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Farmers' Seed Selection Practices and Maize Variety Characteristics in a Traditionally-Based Mexican Community

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CIMMYT

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Abstract

Experimental results and farmer surveys in a Mexican community indicate that farmers' seed selection practices protect the phenological integrity of their maize varieties as they define them, despite numerous factors contributing to genetic instability. Analysis of morphological and genetic data suggests that when subjected to significant gene flow through cross-pollination, ear characteristics are maintained through farmers' selection even though other characteristics may continue to evolve genetically. Because the effects of farmers' selection practices are confined largely to ear characteristics and plant characteristics that are linked to them, their practices appear to offer only limited scope for improving varieties. Farmers' expectations of what they can achieve through seed selection are similarly modest. These findings indicate potentially complementary roles for professional breeders and Mexican farmers in developing methods to improve maize landraces on farms—*if* farmers themselves perceive benefits from the collaboration.

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Introduction

Most genetic resource specialists now agree that *ex situ* and *in situ* conservation approaches are best viewed as complementary, but prospects for *in situ* conservation of cultivated species, as opposed to wild species, are debated. Identifying methods that allow crop populations to evolve at the same time that the farmers who manage them meet their own needs presents unique challenges. Farm families and their social systems adjust to changing economic conditions as plant populations adapt to changing farming practices and environments, although perhaps more rapidly. Numerous questions have been raised about how policies aimed at fostering economic development relate to those designed to conserve genetic resources, and whether conservation can coexist with the integration of communities into commercial markets (Brush 1995; Cohen et al. 1991; Olivier and Chauvet 1991; Montecinos and Altieri 1991; Williams 1988). Prospects are likely to vary by crop (Dempsey 1996). In-depth scientific investigations of the prospects for on-farm conservation of cultivated species are now being undertaken.[1]

In recent years, "participatory" plant breeding has been proposed as a means of providing economic incentives for farmers to continue cultivating genetically desirable crop populations (Eyzaquirre and Iwanaga 1996). According to this point of view, certain techniques used by professional plant breeders may help farmers become more efficient in obtaining varieties adapted to their needs. Close collaboration between farmers and breeders could promote yield increases or other improvements in marginal environments where modern varieties have not been adopted for agronomic, social, or economic reasons. Proponents of this approach argue that while professional plant breeders have sought to develop fewer varieties that are stable over time and adapted to a wide range of environments, participatory crop improvement can support the maintenance of more diverse, locally adapted plant populations (Berg 1995; Ceccarelli, Grando, and Booth 1996; Witcombe and Joshi 1995).

In Mexico, improved seed selection practices for farmers have been recommended by INIFAP (CAECECH 1987) and are currently being promoted by other nongovernmental organizations as a participatory strategy for maize improvement (see Rice, Smale, and

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[1] At the International Rice Research Institute (IRRI), the project "Safeguarding and Preservation of the Biodiversityof the Rice Genepool, Component II: On-Farm Conservation"; in Mexico, the McKnight Foundation project "Conservation of Genetic Diversity and Improvement of Crop Production in Mexico: A Farmer-Based Approach," and at the International Maize and Wheat Improvement Center (CIMMYT), the project "Maize Diversity Management and Utilization—A Farmer-Scientist Collaborative Approach"; in Turkey, the project "Ecology and Ethnobiology of Wheat Landrace Conservation in Central Turkey"; a longitudinal study undertaken by the Institut National de la Recherche Agronomique (INRA) in France; see other initiatives described in Maxted, Ford-Lloyd, and Hawkes 1997.

Blanco 1997). The techniques have been developed with the intention of improving the effectiveness of traditional methods of mass selection.

The fundamental importance of maize seed selection to Mexican farmers is illustrated by the texts gathered in the extensive document published by the Mexican Secretary of Education (SEP 1982), representing the views of farmers from many regions of Mexico. A farmer from Chiapas states, "We will begin saying that seed is where all begins and finishes: it is the beginning and the end." Despite the many anecdotal descriptions and characterizations found in anthropological and scientific literature, however, little is documented concerning farmers' own perceptions of seed selection, their aims in selecting seed, and the effects of their practices on the genetic structure of their varieties. Often, outsiders and farmers attribute a mystical reverence for seed selection practices in traditional societies, portraying seed as a symbol of abundance and fecundity.[2] Some observers convey the impression that farmers who do not select seed before planting are "bad" or disinterested (Brac de la Perrière 1982; Hernandez X. 1985; Sandmeier, Pilate-André, and Pernes 1986).

The purpose of this study is to expand our understanding of the potential for participatory crop improvement in Mexico by improving our knowledge of traditional seed selection practices. A combination of experimental and survey data are used to: (1) relate farmers' selection to variety characteristics; (2) examine the effect of selection in the presence of genetic instability; and (3) record farmers' perceptions of their own practices. Findings are likely to be relevant for, although not necessarily representative of, other systems in traditional communities of Mexico.[3]

Context

Description of the Study Site

Mexico is the center of origin and a primary center of diversity for maize, and is therefore the focus of various initiatives designed to conserve maize genetic resources on farms. The community of Cuzalapa, where this work was undertaken, is located on the Pacific Coast of Mexico, in the municipality of Cuautitlán, State of Jalisco, in a valley in the southern section of the buffer zone of the Sierra de Manantlán Biosphere Reserve (SMBR) (Figure 1).

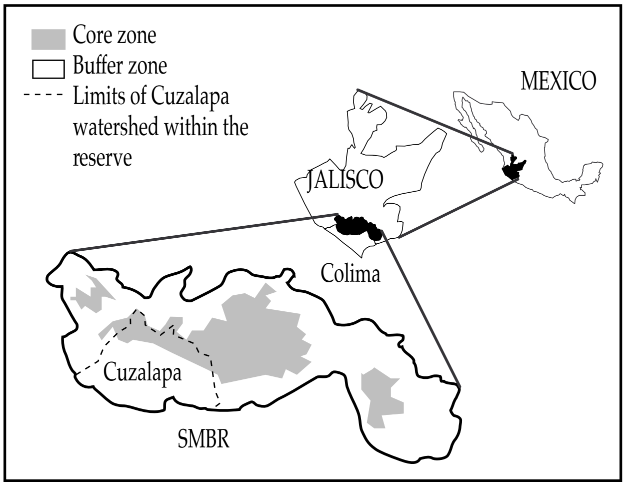

Figure 1. Sierra de Manantlan Biosphere Reserve (SMBR) and Cuzalapa watershed within the reserve.

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[2] For example, see farmers statements cited in SEP, 1982.

[3] Note that we refer to "farmers" with male pronouns because it is appropriate to do so in the case of Cuzalapa. Women may take a greater role in seed selection in other regions of Mexico and in other agricultural systems.

Under the Agrarian Reform of 1950, Cuzalapa was officially recognized as a *comunidad indígena* because its land use history pre-dates the Spanish Conquest. Today, a large proportion of its inhabitants are *mestizos* of combined European and indigenous ancestry. Cuzalapa is located in one of the most marginalized municipalities of the region, when classified according to quality of housing and level of education (Rosales and Graf 1995). Although some of its annual maize crop and cattle are sold outside the valley, Cuzalapa is poorly integrated into commercial markets.

To describe the community, we have used the term "traditionally-based" in recognition of the fact that although farmers share traditional cultural practices and live in a relatively isolated geographical zone, they are affected by numerous modern and external factors, including labor migration and changes in road infrastructure.

The Cuzalapa watershed covers nearly 24,000 ha (most of which lies within the boundary of the biosphere reserve) of mountainous land with extremely irregular topography, ranging from an elevation of 550 m to 2,660 m. The agricultural zone is located in the lowest altitudes. The climate is hot and subhumid, with a mean annual temperature of 22°C and mean annual precipitation of 1,500 mm, which is concentrated during the rainy season (July to October). Crop fields are generally located near rivers on alluvial soils of moderate fertility (Martínez and Sandoval 1993; Martínez, Sandoval, and Guevara 1991).

Each year, about 1,000 ha may be sown to maize in Cuzalapa, of which about 600 ha are irrigated (Martínez and Sandoval 1993). Irrigation and intercropping are reported to have been a feature of agriculture in Cuzalapa since pre-colonial times (Laitner and Benz 1994). Cultural practices continue to be relatively traditional when compared to those found outside the Sierra de Manantlán. Draft animals are used for plowing and cultivation, the crop is sown and harvested manually, and chemical inputs other than fertilizer are seldom used. Maize, the dominant crop, is usually grown in association with squash during the rainy season, and frequently intercropped with beans under irrigation during the dry season. Farmers grow an average of over 2 ha of maize in each season, with a mean maize yield of 2.8 t/ha (unshelled) during the rainy season, and 2.1 t/ha (unshelled) in the dry season (Louette 1994).

Factors Affecting the Genetic Structure of Maize Varieties

Louette (1994) identified 26 varieties grown in the watershed over six cycles of maize cultivation; each farmer growing between one and seven maize varieties each season and, on average, more than two. Most of these cultivars are white-grained dents, although a number are purple-grained or yellow-grained dents, and three are flints. Varieties grown for at least one farmer generation (25 years) were defined as "local," while all others (including traditional varieties and advanced generations of improved varieties) introduced from outside the community have been defined as "foreign" (Table 1). All local varieties are of the Tabloncillo race, while foreign varieties include those of the Tabloncillo race and other distinct races.

