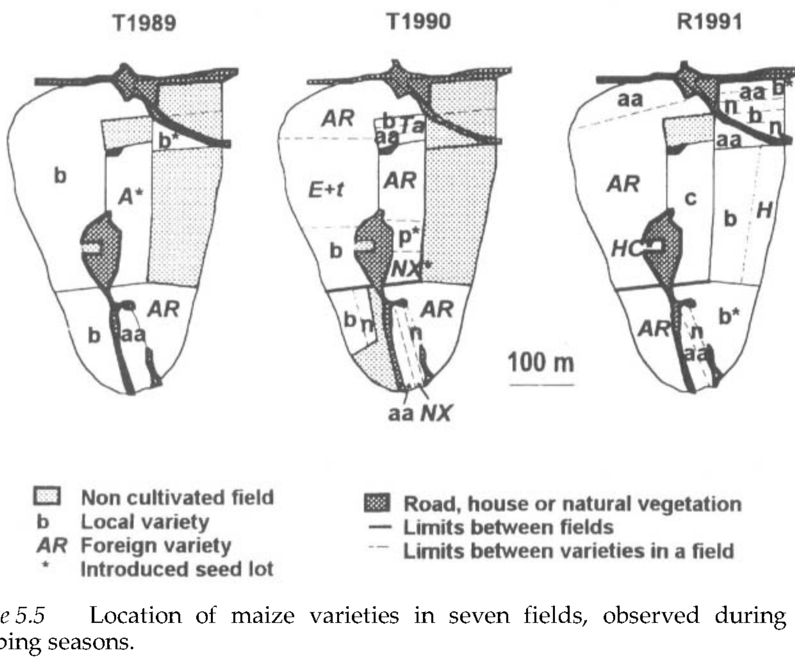

Figure 5.5 Location of maize varieties in seven fields, observed during three cropping seasons.

The planting date does not, however, lead to a sufficient difference of flowering date to permit reproductive isolation, in default of spacing isolation. In assessing the probability of geneflow between the different varieties sown, the work of Basseti and Westgate (1993) has shown that geneflow is more probable between two maize varieties when the difference between the male flowering date of a variety and the female flowering date of the other variety is less than 5 days. Over the three seasons observed in Cuzalapa, the differences of flowering dates between seed lots averaged less than 5 days in 38% of the cases. Different planting dates from farmer to farmer allowed for the synchrony of flowering between long cycle and short cycle varieties in 24% of the cases, although this situation has been more frequent for varieties with similar growing cycles (synchrony of flowering for 65% of the cases for long cycle varieties and for 47% of the cases for short cycle varieties).

Observation on six farmers' fields of the contamination of yellow- or white-grained varieties by a purple-grained variety planted in a contiguous area confirmed the presence of geneflow and provided insight into the level at which it occurs. It was observed, as indicated in the literature (Paterniani and Stort 1974), that the level of contamination of one variety by another diminished rapidly with distance from 20 to 10% in the first row to 1% after the first 2 or 3 m. The level stabilized over a great distance. The concentration of contamination in the first rows of contact between varieties may explain why some farmers think that contamination occurs at the root level.

The management of sowing practices, leading to the development of different varieties on contiguous areas, favors genetic exchange between all cultivar types, independent of the origin and growing cycle of the different varieties. The varieties sown are not genetically isolated. The reproduction of the varieties in the same conditions each cycle can lead to important modifications of their allelic frequencies. Thus, the genetic structure of local varieties is linked to the diversity of the varieties sown in the area and can be particularly influenced by exotic varieties.

Genetic drift

The study of the quantity of seed from which seed lots are reproduced provides evidence which confirms the genetic instability of local varieties and shows why geneflow between seed lots is so important in this system.

Determining the quantity of seed used per seed lot each cycle

Replanting each variety from small samples of seeds theoretically leads to a loss of alleles (Maruyama and Fuerst 1985; Ollitrault 1987). For an open pollinated plant, the theoretical work of Crossa (1988) and Crossa and Vencovsky (1994) has shown that a seed lot formed from less than 40 ears (1) does not permit the conservation of alleles whose frequency in the population in less than 3% (rare alleles), and (2) is conducive to the loss of heterocigosis superior to 1 % when there are less than three alleles per locus. Thus, the use of reduced and variable quantity of seeds leads to the fluctuation of diversity with loss of alleles (Maruyama and Fuerst 1985; Ollitrault 1987).

To determine the effective population size of the seed lots planted in Cuzalapa, the volume of seed of each seed lot was obtained for the 39 farmers participating in the survey during six cultivation seasons. This was converted to the number of shelled ears for each variety based on the weight of one liter of grains and of 100 grains, and an average of 250 grains used for seed per ear.

Fluctuation of diversity

In Cuzalapa, as the field area is reduced (2 ha, on average) and various varieties are sown in the same field, the size of the seed lots planted per variety is reduced. More than 30% of seed lots sown during the six cultivation seasons covered by the survey were constituted from less than 40 ears (Figure 5.6). This phenomenon is important above all for varieties cultivated in small areas, such as the introduced varieties (37.7% of seed lots constituted from less than 40 ears) and the purple and yellow varieties (54.7%). For the main varieties, the phenomenon is less important, although more than 15% of the seed lots of the Blanco variety were constituted from less than 40 ears.

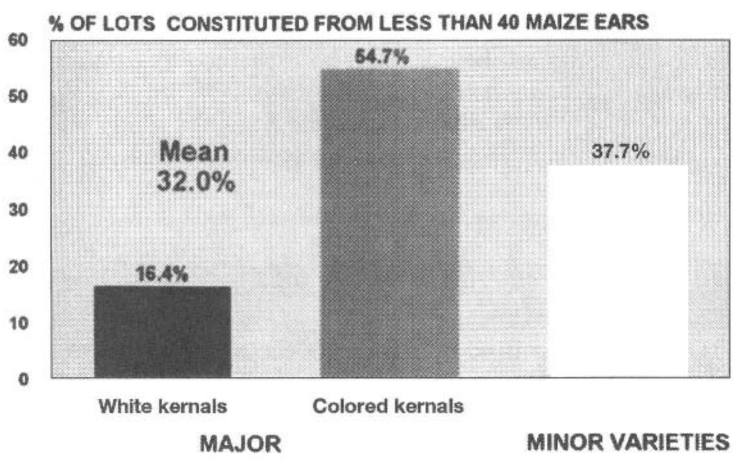

Figure 5.6 Quantity of maize ears shelled to the seed lots, by type of variety.

In conclusion, an important proportion of seed lots are submitted to a regular reduction of their effective population size, leading to the fluctuation of their diversity with loss of rare alleles. Similar findings have been reported by Ollitrault (1987) for rice, millet, and sorghum in Africa. If farmers managed seed lots in isolation from each other from a reproductive point of view, the diversity of some seed lots would probably decrease and consanguinity would probably increase, leading to a loss of production potential. In Cuzalapa, however, this is not the case. Consider, for example, that the genetic

Table 5.4 Isoenzymatic Polymorphism of Four Local Varieties

Variety	Sample (Number of Kernels)	Number of Alleles per Polymorphic Locus	Number of Rate Alleles (Frequency <5%)	Frequency of Polymorphic Locus	Genetic Diversity
Blanco	42	3.4 (0.7)	2	66.7	0.39
Amarillo Ancho	20	2.9 (0.6)	1	66.7	0.34
Negro	41	3.5 (0.3)	5	66.7	0.38
Chianquiahuitl	32	3.3 (0.3)	3	66.7	0.35

diversity of the Negro variety, reproduced from seed lots, of which 70% originate from less than 40 ears, is extremely similar to the diversity of varieties like Blanco, reproduced from significantly larger seed lots (Table 5.4). Geneflow is both responsible and necessary for the restoration of the genetic diversity of seed lots submitted to genetic drift.

Seed selection, conservation of phenotypic diversity, and control of geneflow

In this context, how can varieties maintain unique characteristics within a limited area? This polymorphism cannot be explained by limited geneflow compared to genetic drift. If this were the case, different seed lots of the same variety would tend to differentiate one from the other, which is not the case. seed selection, in fact, seems to be part of the answer.

Farmers' seed selection

Determining seed selection criteria and the influence of selection over the genetic structure of varieties

The seed selection criteria used by farmers in the region were obtained from survey data and from a comparison, for five varieties, between the characteristics of samples of 60 to 140 ears selected by farmers for seed and samples of ears drawn at random from the harvest. As the genetic structure of an open pollinated plant such as maize can be modified by geneflow, an experiment was conducted to verify the extent to which seed selection permits the maintenance of characteristics in conditions of geneflow between seed lots. A random seed sample and a seed sample selected by a farmer were drawn from the farmer's harvest. Those samples were submitted to geneflow over two seasons, using a variety called a "contaminating variety" (Figure 5.7). Each seed sample was constituted from 100 ears and occupied an area of 20 × 20 m within the field planted with the contaminating variety. The initial population (RO) was compared to the last generation of seed selected (52) and of seed drawn a random (R2), in a trial with four replications for their plant, tassel, and ear characteristics. They were also compared at the genetic level for 15