On average, the two principal white varieties (Blanco and Chianquiahuitl) cover about two-thirds of the maize area, and the six local varieties, taken together, account for more than 80% of the maize area. Maize cultivation in Cuzalapa, however, is influenced by a changing and diverse group of foreign varieties introduced continuously through farmer-to-farmer exchanges. The breadth of the genetic structure of maize is expanded for some characteristics by these introductions; the morphophenological characteristics of the local and foreign varieties are distinct and complementary. Local varieties (except for Chianquiahuitl) are characterized in this system by a shorter growing cycle, reduced vegetative development, fewer rows, and, larger kernels. In this system, foreign varieties are characterized essentially by a longer growing cycle, taller plants, more rows, and smaller kernels (Louette, Charrier, and Berthaud 1997) (Table 1).[4]

Table 1. Selected characteristics and importance of maize varieties grown in Cuzalapa, State of Jalisco, Mexico [1]

VARIETIES	% Maize area	% Farmers	Grain color	HPL[2] cm	DIA cm	NLE	WK cm	TK cm	ROW	WEA g	W1K g	Number of days to male flowering during the 1991 irrigation cycle
6 LOCAL (Tabloncillo race)												
Blanco	51%	59%	White	219	1.84	5.9	1.13	0.40	8.7	140	0.42	77
Chianquiahuitl	12%	23%	White	260	1.80	6.2	0.85	0.34	11.7	126	0.27	93
Tabloncillo	5%	6%	White	230	1.65	6.2	0.95	0.33	9.3	104	0.29	85
Perla	0.4%	0.02%	White	235	1.83	6.1	1.08	0.39	8.7	128	0.38	82
Amarillo Ancho	8%	23%	Yellow	231	1.76	6.1	1.00	0.39	9.8	126	0.33	82
Negro	3%	34%	Purple	232	1.83	6.3	0.97	0.37	10.0	123	0.31	83
20 FOREIGN (Distinct races) **3 most cultivated**												
Argentino	5%	10%	White	273	1.96	6.5	0.92	0.36	12.6	158	0.32	96
Enano	3%	12%	White	231	1.99	6.8	0.89	0.40	13.4	160	0.31	93
Amarillo	3%	11%	Yellow	261	1.90	6.6	0.99	0.38	11.3	164	0.36	92
17 minor varieties	< 3% per variety	< 4% per variety	mainly White									

[1] Based on the survey of 39 farmers during 6 growing cycles and on measurement of descriptors in a controlled trial with 3 repetitions established in Cuzalapa during the 1991 irrigation cycle.

[2] For definition see Table 2.

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[4] The characteristics of the varieties were evaluated in a controlled trial established in Cuzalapa during the 1991 irrigation cycle. Growing cycle length was evaluated by counting the number of days to male flowering. See Louette, Charrier, and Berthaud (1997) for details and more extensive discussion.

Louette, Charrier, and Berthaud (1997) have documented that many Cuzalapa farmers also replace, renew, or modify the seed stocks for their varieties by introducing seed obtained from other farmers within and outside the community. Although farmers rarely pool seed lots of different varieties, they commonly mix seed lots considered to be of the same variety to obtain needed seed quantities. Recognition of this practice led to the definition of a "seed lot" as the physical unit of seeds of a given variety used to produce the next season's crop. Farmers appear to identify a seed lot as being of a variety if it resembles it phenotypically, meaning that a variety is then a set of farmers' seed lots bearing the same name. Results of analysis of phenotypic diversity, both among the seed lots of a variety, and among varieties with seed lots bearing different names, support the hypothesis that in Cuzalapa, farmers' concept of a variety corresponds closely to that of a phenotype. The routine utilization of maize seed stocks produced by other farmers also suggests that most of these farmers do not have a strategy for producing and conserving their own seed. Contrary to the stereotype often portrayed in the social science literature, which may hold in other production systems, these landraces are *not* maintained and adapted to the farming system through selective retention of seed from successive generations of the farmers' own harvests.[5]

Farmers in Cuzalapa seem to purposefully encourage the "contamination" that naturally occurs through gene exchange in this cross-pollinating crop. Farmers' management of maize sowing leads to the development of different varieties on contiguous areas—favoring genetic exchange and probably a modest degree of heterosis among all cultivar types—independent of the origin and growing cycle of the different varieties. In effect, differences in sowing dates can lead to the coincidence of flowering among varieties with different growing cycles. The varieties sown are not genetically isolated (Louette 1994; for Chiapas, see Bellon and Brush 1994). The continual reproduction of the varieties with outcrossing and introgression could lead to important modifications of their morphological characteristics and allelic frequencies.

Methods

The methods used combined formal and informal farmer surveys, direct observations of farmers' practices, and experiments. Each are described in greater detail below.

Identifying Farmers' Seed Selection Criteria Preliminary information on seed selection practices and farmers' criteria was obtained through informal interviews and direct observation with different groups of farmers. These were followed by two experiments.

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[5] Franzen et al. (1996) summarize this stereotype well: "in many developing countries . . . smallholders produce, in the traditional cropping systems, their own seed by saving part of the harvest for sowing the next crop. In this way, the seed is handed down from generation to generation . . . " (p. 20). They add that this closed system opens up through exchange of seed with neighbors, hence traditional varieties undergo genetic changes over the centuries. The rate of exchange and extent of the openness encountered among traditional maize farmers in this and related studies in Mexico (Aguirre 1997; Louette, Charrier, and Berthaud 1997; Rice, Smale, and Blanco 1998) is, nevertheless, surprisingly large.

Experiment 1. The purpose of the first experiment was to identify traditional seed selection criteria for the two major white maize varieties grown in Cuzalapa, Blanco and Chianquiahuitl. For each of the two varieties, a plot with 1,500 plants was delimited in the center of a representative farmer's field in Cuzalapa. Each plant within the plot was numbered and after silking, stalk diameter (DIA), ear height (HEA), plant height (HPL), and number of leaves above the ear (NLE) were measured. The index of dry matter ($HD2=HPL*DIA^2$)[6] and the ratio of the plant height to ear height (E/P) were calculated from these descriptors. At maturity, when all plants were completely dry, each ear was harvested and numbered according to the plant that produced it. Each ear was measured for descriptors easily identifiable by the farmer at time of seed selection: total ear length (LEA), length of the ear presenting kernels (LGR), ear weight (WEA), ear diameter (DEA), number of kernel rows (ROW), number of kernels per row (KR), and thickness of the kernel (TK). The width of the kernel (WK) was obtained by dividing the circumference of the ear by the number of kernel rows. The total number of kernels (K) was calculated from the KR*ROW. The alignment or arrangement of the kernels on the row (ALI) was characterized using two categories; the health of the ear (incidence of rots and insects) (PIC) using three categories; and the quality of the filling (FIL) using four categories (Table 2 defines descriptors and shows their abbreviations).

Cuzalapa farmers do not traditionally select seed from plants in the field during the cropping season or at harvest, and their selection is based exclusively on ear characteristics. Each of 25 farmers was asked to select 15 seed ears per variety from the set of previously harvested, husked, and marked ears produced by the 1,500 plants in the experimental field, corresponding to a selection pressure of 1%. Although selection pressure under farmers' conditions will vary from year to year, 1% is equivalent to the usual selection pressure if a farmer selects only enough seed from one harvest to ensure the same number of plants in the subsequent season (given the mean number of kernels per ear used for seed, the germination rate, the survival rate of plants, and the incidence of barren plants). The set of ears selected by the 25 farmers was pooled into one sample, including the ears selected by more than one farmer only once.

A comparison of the characteristics of seed ears selected by the farmers with those of the full set of ears harvested from the plots reveals the farmers' selection criteria. Comparing the characteristics of the set of plants from which farmers selected ears with those of the entire set of plants in the plot allows us to identify the indirect effect of ear selection on plant characteristics. ANOVA analysis was used to compare the characteristics statistically, transforming categorical variables (NLE, ROW, PIC, FIL, and ALI) into ranges. For each descriptor, the mean value for the selected set of ears was compared to the mean value for the population as a percent of the mean value for the population. To determine farmer consensus in selection criteria, the frequency with which the same ear was selected by different farmers was calculated.

Experiment 2. An experiment with five varieties generalized these results across varieties. For each of the five varieties, sets of 15 to 30 seed ears were selected by 2 to 5 individual farmers; sets of 15 to 30 seed ears were also drawn randomly from the farmer's harvest. The selected

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[6] An $r^2 > 0.85$ between HD2 and dry matter has been reported for maize by Navarro (1984) and Scopel (1994).

and random sets of ears were then grouped together by variety and compared. Descriptors included the length, width, and thickness of the kernel (LK, WK, TK), number of kernel rows (ROW), cob and ear diameters (DCO, DEA), ear, cob and kernel weight (WEA, WCO, WK), and total ear length (LEA) (see Table 2). The five varieties were: Blanco, Amarillo Ancho, Negro, Chianquiahuitl, and Argentino. The first three have white, yellow, and black kernels, respectively, with a short growing cycle, reduced vegetative development, 8 to 10 kernel rows, and large kernels. The last two have white kernels, a long growing cycle, taller plants, 10 to 14 kernel rows, and small kernels (Table 1).

To reflect the hypothesis that farmers' selection decisions are based on multiple factors rather than a single factor, a Factorial Discriminant Analysis (FDA), comparable to a multifactorial ANOVA, was used to analyze multifactorial differences among seed samples. Using the data from each ear, FDA distinguishes samples based on the variables for which the ratio of the sum of squared differences within a sample to the sum of squared differences among samples is the greatest.