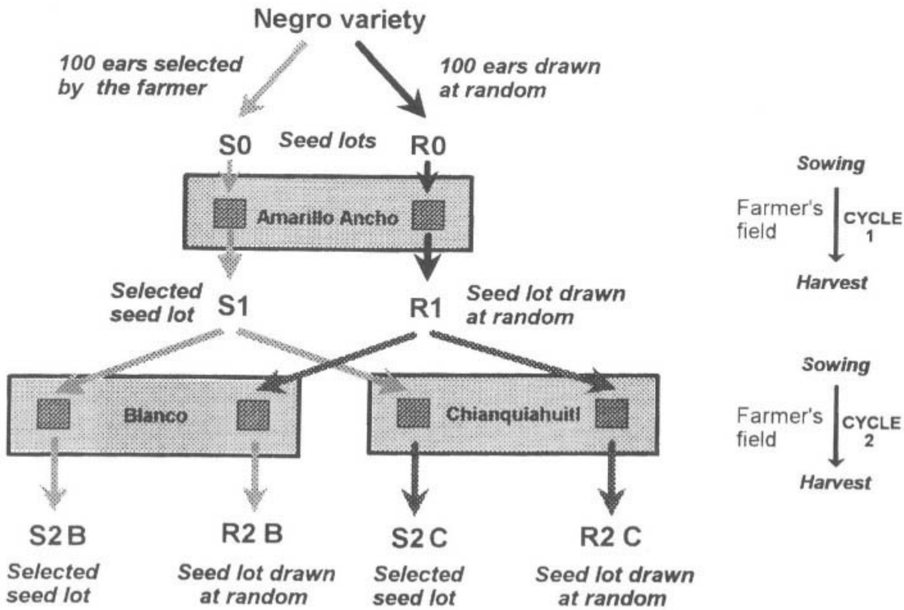

Figure 5.7 Method for determining the influence of seed selection over geneflow.

isoenzymatic loci: ACP-I, ACP-2, CPX-I, CPX-2, CPX-3, EST-8, GOH-2, GOH-3, GOT-I, GOT-2, IDHI-3, PGI-L, PGM-I, PGI-2, and SOH-I.

The trial conducted with Negro as the contaminated variety is considered in this chapter (Figure 5.7). In order to more accurately identify the effect of selection in relationship to the characteristics of the Negro variety, the experiment was subdivided during the second season. A pair of selected and nonselected seed lots were contaminated by the Blanco variety, which displays phenotypic and phenological characteristics similar to those of the Negro variety. Another pair of seed lots were submitted to contamination by the Chianquiahuitl variety, which has significantly different characteristics from the Negro variety (longer growing cycle, bigger vegetative development, more rows of grains, smaller grains, etc.). In this case the initial population (RO) was compared to the last one contaminated either by Blanco (S2B, R2B) or by Chianquiahuitl (S2C, R2C).

Seed selection criteria

Associated with the selection pressure of the environment, the seeds of varieties are mass selected by farmers. The selection does not exclude the ears produced in the borders of the field (with greater probability of contamination). It is based exclusively on the ear after harvest, without control of the pollen source or of the plant characteristics. The selected ears are, according to farmers, the well-developed ears with sane (without fungi or insect damage) and well-filled kernels, characteristics that correspond to the ideotype of the variety. From the selected ears, the kernels of the top of the ear, and sometimes those of the base as well, are not used as seed. These practices have been reported for other regions of Mexico, and for other countries (Bellon 1990; Johannessen 1982; SEP 1982).

The comparison between the characteristics of samples of ears selected for seed and samples of ears drawn at random for the Blanco, Amarillo Ancho, Negro, Chianquiahuitl, and Argentino varieties shows that important differences exist between those two types of ears (Figure 5.8). Selection is oriented to the well-developed ears: axis 2 of the Factorial Discriminant Analysis (FDA) is determined by the weight (WEA) and diameter (DEA) of the ear, the weight of the cob (WCO), and the height of the kernel (HGR). The differences are generally very significant. For example, the mean weight of the selected ears is 30% higher than the mean weight of the unselected ears. As seed selection is oriented to the more developed ears, selection favors the more productive and/or adapted genotypes. This allows for the maintenance of productive varieties. For varieties of a different growing cycle, the selection is divergent on the first axis of the FDA. This axis is related to the characteristics of the ear that distinguish varieties of short and long growing cycle length: number of grain rows (ROW), width (WGR), and thickness (TGR) of the grain. The differences are not always statistically different, although the tendency is evident in the FDA (Figure 5.8) and on the value of the descriptors. In Cuzalapa, the seed selection strengthens the characteristics that distinguish the varieties according to their growing

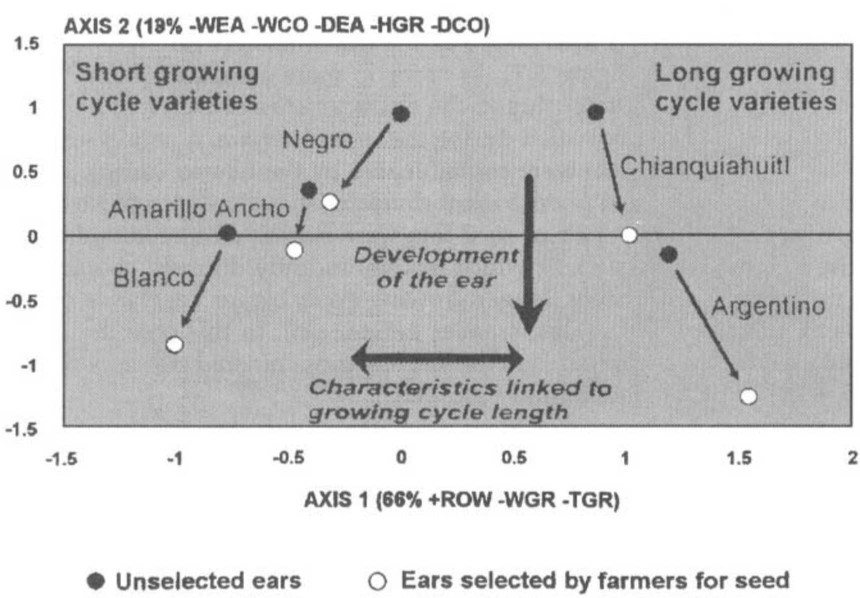

Figure 5.8 Seed selection criteria for five of the main varieties (Factorial Discriminant Analysis).

season. From an agroecological perspective, this has important implications for maize production in a region with two growing seasons.

Control of gene flow for ear characteristics

Comparing traditional seed selection with the random selection of seed in conditions of contamination by another variety shows that the traditional selection of seed efficiently conserves the characteristics of the ear. Let us consider the trial in which the Negro variety (Figure 5.7) was contaminated during the second season by the Blanco variety (similar to the Negro variety from a phenological and phenotypical point of view) and the Chianquiahuitl variety (different from a phenotypical point of view, and having a longer growing cycle; Table 5.3). We compare the characteristics of the initial population (RO) and the population resulting from the two seasons of contamination: populations drawn at random and contaminated by Blanco (R2B) or Chianquiahuitl (R2C), and populations selected for seed and contaminated by Blanco (52B) or by Chianquiahuitl (52C).

As shown by the relative position of RO and R2B in the FDA (Figure 5.9), the contamination by the Blanco variety, similar to the Negro variety, has had little effect on the Negro variety. In contrast, the relative position of RO and R2C indicate that the contamination by Chianquiahuitl, different from Negro, has led to some modifications in the Negro variety. The changes that occurred are related to the characteristics of the Chianquiahuitl variety. R2C presents a vegetative development superior to that of RO. The first axis is defined by the height of the plant (HPL) and of the ear (HEA), the number of leaves (NLE) and the diameter of the stalk (DIA) and smaller kernels arranged on more rows (the first axis is defined by the weight of the kernels, (WG), the width of the grain (WGR) and the number of grain rows (ROW). The values are statistically different only for DIA.

The selection of the seed has had the same effect on the contaminated populations for both contaminating varieties: a higher vegetative development, as indicated by the relative position of 52B and 52C on the first axes of the FDA. What is more interesting to note is that the selection of the population contaminated by Chianquiahuitl has led to the reduction of the effect of contamination over the characteristics of the ears as shown by the relative positions of 52C and R2C on the second axes. The values are statistically different between R2C and 52C for the width of the grain (WGR) and for the number of rows of grain (ROW), which are precisely the characteristics used by farmers to select their seeds.

The effect of selection has also been documented over other characteristics important to farmers when selecting seed: the color of the grain. Over the two growing seasons, the Negro variety was submitted to contamination by white or yellow varieties. The ratio of white or yellow grains in the Negro variety has increased from 7.5 to 16.5% when seed was drawn at random while it stood stable when seed was selected.

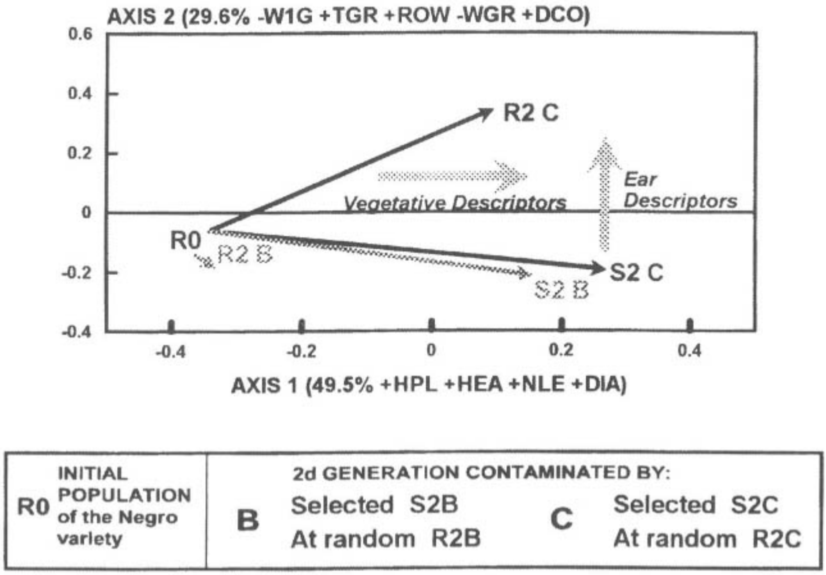

Figure 5.9 Contamination of the Negro variety by Blanco and Chianquiahuitl and contamination control by seed selection.