Table 2. Vegetative and ear descriptors

Vegetative descriptors	
HPL	Total plant height (from the soil to the last node)
HEA	Ear height (from the soil to the upper ear node)
E/P	Ratio of ear height to plant height (HEA/HPL)
DIA	Stalk diameter (biggest diameter measured at 5 cm from the soil, with a caliper)
HD2	Indices of dry matter (HPL*DIA*DIA)
LLE	Ear leaf length (from the ligule to the end of the leaf of the superior ear node)
WLE	Ear leaf width (at the middle length of the upper ear leaf)
NLE	Number of leaves above the superior ear, including the leaf of the superior ear node
Ear descriptors	
LEA	Total ear length (from the base to the tip of the ear)
LGR	Length of the ear presenting kernels (from the base of the ear to the last kernels)
WEA	Ear weight at 15% of humidity
DEA	Ear diameter (measured at the middle length of the ear with a caliper)
WCO	Cob weight at 15% of humidity
DCO	Cob diameter (measured at the middle length of the cob with a caliper)
ROW	Kernel row number (counted at the middle length of the ear)
KR	Number of kernels per row (counted over two rows per ear)
K	Total number of kernels (KR*ROW)
LK	Kernel length (mean of 3 kernels per ear, measured with a caliper)
WK	Kernel width (mean of 10 kernels per ear, measured at the tip of the kernel with a caliper) or Phi*DEA/ROW
TK	Kernel thickness (mean of 10 kernels per ear, measured at the top of the kernel with a caliper)
W1K	1 kernel weight at 15% of humidity (mean of 3 samples of 100 kernels/100)
ALI	Alignment of kernels on the row 0 = kernels not aligned; 1 = kernels aligned
PIC	Degree of infection of the ear by pest and fungi 0 = ear rot or heavily affected by insects or fungi, 1 = only the tip of the ear affected, 2 = ears not affected
FIL	Quality of filling of the ear 0 = no ear (less than 50 kernels), 1 = kernels missing on some rows and on the tip of the ear, 2 = kernels missing only on the tip of the ear, 3 = well filled ear

Determining the Influence of Selection over the Genetic Structure of Varieties

Experiment 3. A third experiment was conducted to determine the effects of farmer seed selection criteria on the maintenance and conservation of variety characteristics. The influence of farmer selection was determined by comparing seed lots selected by farmers to those selected at random under conditions of strong genetic contamination. At the beginning of the first cycle, two sets of ears of the *Negro* variety were constituted from the harvest of one farmer: a set of 100 ears drawn at random and a set of 100 ears selected by the farmer for seed. From each set, a sample of seed was constituted using two kernels per ear (S0, initial selected seed sample; R0, initial random seed sample). Each sample was sown in a 20m x 20m area within a farmer's field in Cuzalapa. In the first season, the surrounding field was planted to Amarillo Ancho, which is referred to as the "contaminating variety, cycle 1" (Figure 2). At the end of the first cycle, a set of 100 ears was drawn at random from the plot sown with R0 and a set of 100 ears was selected by the same farmer from the plot sown with S0. Samples of seed were constituted from each set of ears (S1, first generation of selected seed; R1, first generation of randomly selected seed).

Farmer conditions did not permit the reestablishment of the experiment with the same contaminating variety in the second season, and the experiment was then subdivided. In cycle 2, one pair of seed lots selected by farmers (S1) and at random (R1) were contaminated by Blanco, while another pair was submitted to contamination by Chianquiahuitl. Both

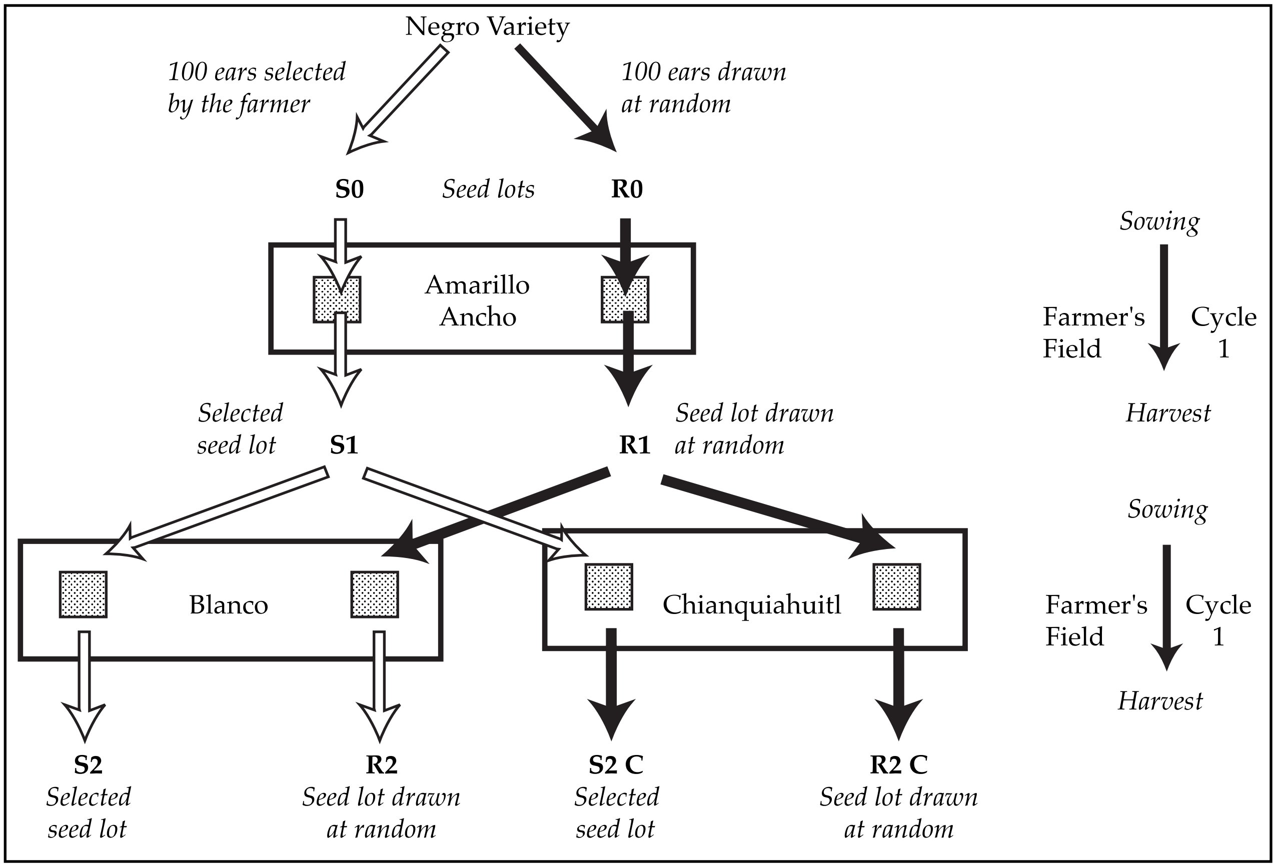

Figure 2. Method for determining the influence of seed selection over geneflow.

pairs were sown with the same arrangement as the R0 and S0 seed lots. Blanco has phenotypic and phenological characteristics that are more similar to those of the Amarillo Ancho and Negro varieties, than those of the Chianquiahuitl variety (Table 1). Chianquiahuitl has a longer growing cycle, greater vegetative development, and more rows of smaller kernels. At harvest S2 and R2 were constituted in the same way as S1 and R1.

Several duplicates of R0, S0, R1, and S1, constituted in the same way, were stored in the genebank at CIMMYT until the end of the last cycle of contamination. A controlled experiment with four complete blocks (6 furrows per 4 m plots) was established at the INIFAP Experiment Station at La Huerta near Cuzalapa. The initial population of Negro (represented by R0) was compared to the populations of the last generation of selected seed (S2B and S2C) and to seed drawn at random (R2B and R2C). Per plot, 20 plants and 15 ears produced by these plants were measured for plant and ear characteristics: HEA, HPL, DIA, LLE, WLE, NLE, LK, WK, TK, DEA, DCO, LEA, ROW, WEA, WCO, WK (see Table 2 for abbreviations and methods of measure). Fewer ears than plants were measured because ear descriptors appeared to vary less than plant characteristics reported in earlier research (see Louette 1994). Sixty plants per treatment (15 per block) were measured completely for ear and plant characteristics.

S0, S1, and S2 represent the usual farmer practice, and R0, R1, and R2 represent what would happen in the absence of farmer selection pressures: R2B, R2C, S2B, and S2C were subjected to contamination by two different varieties during the two cycles, but because Amarillo Ancho and Blanco are close phenotypically, the conditions of contamination were similar during the two cycles for R2B and S2B. Conditions were very different for R2C and S2C, which were contaminated by Chianquiahuitl during the second cycle.

The data were compared using an ANOVA procedure with two factors: (1) contamination (0, 2B, and 2C), and (2) selection (selected by farmer or selected at random). FDA was used to analyze multivariate differences among treatments, considering for each treatment the plants with full sets of data for ear and plant descriptors.

The seed samples (R0, R2B, R2C, S2B, and S2C) were also compared for nine enzymatic systems at 15 isoenzymatic loci. The systems were: (1) Acid phosphatase (ACP) EC 3.1.3.2; (2) Peroxidase CPX EC 1.11.1.7; (3) Esterase (EST) EC 3.1.1.1; (4) Glutamate deshydrogenase (GDH) EC 1.4.1.3; (5) Glutamate-Oxaloacetate Transaminase (GOT) EC 2.6.1.1; (6) Isocitrate Dehydrogenase (IDH) EC 1.1.1.42; (7) Phosphoglucose isomerase (PGI) EC 5.3.1.9; (8) Phosphoglucomutase (PGM) EC 2.7.5.1; and (9) Shikimic Acid Deshydrogenase (SAD) EC 1.1.1.25). The loci were: ACP-1 and 2, CPX-1, 2 and 3, EST-8, GDH-2 and 3, GOT-1 and 2, IDH-1, PG-1, PGM-1 and 2, and SDH-1. The techniques used were those recommended by Stuber et al. (1988). Based on the allele frequencies for the nine polymorphic alleles, pairwise χ^2 distances were calculated between R0 (Negro) and samples for the Blanco and Chianquiahuitl varieties, and between R0 and R2B, R2C, S2B, and S2C.

Eliciting Farmers' Perceptions of Seed Selection

Farmers' perceptions of the purpose of seed selection and additional details on their practices were obtained through participant observation during the period of the experimental research, semi-structured interviews, and structured interviews with 25 farmers. In the first series of semi-structured, personal interviews, farmers were informally asked questions from a checklist, and responses were discussed. Questions were clustered into three themes: (1) on which characteristics do farmers focus when selecting seed ears, (2) what do farmers believe is the purpose of selection, and (3) what do farmers believe can be accomplished through seed selection. The questions elicited their opinions about seed selection and its potential for improving their maize landraces, thus providing additional information about farmers' knowledge systems and the potential for on-farm maize improvement through seed selection strategies. In the second set of interviews, questions were reduced to those shown in Table 9 (see page 20). To more fully interpret their responses, farmers were asked how they believed they might modify (a) row numbers and (b) flowering date. To reduce confusion over interpretation, the Spanish phrases they used are reported below with English translations.

Results

Seed Selection Practices

Cuzalapa farmers do not select seed from plants in the field during the cropping season or at harvest, but from the pile of harvested ears that constitutes the household's grain stocks. These stocks are composed of husked ears and include ears from the entire population of maize plants in the farmers' fields—those in the center and those on the borders of the field, which are more likely to be contaminated by adjacent maize fields. Sometimes farmers select their ears for seed immediately before planting, choosing them from the ears remaining after consumption of the previous season's harvest.

Among the farmers studied here, seed selection was based exclusively on ear characteristics. Farmers do not control pollen sources or consider the vegetative and agronomic characteristics of the plants that produce the ears. Although cases are occasionally reported of seed selection in the field during harvest, selection on ear characteristics alone seems to be the common practice for maize in Mexico (SEP 1982). The absence of plant selection is not, however, common to all traditional agricultural systems. Berg (1993), Sandmeier, Pilate-André and Pernés (1986), and Mushita (1992) have described selection methods based on plant characteristics for sorghum and pearl millet in Africa.

Most farmers in Cuzalapa use only the kernels from the center of the ear for seed. The 2 to 3 kernels of the base and the 5 to 6 kernels of the top of each row of kernels are excluded. A farmer from Guerrero explains: "After harvest, we choose the biggest ears (*hueycintli*) from which we take off the badly filled kernels (*popoyotl*), those which have begun to rot because of the humidity (*tlayolpoyaque*) and those damaged by insects (*tlayolcoyonqui*). Once this cleaning is complete, we shell the tip (*coaoya*) and the base (*zinhoya*) of the ear so that only the finest kernels of the center of the ear remain. These are the selected seed (*xinaxli*) for the next sowing" (SEP 1982). The practice of using only kernels from the center of the ear appears to be widespread in Mexico (SEP 1982), and has been reported for the K'ekchi of Guatemala, the Mandan of the USA, the Guaymi of Panama (Johannessen 1982), and among other peoples and regions where maize is grown, but did not originate (for Nepal, see Leslie 1986; for Malawi, Smale et al. 1992).

The significance of the practices is not fully understood, however, farmers generally believe that kernels from the ear tip will not germinate or will produce badly developed ears with small kernels. The kernels from the ear tip are usually smaller, have poor reserves, and are often damaged by birds, insects, and fungi, which may justify their exclusion. Unpublished results of germination tests (conducted by the first author) indicate that the upper kernels have a slower and lower germination rate than those of the base or center. No clear justification exists for the base kernels. Kernels at the base of the ear (called "male" kernels) are thought to produce no ear or an ear with deformed kernels. Since the first silks emerge from the base of the ear, these kernels have a greater probability of self-pollination and inbreeding.

Farmers' Selection Criteria

"Big, clean ears" and "big kernels" are the selection criteria mentioned by farmers in most areas of Mexico in the texts gathered by SEP (1982). Cuzalapa farmers involved in the experiments and surveys reported that they select well-developed, well-filled ears without fungi or insect damage.

For both Blanco and Chianquiahuitl, a comparison of the characteristics of the ears selected by farmers with those harvested from the total population of plants confirms the importance of farmers' criteria. All descriptors, except the ratio of ear height on plant height (E/P) and the thickness of the kernel (TK), had a significantly higher level in the selected set of ears than in the population. The thickness of the kernel (TK) was the only characteristic with a significantly lower value on seed ears (Table 3).

For both varieties, the ear descriptors on which farmers exerted the greatest selection pressure (see variation in percent) were those most related to the criteria they identified as important: ear weight (WEA), ear length (LEA), length of the ear presenting kernels (LK), total number of kernels (K), and kernel filling (FIL). The alignment of kernels on the rows (ALI) appeared to have some importance also, although it may only be aesthetic.

Although farmers select seed only on the basis of ear characteristics, some indirect selection on plant characteristics is observable—especially for the indices of dry matter (HD2) and stalk diameter (DIA), which are correlated. For other vegetative descriptors, however, differences between the set of plants from which ears were selected and the set of plants from which ears were discarded for seed were less than the differences observed for ear characteristics between selected and non-selected ears (Table 3). The indirect effect of selection on plant characteristics can be explained by their correlation with the descriptors linked to ear development (Table 4). A well developed plant has a good chance of producing a well developed ear, and a well developed ear has a higher probability of being selected by farmers. In general, for both ear and plant characteristics, large differences were found for descriptors that are linked to the development of the ear.

Table 3. Experiment 1. Comparison between the total population of plants and ears and the set of ears selected for seed by 25 farmers

	BLANCO				CHIANQUIAHUITL			
	Population Mean (SDev.)	**Seed Selected Mean (SDev.)**	**% var [3]**	**Significance of the difference [4]**	**Population Mean (SDev.)**	**Seed Selected Mean (SDev.)**	**% var**	**Significance of the difference**
Vegetative[1]	**1500 plants**	**142 plants**			**1500 plants**	**168 plants**		
HPL	181.1 (28.4)	200.9 (25.6)	+ 10.9	***	198.6 (32.0)	213.5 (26.4)	+ 7.5	***
HEA	103.6 (21.5)	117.6 (20.7)	+ 13.5	***	103.3 (23.4)	109.2 (21.1)	+ 5.7	***
E/P	0.57 (0.07)	0.58 (0.06)	+ 1.8	*	0.51 (0.07)	0.51 (0.06)	0.0	**NS**
DIA	1.40 (0.29)	1.69 (0.30)	+ 20.7	***	1.88 (0.45)	2.27 (0.38)	+ 20.7	***
HD2	384.0 (198.7)	605.0 (250.0)	+ 57.6	***	771.3 (418.1)	1130.1 (399.1)	+ 46.5	***
NLE [2]	5.28 (0.64)	5.51 (0.63)	+ 4.4	***	6.39 (0.94)	6.65 (0.90)	+ 4.1	***
3-4	8.1 %	2.8 %			1.6 %	0.0 %		
5	57.4 %	47.2 %	- 17.0		7.4 %	2.9 %		
6	32.3 %	45.8 %	+ 41.8		61.8 %	54.8 %	- 11.3	
7	2.1 %	4.2 %			9.7 %	17.3 %	+ 78.4	
8	0 %	0 %			19.4 %	24.4 %	+ 25.8	
9	0 %	0 %			0.2%	0.6%		
Ear [1]	**1233 ears**	**142 ears**			**1125 ears**	**168 ears**		
LEA	14.0 (3.0)	17.2 (2.6)	+ 22.9	***	15.6 (3.5)	17.9 (2.6)	+ 14.7	***
LGR	11.5 (3.0)	15.0 (2.9)	+ 30.4	***	13.7 (3.6)	16.4 (2.8)	+ 19.7	***
WEA	72.2 (33.6)	121.5 (33.1)	+ 68.3	***	128.6 (55.4)	185.3 (50.7)	+ 44.1	***
DEA	3.51 (0.38)	3.87 (0.33)	+ 10.3	***	3.87 (0.44)	4.20 (0.38)	+ 8.5	***
ROW [2]	8.36 (1.17)	8.42 (1.23)	+ 0.7	***	10.87 (1.6)	11.40 (1.38)	+ 4.9	***
<8	6.7 %	4.2 %			0 %	0 %		
8	69.0 %	71.8 %	+ 4.1		8.3 %	1.2 %		
10	23.3 %	21.8 %	- 6.4		50.0 %	40.5 %	- 19.0	
12	0.8 %	1.4 %			32.0 %	46.4 %	+ 45.0	
>12	0.2%	0.7 %			9.7 %	11.9 %		
K	206.3 (77.4)	294.6 (71.5)	+ 42.8	***	324.4 (114.6)	432.4 (79.3)	+ 33.3	***
WK	1.31 (0.16)	1.44 (0.15)	+ 9.9	***	1.13 (0.15)	1.17 (0.12)	+ 3.5	***
TK	0.40 (0.09)	0.37 (0.05)	-7.5	***	0.38 (0.06)	0.37 (0.05)	-2.6	**
ALI [2] *0*	27.7%	10.6%		***	34.4%	17.3%		***
1	72.3%	89.4%	+ 23.7		65.6%	82.7%	+ 26.1	
PIC [2] *0*	3.6%	1.4%		***	0.2%	0.6%		***
1	32.6%	4.9%			3.3%	2.4%		
2	63.7%	93.7%	+ 47.1		96.5%	97.0%	+ 0.5	
FIL [2] *1*	11.9%	2.1%		***	18.3%	3.0%		***
2	70.1%	52.1%			34.0%	23.2%		
3	18.0%	45.8%	+ 154.4		47.7%	73.8%	+ 54.7	

[1] For definition see Table 2

[2] Data were transformed in ranges to apply the ANOVA test, and % of var was calculated for the main classes

[3] % var: (mean value in the selected set— mean value in the population) / mean value in the population