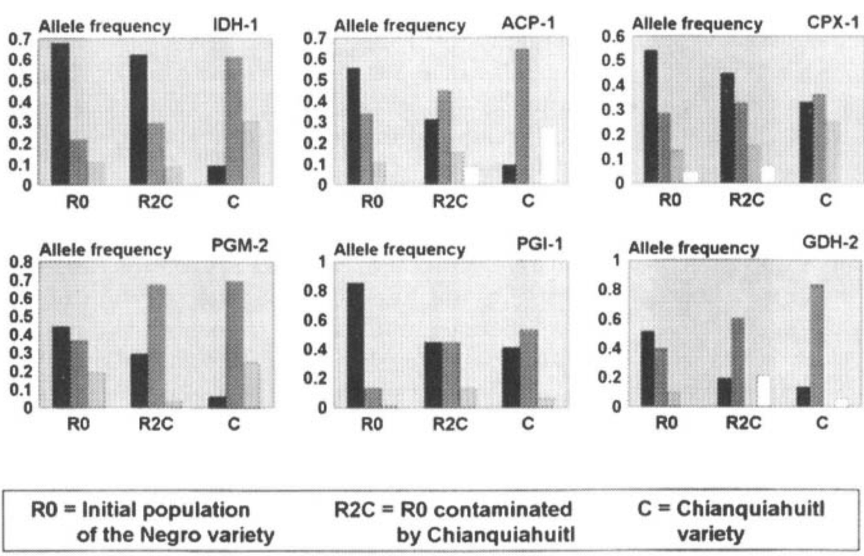

Figure 5.10 Genetic effect of the Negro variety contamination by the Chianquiahuitl variety.

At the genetic level, we were able to observe the effect of contamination on six of the ten polymorphic loci examined (Figure 5.10). The population without selection (R2C) has frequencies intermediate between those of the initial population (RO) and those of the contaminating variety Chianquiahuitl (C). Nevertheless, no effect of selection could be observed at the genetic level.

Discussion and conclusions

Cuzalapa as an open system from the germplasm point of view

The study of seed exchange and the morphological structure of diversity suggests that on-farm conservation projects must not isolate a rural community or a variety. The assumption that traditional systems are closed and isolated with respect to the flow of genetic material is clearly contradicted by the results of this study. A small group of local landraces is continuously cultivated, while varieties with diverse origins that are morphologically diverse among themselves and distinct from the local landraces succeed each other over time. These exotic varieties are introduced for testing by farmers, but they may also be integrated into the group of local landraces. This case study shows that over 3 years alone, in a traditional farming system located in what some regard as the geographic center of origin for maize, introduced materials represent a substantial proportion of the maize seed planted and local varieties are not generally the product of exclusively local seed selection and management.

Similar results have been reported by researchers investigating the use of rice (Dennis 1987), maize (Bellon and Brush 1994; Ortega 1973), bean (Sperling and Loevinsohn 1993), and potato varieties (Brush et al. 1981). Dennis (1987) and Bellon (1995) characterize similar situations as an "excess of diversity" with respect to what is necessary to keep the agricultural system functioning.

Rather than displacing local cultivars, exotic varieties occupy a small proportion of the area planted to maize, and local landraces continue to dominate maize area in Cuzalapa. Introduced varieties more often have uses and modes of management that are complementary, rather than substitutable for, those of the dominant cultivars (Bérard et al. 1991). Our findings in Cuzalapa are similar to what Bellon and Brush (1994) described in Chiapas, although the proportion of local and exotic maize varieties is reversed in the two cases.

The appropriate geographic scale over which we can define a variety as "local" is problematic because the mechanisms that explain the phenotypic diversity of maize in Cuzalapa suggest a constant influx of genetic material. Exotic varieties, as well as introduced seed lots that are then integrated into local varieties, are probably a source of phenotypic and genetic diversity. It is questionable whether any particular geographic scale would necessarily include all of the factors affecting "local" varieties.