[4] Significant differences at 5% (*), 1% (**), 0.1% (***); Non-significant differences at 5% (NS)

Some descriptors were affected differently according to varietal characteristics. Selection increased the proportion of ears with eight rows and the width of the kernels in the Blanco variety. In the Chianquiahuitl, selection increased the proportion of ears with more than 12 rows, inducing little change in width of kernel (Table 3). The change in the Blanco was less pronounced than in the Chianquiahuitl, because more than two-thirds of the Blanco ears in the population had eight rows. The percent of Chianquiahuitl ears with more than 12 rows

Table 4. Experiment 1. Pearson correlation coefficient between descriptors measured on 1,500 plants and on the ears produced by these plants, Blanco and Chianquiahuitl varieties

BLANCO VARIETY

		Plant descriptor[1]					**Ear descriptor[1]**							
		HEA	**HPL**	**DIA**	**HD2**	**NLE**	**LEA**	**LGR**	**DEA**	**ROW**	**WK**	**TK**	**K**	**WEA**
Plant Descript.	**HEA**	1.00												
	HPL	**0.81**	1.00											
	DIA	**0.54**	**0.58**	1.00										
	HD2	**0.65**	**0.72**	**0.96**	1.00									
	NLE	**0.17**	**0.49**	**0.28**	**0.35**	1.00								
Ear Descript.	**LEA**	**0.41**	**0.49**	**0.53**	**0.56**	**0.29**	1.00							
	LGR	**0.40**	**0.48**	**0.55**	**0.58**	**0.29**	**0.88**	1.00						
	DEA	**0.31**	**0.40**	**0.49**	**0.48**	**0.27**	**0.41**	0.41	1.00					
	ROW	0.08	**0.12**	**0.16**	**0.15**	**0.12**	-0.02	0.00	**0.42**	1.00				
	WK	**0.21**	**0.27**	**0.32**	**0.31**	**0.16**	**0.39**	**0.37**	**0.58**	**-0.56**	1.00			
	TK	-0.08	-0.09	**-0.12**	**-0.10**	-0.06	**-0.16**	**-0.18**	**-0.22**	-0.09	**-0.14**	1.00		
	K	**0.35**	**0.43**	**0.50**	**0.52**	**0.26**	**0.66**	**0.72**	**0.56**	**0.39**	**0.20**	**-0.46**	1.00	
	WEA	**0.40**	**0.49**	**0.60**	**0.62**	**0.30**	**0.75**	**0.76**	**0.74**	**0.20**	**0.52**	**-0.28**	**0.81**	**1.00**

CHIANQUIAHUITL VARIETY

		Plant descriptor[1]					**Ear descriptor[1]**							
		HEA	**HPL**	**DIA**	**HD2**	**NLE**	**LEA**	**LGR**	**DEA**	**ROW**	**WK**	**TK**	**K**	**WEA**
Plant Descript.	**HEA**	1.00												
	HPL	**0.76**	1.00											
	DIA	**0.20**	**0.31**	1.00										
	HD2	**0.39**	**0.55**	**0.94**	1.00									
	NLE	0.08	**0.38**	**0.24**	**0.31**	1.00								
Ear Descript.	**LEA**	**0.30**	**0.43**	**0.62**	**0.63**	**0.24**	1.00							
	LGR	0.26	**0.37**	**0.62**	**0.62**	**0.19**	**0.92**	1.00						
	DEA	**0.25**	**0.30**	**0.49**	**0.49**	**0.15**	**0.51**	**0.51**	1.00					
	ROW	0.07	0.09	**0.20**	**0.21**	0.10	**0.16**	**0.17**	**0.50**	1.00				
	WK	**0.14**	**0.16**	**0.20**	**0.20**	0.03	**0.26**	**0.26**	**0.32**	**-0.64**	1.00			
	TK	**0.10**	**0.18**	0.08	**0.13**	**0.12**	**0.15**	**0.13**	0.02	-0.08	0.10	1.00		
	K	**0.14**	**0.18**	**0.46**	**0.42**	**0.11**	**0.60**	**0.66**	**0.60**	**0.57**	-0.10	**-0.27**	1.00	
	WEA	**0.28**	**0.38**	**0.62**	**0.63**	**0.21**	**0.77**	**0.80**	**0.79**	**0.36**	**0.28**	0.06	**0.74**	1.00

[1] For definition see Table 2.

[2] All correlations are statistically significant. Those marked in bold have a magnitude > 0.5.

rose from 41.7% to 58.3%. Row number is part of the ideotype of a variety and is a trait on which farmers can directly select. Because the number of rows is a distinguishing feature of the varieties, the results suggest a link between the selection pressures of farmers and their variety ideotypes.

Other characteristics were affected differently because of field conditions where the crop was cultivated. For example, in comparing the Blanco to Chianquiahuitl, selection greatly reduced the proportion of ears affected by fungi or insects. Because of better field conditions or differences in susceptibility, the Chianquiahuitl produced a smaller proportion of rotten ears (3.5% for the classes 0 and 1 of PIC) than the Blanco (36.2%).

These results need to be interpreted with some caution. Because the comparison was made on the characteristics of the seed selected by farmers or at random, rather than on their progeny (after simultaneously growing out the ears from the 1,500 plants and those from the selected sample), the observed differences cannot be assumed to represent genetic differences. They may reflect, for example, the effects of isolated plants with less competition from neighbors than the average of the other plants.

The consensus test revealed the consistency of seed selection criteria among farmers. Out of the ears selected for the Blanco, 43% were selected by farmers more than once. Six of the same ears were selected by 10 different farmers. For Chianquiahuitl, 38% of all of the ears selected by farmers were selected more than once, and the same six ears were selected by seven. The total number of ears selected more than once represents no more than 5-6 % of all of the ears displayed by either variety (Table 5).

Criteria and Variety Ideotype

The findings of Experiment 1 are generalized by Experiment 2. Results confirm that seed selection: (1) is oriented to heavier, bigger, and better-developed ears, and (2) reinforces differences between varieties with long and short growing cycles.

In Figure 3, the descriptors that are strongly linked to the first axis of the FDA are those that distinguish varieties in Cuzalapa based on the length of their growing cycle (ROW, WK, and TK), while those linked to the second axis are related to ear development (WEA, DEA, or LK).

Table 5. Experiment 1. Farmers consensus on seed selection criteria

	Total number of ears produced by the plants	Total number of distinct ears selected by the 25 farmers[1]	Ears selected once		Ears selected more than once		
			Number of ears	% of selected ears	Number of ears	% of selected ears	% of ears produced by the plants
BLANCO	1233	142	81	57%	61	43%	5%
CHIANQUIAHUITL	1125	168	103	62%	65	38%	6%

[1] The same ear selected by several farmers is counted as one ear. Total of 25 farmers selecting ears.

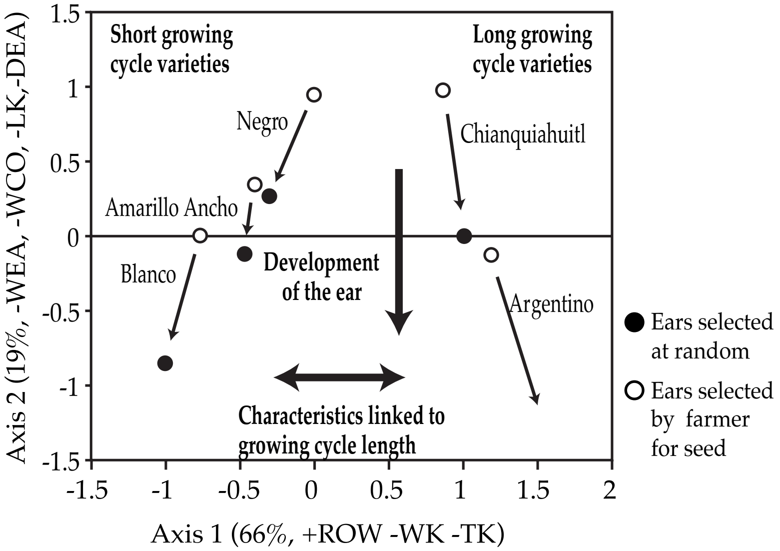

Figure 3. Seed selection criteria for five of the main varieties (Fact. Disc. Anal.).
Note: Percent following axis number indicates the proportion of the total variation explained by the axis. Descriptors refer to those most correlated with the axis, and number in parentheses indicates direction of correlation. See Table 2 for definition of descriptors.

For each of the five major varieties (Blanco, Chianquiahuitl, Amarillo Ancho, Argentino, and Negro), relative to the randomly drawn sample, the selected sample is always located along axis 2 in the direction of more developed ears. In general, the differences are highly significant between the samples of ears selected for seed and the samples drawn at random for the descriptors that define that axis (Table 6).

As shown by the relative position of the selected and random samples on axis 1 (Figure 3), selection causes

Table 6. Experiment 2. Comparison between the set of selected ears and the set of ears drawn at random for 5 varieties[1]

VARIETY	Sets of ears	No. of ears	WEA[2]	WCO	DEA	DCO	LK	LEA	ROW	WK	TK
BLANCO	Random	90	109.5	15.3	3.76	2.12	0.95	16.1	8.74	1.06	0.38
			(31.2)	(5.9)	(0.34)	(0.26)	(0.13)	(2.8)	(1.10)	(0.09)	(0.04)
	Selected	103	148.6	20.6	3.98	2.12	1.04	18.5	8.62	1.23	0.40
			(24.9)	(5.3)	(0.24)	(0.21)	(0.08)	(2.1)	(0.97)	(0.08)	(0.03)
			***	***	***	NS	***	***	NS	***	**
AMARILLO ANCHO	Random	140	105.6	16.5	3.73	2.15	0.92	16.1	9.33	1.00	0.38
			(29.4)	(5.2)	(0.30)	(0.27)	(0.10)	(2.4)	(1.33)	(0.09)	(0.04)
	Selected	100	130.3	19.1	3.88	2.23	0.94	17.5	9.28	1.02	0.38
			(27.9)	(5.4)	(0.31)	(0.30)	(0.09)	(2.0)	(1.32)	(0.08)	(0.04)
			***	***	***	*	NS	***	NS	*	NS
NEGRO	Random	60	81.4	12.1	3.57	1.99	0.82	14.1	9.33	0.94	0.35
			(32.4)	(4.4)	(0.28)	(0.28)	(0.09)	(2.7)	(1.31)	(0.09)	(0.04)
	Selected	60	119.5	17.7	3.70	2.05	0.90	17.4	9.30	0.99	0.36
			(26.4)	(4.5)	(0.26)	(0.17)	(0.08)	(1.9)	(1.32)	(0.08)	(0.04)
			***	***	**	NS	***	***	NS	**	NS
CHIAN-QUIAHUITL	Random	71	97.6	15.3	3.70	2.01	0.94	14.6	11.44	0.82	0.34
			(38.0)	(7.0)	(0.38)	(0.26)	(0.12)	(2.8)	(1.44)	(0.08)	(0.04)
	Selected	79	145.9	20.2	4.03	2.09	1.01	17.0	12.00	0.83	0.34
			(28.7)	(5.7)	(0.29)	(0.22)	(0.09)	(2.0)	(1.54)	(0.07)	(0.03)
			***	***	***	*	***	***	*	*	NS
ARGENTINO	Random	60	130.3	20.7	4.22	2.32	0.99	14.5	12.30	0.88	0.33
			(60.2)	(10.4)	(0.46)	(0.32)	(0.12)	(3.3)	(1.70)	(0.07)	(0.05)
	Selected	60	187.0	28.7	4.58	2.46	1.07	16.4	13.10	0.90	0.34
			(66.0)	(11.8)	(0.38)	(0.24)	(0.12)	(3.0)	(1.40)	(0.08)	(0.03)
			***	***	***	**	**	**	**	NS	NS

---

[1] Mean with standard deviation in brackets. Significant differences at 5% (*), 1% (**), 0.1% (***); non-significant differences at 5% (NS).
[2] See Table 2 for definitions of variables.

divergence among the varieties of different growing cycle length, with respect to number of rows and kernel width. In Cuzalapa, number of rows and kernel width are related to length of growing period, since fewer rows and wider kernels are associated with early-maturing varieties, and more rows with smaller kernels are characteristics of later-maturing varieties (Table 1). Maintaining this distinction is economically important in a farming system with two growing seasons, each of which is associated with its own agroecological features. The farmers also exclude ears that have mixed color kernels, in order to maintain the kernel color of their varieties. Kernel color also distinguishes varieties according to their use by farm families as either food or feed.

Selection Effects on Gene Flow

The results of the third experiment demonstrate that seed selection serves to maintain the ear characteristics that define varieties. Both the effects of contamination and the counteracting effects of seed selection can be observed by comparing the characteristics of the first and last generation of the seed selected by farmers to those of the seed selected at random. The comparison was conducted for morphological descriptors (visible to farmers) and for allele frequencies (invisible to farmers).

Morphological characteristics. Analysis of variance (ANOVA) reveals a low number of significant differences in morphological characteristics between the initial Negro population and seed drawn at random or selected from the contaminated Negro population (Table 7). However, the values of the characteristics in R0 (initial population), R2B (second generation drawn at random and contaminated by Blanco), and R2C (second generation drawn at random and contaminated by Chianquiahuitl) are nearly always classified in the same order as the value for the three varieties Blanco, Chianquiahuitl, and Negro, except for kernel thickness (Table 1 and 7). As expected, given the differences between the varieties, the differences always appear greater between R0 and R2C than between R0 and R2B.

The factorial discriminant analysis (FDA) shows the same trends graphically (Figure4). The plane defined by the two first axes accounts for 80 percent of the total variation (50 on axis 1 and 30 on axis 2). The descriptors that are highly linked to the axis 1 are plant characteristics (HPL, HEA, NLE, and DIA), while those more strongly linked to axis 2 are ear characteristics (W1G, TK, ROW, and WK).

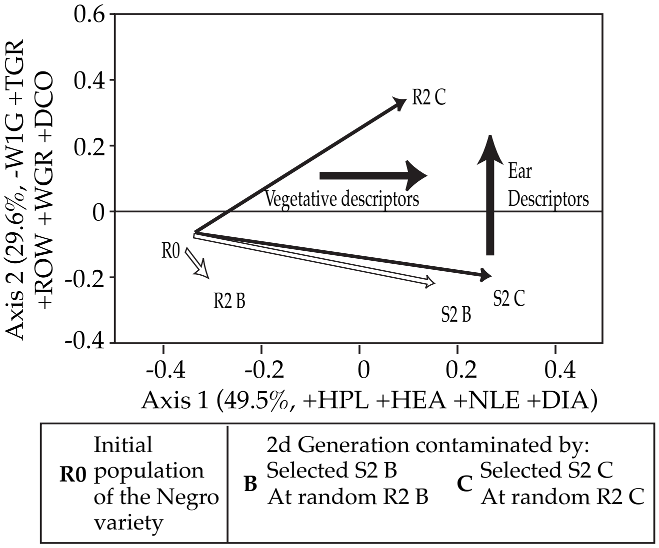

Figure 4. Contamination of the Negro variety by Blanco and Chianquiahuitl and contamination control by seed selection.

Note: Percent following axis number indicates the proportion of the total variation explained by the axis. Descriptors refer to those most correlated with the axis, and number in parentheses indicates direction of correlation. See Table 2 for definition of descriptors.

Figure 4 illustrates both the effects of contamination and the effects of selection. The proximity of R0 to R2B demonstrates that the contamination of the Negro by the Blanco, which is phenotypically similar to the Negro, has little effect on plant and ear descriptors. By contrast, contamination by the Chianquiahuitl, which is phenotypically different from Negro, induces changes related to the characteristics of the Chianquiahuitl. R2C has greater vegetative growth than R0, as expressed by the plant height (HPL), ear height (HEA), number of leaves (NLE), and stalk diameter (DIA) on the first axis of the FDA. R2C also presents smaller kernels arranged on more rows (weight of one kernel W1K, width of the kernel WK, and number of kernel rows ROW), as indicated by the second axis. The values are statistically different for DIA only (Table 7).

Table 7. Experiment 3. Comparison of ear and plant descriptors for R0 , S2B, R2B, S2C, and R2C

Treatments		**HPL**	**HEA**	**DIA**	**NLE**	**ROW**	**WK**	**TK**	**W1K**
R0	**Mean**	293.9	169.6	2.21	6.31	10.07	1.04	0.37	34.2
	SD.	(6.7)	(3.4)	(0.13)	(0.14)	(0.28)	(0.02)	(0.01)	(2.7)
S0	**Mean**	286.4	164.0	2.19	6.55	10.00	1.03	0.36	34.5
	SD.	(6.2)	(3.5)	(0.09)	(0.29)	(0.24)	(0.02)	(0.01)	(0.6)
R2B	**Mean**	285.4	164.6	2.15	6.41	9.90	1.05	0.37	35.5
	SD.	(10.6)	(5.6)	(0.11)	(0.12)	(0.37)	(0.02)	(0.00)	(2.2)
S2B	**Mean**	296.5	171.7	2.19	6.60	9.25	1.03	0.37	35.0
	SD.	(5.6)	(4.4)	(0.06)	(0.37)	(0.38)	(0.01)	(0.01)	(1.4)
R2C	**Mean**	295.2	176	2.32	6.55	10.23	1.01	0.38	33.8
	SD.	(6.1)	(4.9)	(0.08)	(0.14)	(0.38)	(0.03)	(0.01	(1.0)
S2C	**Mean**	301.3	178.2	2.28	6.55	9.33	1.06	0.36	35.3
	SD.	(6.9)	(2.2)	(0.14)	(0.04)	(0.36)	(0.02)	(0.01)	(1.8)
CONTAMINATION									
F observed		2.76	16.2	7.51	0.56	5.45	0.00	0.01	0.54
Significance [1]		**NS**	**	**	**NS**	*	**NS**	**NS**	**NS**
Newman Keuls groups [2]			**0 a** **2B a** **2C b**	**0 a** **2B a** **2C b**		**0 a** **2B b** **2C ab**			
SELECTION									
F observed		1.09	0.6	0.07	2.31	22.53	0.72	5.47	0.30
Significance		**NS**	**NS**	**NS**	**NS**	**	**NS**	*	**NS**
Newman Keuls groups						**R a** **S b**		**R a** **S b**	
GENER.xSELECT.									
F observed		3.23	5.3	0.81	0.61	4.73	4.83	0.35	0.55
Significance		**NS**	*	**NS**	**NS**	*	*	**NS**	**NS**
Newman Keuls groups			**R0 ab** **S0 ab** **R2B a** **S2B abc** **R2C bc** **S2C bc**			**R0 a** **S0 a** **R2B a** **S2B b** **R2C a** **S2C b**	**R0 ab** **S0 ab** **R2B ab** **S2B ab** **R2C a** **S2C b**		

[1] Significant differences at 5% (*) and 1% (**); non-significant differences at 5% (NS).

[2] Two treatments with identical letters indicates that both samples are part of the same group, based on the Newman-Keuls test.