In Cuzalapa the morphophenological characteristics of the local and exotic varieties seem complementary, and the two groups rarely compete with respect to growing cycle, vegetative characteristics, or ear attributes. Introductions do not necessarily lead to a large shift away from local cultivars. This finding suggests that a variety is more easily adopted by farmers if it satisfies a need that is not currently met by local varieties or if it occupies a place in the morphological continuum that has not yet been exploited (Boster 1985). In Cuzalapa, survey farmers clearly sought new or different genetic materials from among exotic varieties.

At the level of introduction observed in Cuzalapa, exotic varieties are more a source of phenotypic diversity than a factor inducing genetic erosion. As indicated by Brush (1992), genetic erosion seems to be a phenomenon that is too complex to be captured in the equality "introduction of varieties = loss of genetic diversity." Genetic erosion is a complex function of the area occupied by introductions vs. area planted to local cultivars, the diversity within and between the introduced and local cultivars, and the extent to which local varieties have been abandoned or displaced. As long as the function of the introduced material is complementary to that of the local germplasm, diversity probably increases. When introduced and local materials compete, exotic varieties can displace local material, but this displacement leads to a loss of diversity only if the introduced material is less diverse, replaces several local landraces, or displaces genetic uniqueness of local material. Identifying the factors that affect the extent of genetic erosion, and determining their critical values, is likely to be difficult, and especially so in a system as dynamic as that of Cuzalapa.

The regular acquisition of genetic material by farmers is evidence of their interest in, rather than resistance to, the introduction of new cultivars. In Cuzalapa, farmers are generally experimenters who do not hesitate to test new cultivars planted by farmers in other regions against their respective local varieties. Brush et al. (1981) have indicated that in the Mantaro Valley in Peru farmers may travel more than 50 km in search of new potato varieties. Farmers in Cuzalapa will adopt a maize variety, however, only if it demonstrates its advantages consistently over a large number of cropping seasons. One unsuccessful trial can lead a farmer to abandon a variety, regardless of the reason for the failure. In Dennis' (1987) study in Thailand, farmers in the eight survey villages, on average, cultivated ten varieties in the first year, adopted four introduced varieties in 5 years, and abandoned four cultivars during the same period. Over the past 40 years in Cuzalapa, of all of the varieties introduced by the survey farmers of Cuzalapa, only Chianquiahuitl has been fully adopted.

A local variety as an open genetic structure

Another major research finding concerns the definition of a local variety itself. The magnitude of seed exchange among farmers and the fluctuation of the diversity of seed lots, caused by the amount of seed used and by the regular geneflow between seed lots, raise questions about farmers' concepts of a variety and the distinction between "local" and "exotic" varieties.

First of all, in Cuzalapa, it is not only the set of cultivars but also the set of seed lots that constitute the cultivars which vary in time. A certain number of seed lots disappear in each crop cycle because they are not replanted by the farmer who selected them; on the other hand, one introduced seed lot may evolve into a number of seed lots once farmers begin to exchange seed. The composition of the group of seed lots that constitute a variety is mutable over time. The geographical point of reference for the term "local variety" is larger than the community itself. Introduced seed lots that phenotypically resemble seed of local landraces are adopted as part of these landraces. Thus, the genetic diversity of a variety can be traced beyond the community itself. No geographic scale can exactly define a variety.

Finally, seed lots are submitted to fluctuations in their levels of diversity due to the changing amount of seed from which they are reproduced and continuous geneflow from other seed lots. A farmer variety is, therefore, mutable in terms of the number, origin, and genetic composition of the seed lots of which it is composed. Contrary to the modern concept of variety, traditional cultivars are not genetically stable populations that can be well defined for conservation purposes. Rather, local varieties constitute systems that are genetically open.

Seed selection for maintaining productivity and morphological characteristics

The traditional selection described in Cuzalapa has several utilitarian functions: to maintain the agronomic characteristics of the varieties by selecting the best ears, to maintain distinct morphological characteristics by selection based on those criteria, and to maintain diversity when the pollen source is not controlled (Sandmeier et al. 1986). Although the effect of selection over the conservation of phenotypic characteristics is not as strong as the effect of selection over agronomic characteristics, it seems systematic and has been demonstrated both by the experimental results and by statements of farmers. Traditional seed selection seems, therefore, to be an efficient means of conserving the integrity of the ear characteristics even when geneflow is a significant factor. As indicated by Boster (1985), varieties must be distinct in order to be selected for more utilitarian characteristics. If a variety is not easily distinguishable at the moment of seed selection, it can be lost in favor of varieties sown on more extensive areas. In Cuzalapa, seed selection facilitates the conservation of differences between varieties that have distinct functions within the area, particularly varieties of different growing cycles, length, or grain color. Seed selection does not, however, control geneflow that affects the characteristics of the ears at the genetic level or for vegetative characteristics. Therefore, traditional seed selection conserves phenotypic characteristics of the ear, but not the genetic integrity of the different seed lots.