Seed selection appears to have had the same effect on contaminated populations for both contaminating varieties. The selected seed (S2C, S2B) has better plant growth than the initial population.[7] A greater degree of vegetative growth could indicate selection for hybrid vigor. The results are inconclusive, however, because the differences between R0 and S2B for vegetative characteristics were not significant. In the case of the seed contaminated by Chianquiahuitl, the effect of selection is difficult to separate from the effect of contamination. Both R2C and S2C were significantly different from R0 for HEA, DIA, and HD2, which are characteristics of the Chianquiahuitl.

For ear characteristics, seed selection appears to have reduced the contaminating effect of the Negro by the Chianquiahuitl population. Relative to R0, R2C is located in a positive direction on the second axis, while S2C is at the same level or lower, indicating the effect of selection over the descriptors that define the second axis (Figure 4). The values are statistically different between R2C and S2C for the width of the kernel WK and for the number of rows of kernel ROW, the principal characteristics that distinguish Negro from Chianquiahuitl.

Another indicator that confirms the effect of selection over the control of gene flow is the evident effect of selection in the color of the kernel. During two seasons, the Negro was submitted to contamination by white or yellow varieties. The ratio of white or yellow kernels in the Negro variety more than doubled from 7.5% to 16.5% when seed was drawn at random, while it remained stable when seed was selected each season. We conclude that the influence of farmers' seed selection over gene flow is significant and can be observed in as few as two growing cycles for descriptors for which they select and those that have high heritability, such as ear characteristics.

Genetic characteristics. The results of the isoenzyme analysis are similar to those of the morphological analysis with respect to contamination. As was found in the case of morphological characteristics, the χ^2 distance calculated from the allele frequency of the nine polymorphic loci shows that the genetic distance between the Negro and Chianquiahuitl varieties is greater than the distance between the Negro and Blanco varieties. Table 8 shows how this situation relates to the distance between R0 and the contaminated samples; the distances between R0 and samples contaminated by Chianquiahuitl (R2C and S2C) are greater than between R0 and the samples contaminated by Blanco (R2B and S2B). The effects of contamination by the Chianquiahuitl were observable at six of the nine polymorphic loci examined. For the population without farmer selection (R2C), the frequencies of the two most frequent

Table 8. Experiment 3. χ^2 distances between the Negro, Blanco, and Chianquiahuitl varieties and between R0 and S2B, R2B, S2C, and R2C[1]

	Blanco	Chianquiahuitl	S2B	R2B	S2C	R2C
R0 (Negro)	9065	11778	5806	6554	7456	7843

[1] Calculated from the allele frequencies of the polymorphic loci: ACP-1, ACP-2, CPX-1, EST-8, GDH-2, IDH-1, PHI/PGD-1, PGM-2, and SDH-1.

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[7] Differences in seed age probably do not affect this result, because samples of R0 were stored under good conditions.

alleles are intermediate between the two populations which crossed, the initial population (R0) and the contaminating variety Chianquiahuitl (C) (Figure 5).

No effects of seed selection are visible at any of the loci, and no particular trend could be identified (graphics not shown). However, the c-squared distance calculated from the allele frequencies shows that S2C is closer to R0 than R2C, and that S2B is closer to the initial population than R2B, which suggests a global selection effect. Through selection, farmers seem to have reduced the genetic differences between the initial population and the last contaminated generation of seed.

Contamination through cross-pollination affects both the morphological descriptors and allele frequencies, which are invisible to farmers. Farmers' seed selection, on the other hand,

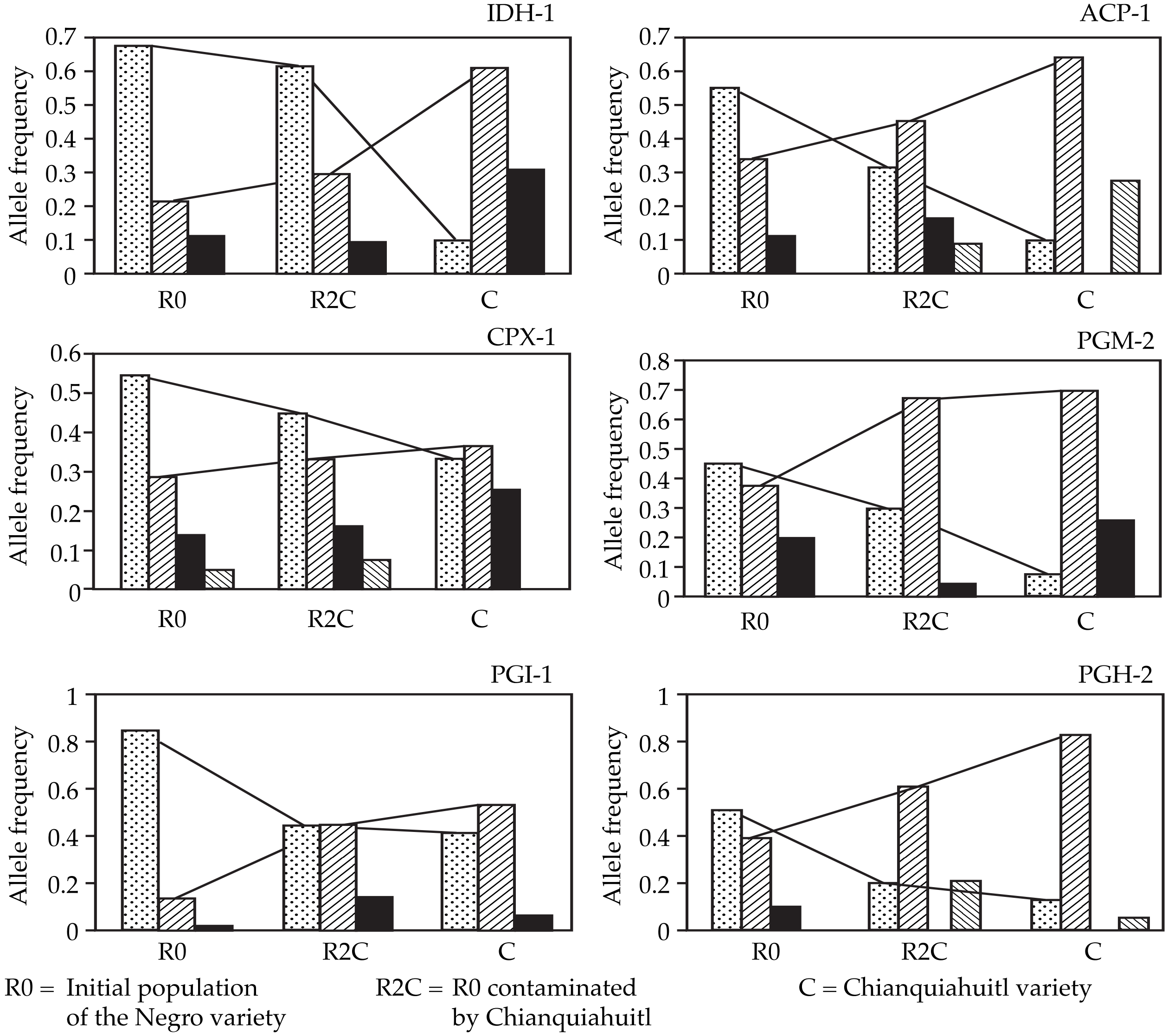

Figure 5. Effect on allele frequencies of the contamination of the Negro variety by the Chianquiahuitl variety.

Note: For each locus, a color bar represents the frequency of one allele. For each of the six loci represented here, 3 to 4 alleles were detected. Lines join the bars that represents the same allele in the three samples (R0, R2B, R2C), for the two most frequent alleles per locus in wich a tendency was observed.

affects morphological descriptors, but has little influence on allele frequencies, at least when observed over a short time period. Seed selection can be expected to observably affect a locus only when there is a strong linkage between selection criteria and the locus under study. This does not preclude the possibility that selection affects allele frequencies at loci other than those studied.

Farmers' Perceptions of Seed Selection

Farmers responses to questions about seed selection criteria and perceptions are shown in Table 9, in decreasing order of frequency.

When asked to describe their personal selection criteria, all 25 farmers interviewed stated that they selected ears that were well-filled and had healthy kernels (in their words, "*grano bien llegado*"; "*mazorca llenita*"). Most specified that seed ears should also be large—although some insisted that size is not important as long as the kernels are healthy and the ears are well-filled. These findings are consistent with those reported by Ocampo and Segovia (1997) for the same community and with the texts gathered in SEP (1982) in which farmers of different regions of Mexico describe "clean ears", "big ears", and "big kernels".

Most survey farmers also explained that seed ears should be typical ("*legítimo*") or representative of the variety or ideotype. The seed ear should resemble the maize the farmer wants to harvest (*"para que salga igual"*); the farmer should recognize in the seed ear the variety he seeks to reproduce (*"hay que reconocer la mazorca que sea del maíz que uno va a apartar"*). Other farmers expressed the same concept indirectly. When asked if they would select an ear with a different color or more kernel rows than is commonly found in a given variety, they responded that such an ear is not of the same variety.

How do farmers perceive the purpose of seed selection and its potential for crop improvement? For the majority of farmers surveyed in Cuzalapa, the principal reason for selecting seed is to ensure seed quality and good germination (*"para que nasca bien la milpa"*, *"nace con más fuerza"*), because good plant density is important for ensuring good production.

Table 9. Farmers' perceptions of seed selection and its purpose, Cuzalapa[1]

Question	Most Frequent Responses
Which ears do you select?	Well-developed, healthy kernels Large ears Ears that are typical of the variety
Why do you select seed?	To ensure germination To reproduce the variety
Can you modify the characteristics of a variety?[2]	By changing the planting date, applying fertilizer, or planting the variety next to a different variety, but not by selecting seed

[1] Most frequent responses among 25 farmers, in order of decreasing frequency.

[2] Two examples were discussed: growing cycle length (plant characteristics) and number of rows of kernel (ear characteristics).

Another purpose mentioned by the farmers is to maintain the purity or ideotype of the variety (*"para que sea legítimo*"). This point has already been highlighted by Hernandez X. (1985), a leading ethnobotanist who has studied maize in Mexico. In the Cuzalapa survey, however, some farmers expressed doubt over the utility of seed selection, reporting that while it is customary to select seed, any healthy seed grows (*"toda semilla sana nace"*).

When asked if they could modify the characteristics of a variety, the first reaction of most farmers was astonishment and disbelief (*"no se puede . . . ¿como ?*). Farmers then suggested an exchange of seed with another farmer, or a change of variety through obtaining a new seed lot, rather than selecting from their own. When asked specifically how they might change the time to silking *with the same seed,* they proposed changes in crop management, such as fertilizer application, fertilizer quantities, or planting date. To change the number of kernel rows, some suggested planting different varieties in contiguous plots to permit cross-pollination. In fact, most of the farmers had noticed the contamination produced by the outcrossing of maize planted in adjacent plots, however, they only detected very observable changes, such as kernel color or row number, rather than characteristics such as plant height or length of growing cycle. Only one farmer mentioned the possibility of using seed selection to change the characteristics of a variety. Although some agreed that by selecting ears with more rows of kernel for seed, harvested ears would eventually also carry larger numbers of rows, most were convinced that a variety cannot be modified. Each variety is defined by its own time to silking (*"cada variedad tiene su tiempo para espigar*"); a variety always "comes out the same" (*"el maíz vuelve a salir igual").*

Contrary to the perspective of professional maize breeders, these maize farmers did not perceive seed selection as a means of modifying a variety or increasing yield. For them a variety is stable and cannot be modified; modifying it would make it another variety. This view makes sense: as suggested above by the analysis of trial data, the principal role of selection in this environment may be to counteract the destabilizing effects of the multiple factors contributing to gene exchange. A more extreme view is represented by the comments of a Chiapas farmer cited by SEP (1982): "Our earth should be sad to see the adulterations and modifications that suffer the plant on the hands of man that try, with hybridization, to make it produce more grain than it should." The Cuzalapa farmers we interviewed are more likely to think of changing from one variety to another or replacing the seed for a variety than of attempting to modify its characteristics through seed selection practices.

Finally, none of the survey farmers in Cuzalapa seemed concerned about past or future "losses" of varieties. Nor did they appear worried about reduced areas planted to some varieties. When asked why the varieties disappeared, most farmers cited certain undesirable characteristics such as propensity to lodge because of tall stature, late maturity, or low yield. They also mentioned farmers' "carelessness" (*descuido*) and that the variety was no longer "legitimate" (*legitimo*)—suggesting that its characteristics deteriorated through crossing. Most of the farmers interviewed had recently tested varieties using seed they found with another farmer, either on the road or in fields. Most of these experimental varieties were rejected in a season or two because they were of little interest to the farmers. In the Cuzalapa system, farmers continually compare and enrich their set of varieties with new materials of both local and foreign origin—including modern varieties developed by plant breeding programs and traditional varieties (Louette, Charrier, and Berthaud 1997).

Discussion

In Cuzalapa, farmers practice mass selection based exclusively on ear characteristics. As maize is an open-pollinated crop, farmer selection is based solely on the female plant, which could contribute to the maintenance of diversity because the pollen source is not controlled (Sandmeier, Pilate-André, and Pernès 1986). Selection includes male characteristics only in the case of characteristics presenting xenia effects, such as kernel color and kernel texture.

Farmers' seed selection in Cuzalapa can be interpreted as a double selection or a selection that exerts two types of pressures. The first involves selection for production criteria: well-developed ears with healthy kernels ensure good germination and favors the more productive genotypes for the region's growing conditions. The second selection pressure protects ideotypes by reinforcing the characteristics of the variety as defined by farmers. Farmers use ear characteristics to distinguish their variety because they vary less with growing conditions than plant characteristics. The farmer selects the ear that resembles the ear he wants to harvest. Although the effects of the second selection pressure may be weaker than those of the first, they are systematic and are verified by both experimental results and farmers' statements. The data presented here are not sufficient to test whether these are crossed or nested criteria: do farmers choose typical ears from healthy ears, or do they first select good ears and then exclude those that are not typical of the variety? Double selection of this type has also been reported by Johannessen (1982) for Guatemala and was recommended for Mexican farmers decades ago (Chavez 1913).

As argued by Bellon and Brush (1994) in their study of maize farming in Chiapas, the quantitative results presented here demonstrate that farmers' seed selection conserves the integrity of the ear characteristics of their varieties even in the presence of significant gene flows due to cross-pollination. The selection against off-types can lead to the maintenance of a phenotypic polymorphism among varieties planted in adjacent areas (Dickinson and Antonovics 1973). This finding could explain, at least in part, the continued coexistence of so many different varieties in Cuzalapa, even though growing conditions favor large gene flows among them. Traditional seed selection practices have the effect of maintaining the ear characteristics that correspond to variety ideotypes and any genetically linked characteristics, while permitting other characteristics to evolve genetically.

The selection practices of Cuzalapa farmers appear to serve both a utilitarian purpose and the purpose of distinguishing varieties. Since their maize farming system is based on two cultivation cycles with distinct growing conditions, these farmers need to ensure that their early and late-maturing varieties maintain their characteristics and that they can be clearly differentiated. Similarly, Boster (1985) found that the varieties of manioc cultivated by the Jivaros Aguaruna of northern Peru are selected for a set of characteristics whose primary function is to assure the distinction between varieties. Boster argued that varieties must be easily distinguishable before they can be selected for survival or use. If a variety is not easily distinguished at the moment of seed selection, it can be replaced by more extensively planted varieties.

Implications for Participatory Plant Breeding

The results of the experiments, surveys, and secondary literature summarized here suggest a complementary role for professional plant breeders in the mass selection of maize by farmers in Mexican communities. Important questions are also raised about the likelihood of achieving a genetic gain or productivity impact through the recommendation of "improved" seed selection and management practices.

Modern plant breeding may complement farmer seed selection in communities like that of Cuzalapa in three ways. First, farmers' methods of mass selection do not create a strong pressure for productivity. Although there is a clear difference between the characteristics of the harvested population of ears and those of the ears selected for seed, the variance in the selected set of ears continues to be large, indicating that higher seed selection pressure could be used. It is possible, of course, that this variation provides stability over years and locations, which is important to farmers. Second, farmer selection in Cuzalapa ignores environmental effects because no system of stratifying fields is used. Finally, farmers do not consider plant characteristics directly in their seed selection, even though most complain about the plant characteristics of their varieties, such as plant height and stalk diameter. Intensifying selection pressure could improve the agronomic characteristics of varieties without significantly modifying their diversity, because gene flow between fields would continue.

Some characteristics of the traditional management of seed in this zone, however, raise serious questions about the genetic gains that may be achieved, and, therefore, the economic benefits that may be realized by of attempting to render more effective farmers' mass selection practices. Few farmers follow the practice of saving seed from their own harvest. Research by Aguirre (1997) in southeast Guanajuato and Rice, Smale, and Blanco (1998) in the Sierra de Santa Marta shows the extent to which farmers in Mexico intentionally replace and renew the seed for their maize varieties through seed exchange with other farmers. In Cuzalapa, Louette, Charrier, and Berthaud (1997) found that 47% of the 484 seed lots planted by 39 survey farmers over six cycles were obtained from other farmers in Cuzalapa or outside the community.

Farmers interviewed in this study exchanged seed for several reasons, including loss of seed because of poor harvests, insect damage in storage, and lack of seed choice because they sharecrop. A principal reason, however, is the belief that the same seed should not be planted in the same plot in successive seasons, because its yield will decline. This concept of a 'tired' variety and the need to exchange seed to "renew" it may not be uncommon among farmers (Almekinders, Louwaars and de Bruijn 1994; Li and Wu 1996; Sequeira, Bos, and Pasquier 1993; Sperling, Scheidegger, and Buruchara 1996; Wood and Lenné 1997).

If farmers are not concerned about losing their varieties it may mean either that they are unaware of the dangers of losing their genetic resources or that they are aware—and the threat is not considered significant. They may also be more pragmatic—varieties are simply abandoned or replaced when they have outlived their usefulness. Only some farmers can afford to be curators of tradition. In his overview of the literature, Tripp (1996) concludes that local varieties "are not the unchanging embodiment of ancient germplasm, but rather the outcomes of imperfect and iterative choices regarding the qualities judged useful or attractive at a particular point in time." If many farmers share the views portrayed here, it may be difficult to make varieties more useful by enhancing only mass selection practices. Any efforts to recommend a strategy for on-farm improvement, and any expectations of its economic impact, would need to recognize the fluidity of such a system.

Finally, farmers may not perceive that seed selection is a viable way of modifying a variety or improving it. To the farmers interviewed in Cuzalapa, seed selection is a means of guaranteeing good production or maintaining varieties, but not a means of transforming them. Farmers we interviewed would likely think of changing from one variety to another or replacing the seed for a variety before attempting to modify its characteristics through seed selection practices. Farmers may not be interested in intensifying their seed selection pressures through new practices if several cycles are required to generate an observable, significant result. Depending on the characteristics farmers want to modify, "improved" seed selection could be less effective and much more labor-intensive. If so, participatory plant breeding would not represent a viable means of providing benefits to farmers while maintaining or enhancing the diversity of their varieties. On the other hand, the high rate of seed exchange in traditional maize varieties may reflect the fact that farmers do not possess the tools to modify their varieties by any other means. Their continual experimentation and attempts to enrich their varieties with their own tools is an expression of their willingness to modify them, even if they doubt their capacity to do so through seed selection alone. Providing innovative farmers with new tools could further stimulate their interest in crop improvement.

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