Metapopulation structure

In Cuzalapa, what do farmers conserve? What is a landrace? What should be considered as the unit of conservation? The structure and processes described for maize cultivation in Cuzalapa can be compared to a metapopulation structure, defined as a group of subpopulations interconnected by geneflow and submitted to local colonization and replacement by new populations (Olivieri and Couyon 1992; Slatkin and Wade 1978) (Figure 5.11). In the case of Cuzalapa, the metapopulation is integrated into the various seed lots of the different varieties sown, through geneflow. The phenomenon of replacement corresponds to the disappearance of seed lots when they are not replanted, and the phenomenon of colonization corresponds to the creation of new seed lots through the interchange of seed between farmers. The maize metapopulation in Cuzalapa is interconnected with other metapopulations as seed lots are introduced from other regions and seed from Cuzalapa is sown in other areas.

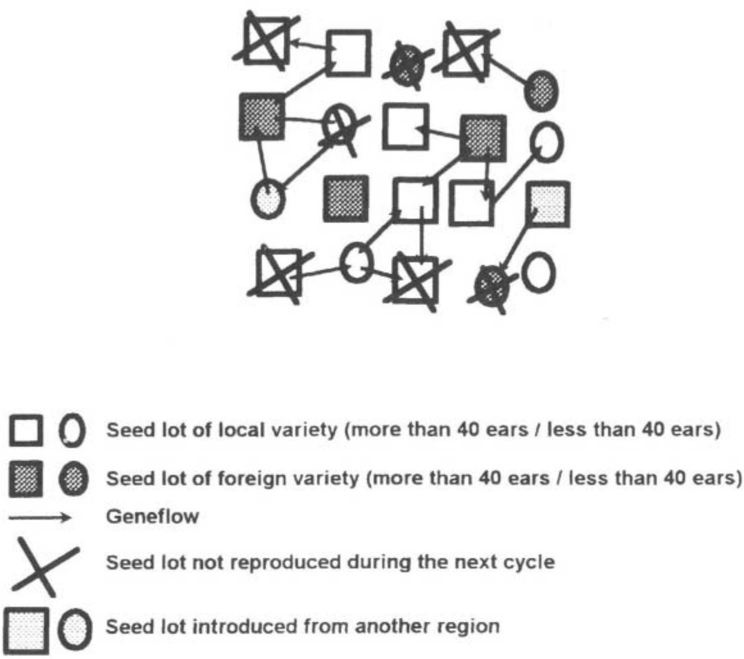

Figure 5.11 Metapopulation in Cuzalapa.

Based on the various models which have elaborated on metapopulation structures (David 1992; Dickinson and Antonovics 1973; Hedrick 1986; Michalakis and Olivieri 1993; Nagylaki 1976; Roof 1994; Slatkin 1981; Slatkin 1989; Varvio et al. 1986; Zhivotovsky and Feldman 1992), we can interpret the genetic functioning of this metapopulation. First of all, this structure warrants the conservation of the global allelic diversity (Varvio et al. 1986). For example, in

Cuzalapa, as a variety is represented by several seed lots, an allele which is lost when selecting a seed lot from an insufficient number of ears (genetic drift with loss of alleles) can be retained in one or more other seed lots selected by other farmers and then conserved, at least temporarily, at the watershed scale. Geneflow between seed lots can then restore the genetic diversity of the seed lots submitted to genetic drift. Furthermore, Michalakis and Olivieri (1993) and Slatkin (1989) have shown that the effect of geneflow is reinforced by the phenomenon of colonization and replacement.

Analysis of metapopulation structures has also shown that it favors a dynamic evolution of diversity. Genetic drift and the introduction of new varieties favor the appearance of new genetic structures that are impossible to obtain in a unique population in panmixis and geneflow allows them to spread (Slatkin 1981). The management of varieties in such a system permits introduced varieties to serve as new material for the local varieties. Slatkin (1981) has shown that in a meta population structure, recessive or subdominant alleles respond better to selection than in a unique population in panmixis, the contrary being true for dominant alleles. That is, even if dominant alleles are selected, they have less potential to dominate. Likewise, the proportion of the recessive or subdominant alleles is easier to increase than in a population in panmixis. By permitting the permanence of all types of alleles, this structure warrants some level of diversity that can be considered "useless" at present, but which may prove important for the continuous adaptation of varieties.

Finally, in a meta population structure, polymorphism is favored by variable selection pressure over different subpopulations and reduced geneflow between them (David 1992; Dickinson and Antonovics 1973; Hedrick 1986; Nagylaki 1976; Roof 1994; Zhivotovsky and Feldman 1992). Strong geneflow — relative to selection pressures — would lead to uniformity over the set of subpopulations and reduction of global diversity, while the absence of geneflow would lead to inbreeding and to the death of some subpopulations. The phenotypic integrity present in Cuzalapa is maintained by different farmer selection criteria for different varieties, and by reduced geneflow.

While seed selection conserves the phenotypic integrity of the varieties, the processes occurring within the metapopulation structure formed by the group of varieties sown suggest that landraces are genetically variable over time. The traditional management of maize in Cuzalapa contributes more to the conservation of a general level of diversity than to the conservation of genetically stable and distinct maize populations. A landrace is far from a stable, distinct, and uniform unit. Its diversity is linked to the diversity of the material sown in the area, and then related to the diversity of the introduced varieties.

Implications for in situ *conservation*

The characterization of the maize farming system in the Cuzalapa watershed as open with respect to genetic material contrasts with the original model for conserving crop genetic resources *in situ,* in which farmers would be motivated not to change their cultural practices or introduce exotic genetic material (Altieri and Merrick 1987; Iltis 1974). A farming system is affected by exchange with other communities, and a variety is the product of genetic exchange with materials that mayor may not be replanted locally.

Conservationists may argue that if a community under study reveals these characteristics, it is not traditional, because traditional systems are autarchic. In fact, the characterization of a society or community is normative and relative: a community is traditional only with respect to what is perceived as modem and with respect to other contemporary human groups. In any case, the system of seed exchange that has been described by farmers and observed in Cuzalapa appears "traditional" in the sense that it is customary and long-lived. With time and improved communication with other regions, the level of seed exchange might have changed, but not the interest in looking for new genetic materials. It is likely that the major findings reported can be generalized to other rural areas of Mexico, because the factors that explain seed exchange system in Cuzalapa appear neither new nor specific to this region. To be convinced of this point, it is enough to observe the extent to which the world is the fruit of an ancient and continuous evolution that includes the diffusion of plants from their centers of domestication, the adoption and abandonment of cultivars or of cultivated plants, the differentiation of races and varieties within species, and the adaptation of cultivars to various agrosystems and techniques of cultivation (Harlan 1992; Haudricourt and Hedin 1987).

This study has shown that the set of seed lots that constitute a variety and its diversity is mutable in time. The seed exchange between farmers and the geneflow between seed lots implies that varieties evolve within the entire set of genetic material planted in the region. A seed lot does not evolve as a specific farmer line. As Berg stated (1992), it has become clear that the proper conservation unit is not a variety, and never one single seed lot per variety, but the group of cultivated varieties in their subdivision and mixture.

The diversity found in this region is the fruit of collective management of local and exotic varieties. Although individual farmers cultivate several varieties, they cannot maintain the processes that support regional diversity in isolation from other farmers. Therefore, we must focus on the mechanisms that influence the metapopulation formed by all exotic and local varieties. What is important to preserve is not the genetic material in and of itself, but the processes that create and preserve genetic diversity.

Finally, what is the significance of on-farm conservation of local varieties and what are the optimum tools for implementing on-farm conservation strategies? Is the term "conservation" appropriate? There is no single answer. Rather, the answer depends on the objective of on-farm conservation, as well as the definition of the diversity to be conserved. On this topic, the positions are not clear. In most cases, the objectives of on-farm and *ex situ* conservation are considered the same. There is a lack of debate about the role of on-farm conservation in relation to the efforts of genetic resources conservation. In

Cuzalapa, for example, it seems clear that we cannot expect complete preservation of the genetic diversity actually present in the watershed. In this case, the conservation of the material in a gene bank would be a more appropriate option, provided that appropriate methods are used to collect samples. Equally, *ex situ* conservation would be the best alternative if the objective is to conserve specific alleles.

If conservation of the phenotypic characteristics of the local varieties is considered to be the objective of an on-farm conservation project in the zone, it would be sufficient to sow the varieties on areas of adequate size to reduce genetic drift and to ask farmers to select the seed. This material can alternately be sown in farmers' fields and conserved in an official or community gene bank. If the objective is to conserve the characteristics related to environmental adaptation of this material, diverse varieties could succeed one to the other if cultivated long enough in the zone to be locally adapted, acquiring these characteristics by geneflow or environmental selection. New cultivars could also be produced from the local ones (Oldfield and Alcorn 1987).

One could also ask if it is both realistic and necessary — for world agriculture and the development of the Cuzalapa community or its agrosystem — that the Blanco, Amarillo Ancho, Perla, Negro, and Chianquiahuitl varieties are cultivated during the next century? Perhaps what is more important than the preservation of these varieties is the maintenance of a high level of phenotypic and genetic diversity: assuring that 20 different varieties continue to be cultivated in Cuzalapa, though not necessarily the same ones, and ensuring a high level of diversity for the introduced material, as massive introduction of varieties with low genetic diversity can lead to a reduction of the overall diversity. In this way, we turn the discussion from on-farm conservation of varieties to on-farm conservation of diversity.

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