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Farmers' seed selection practices and traditional maize varieties in Cuzalapa, Mexico

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Summary

Experimental results and farmer surveys from a Mexican community located in the buffer zone of a biosphere reserve indicate that farmers' seed selection practices protect the phenological integrity of their traditional 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. Because the effects of farmers' selection practices are confined largely to ear characteristics, their practices appear to offer only limited scope for variety improvement. Farmers' expectations of what they can achieve through seed selection are similarly limited. These findings suggest complementary roles for professional breeders and Mexican farmers in enhancing mass selection methods to improve maize landraces on farms – if farmers themselves perceive benefits from the collaboration.

Introduction

Participatory plant breeding, including variety selection and seed selection practices, has been proposed as a means of providing economic incentives for farmers to continue cultivating genetically desirable crop populations, supporting the *in situ* conservation of crop genetic resources (Eyzaquirre & Iwanaga, 1996; Qualset et al., 1997). 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 encourage the maintenance of more diverse, locally adapted plant populations (Berg, 1995; Ceccarelli et al., 1996; Joshi & Witcombe, 1996). Techniques used by professional plant breeders may help farmers become more efficient in selecting crop populations adapted to their needs; farmer involvement in selection can help breeders target environments where modern varieties have not been adopted (Komegay et al., 1996; Sperling et al., 1993).

In Mexico, improved seed selection practices have been recommended in the past by the national agricultural research institution (CAECECH, 1987) and are currently promoted by some nongovernmental organizations as a participatory strategy for maize improvement (Rice et al., 1998). In order to improve the effectiveness of methods used by farmers in Mexico, researchers have recommended for example that they not select maize seed exclusively on the characteristics of harvested ears (SEP, 1982) but that they select superior maize plants in the field as in other traditional agricultural systems (Berg, 1993; Mushita, 1992; Sandmeier et al., 1986). Nevertheless, the assumption that such techniques would prove successful under farmers' conditions has not been challenged.

The texts gathered by the Mexican Secretary of Education (SEP, 1982) represent the views of farmers from many regions of Mexico and illustrate the importance they attribute to maize seed selection. Farmers' acceptance of new seed selection practices, rather simple or complex, depends on a number of factors, including their perceptions of what they might hope to achieve relative to current practices, how well proposed practices can be integrated into current practices, and their own assessment of whether it is worth the time and effort. While many anecdotal descriptions are found in the scientific literature, neither the effect of their seed selection practices on the genetic structure of their varieties nor farmers' perceptions of those effects has been documented.

This study addresses the potential for enhancing mass selection practices as one of many possible participatory strategies to improve maize landraces in Mexico (see McGuire et al., 1999). A combination of experimental and survey data are used to: (1) relate farmers' selection criteria to variety characteristics; (2) examine the effect of farmers' seed selection in the presence of genetic instability; and (3) record farmers' perceptions of their practices. Findings are likely to be relevant for, although not necessarily representative of, other systems in traditional communities of Mexico.

Context

Description of the study site

The study community of Cuzalapa is located on the Pacific Coast of Mexico, in the buffer zone of the Sierra de Manantlán Biosphere Reserve, municipality of Cuautitlán, State of Jalisco. Under the Agrarian Reform of 1950, Cuzalapa was officially recognized as a *comunidad indígena* because its land use history pre-dates the Spanish Conquest. Cuzalapa is located in one of the most marginalized municipalities of the region when classified by housing quality and education (Rosales & Graf, 1995). Although some of its annual maize crop and cattle are sold outside the valley, Cuzalapa is poorly integrated into commercial markets.

Each year, about 1,000 ha may be sown to maize in Cuzalapa. 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 2.5 t/ha (unshelled) (Louette, 1994). Detailed descriptions of the study site and maize production system are found in Louette (1994), Martínez et al. (1991), Martínez et al. (1993) and Laitner & Benz (1994).

Previous research on the genetic structure of maize varieties

Louette et al. (1997) identified 26 varieties grown in the Cuzalapa community 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. Four farmer practices shape the genetic structure of these varieties and influence the effectiveness of maize seed selection.

The first is the introduction of varieties from surrounding communities. While the two principal local varieties (Blanco and Chianquiahuitl) cover about two-thirds of the maize area and the six local varieties account for more than 80%, a changing group of foreign varieties is introduced continuously through farmer-to-farmer exchanges. Louette et al. (1997) defined varieties grown for at least one farmer generation (25 years) as 'local' and all others as 'foreign'. The vast majority of foreign varieties are traditional varieties from other communities and a few are 'rusticated' improved varieties of advanced generations.

The breadth of the genetic structure of maize is expanded for some characteristics by these introductions because the morpho-phenological characteristics of the local and foreign varieties are distinct. Local varieties (except for Chianquiahuitl) are characterized by a shorter growing cycle, reduced vegetative development, fewer rows, and larger kernels. Foreign varieties are characterized by a longer growing cycle, taller plants, more rows, and smaller kernels. All local varieties are of the Tabloncillo race, while foreign varieties include those of the Tabloncillo race and other distinct races. Details of a controlled experiment to evaluate variety characteristics are found in Louette et al. (1997) and are summarized in Table 1.

Second, Cuzalapa farmers also replace or modify the seed stocks for their varieties with seed obtained from other farmers within and outside the community. Instead of relying on their own production as a seed

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

Varieties	% Maize area	% Farmers	Grain color	PlHgt[b] cm	StDia cm	LeaNb	KeWid cm	KeBr cm	KeRow	EarWt g	1KeWt g	Flo days
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									

[a] Based on: (a) a survey of 39 farmers during 6 growing cycles and (b) measurement of descriptors in a controlled trial with 3 repetitions during the 1991 irrigation cycle in Cuzalapa.
[b] PlHgt = plant height, StDia = stalk diameter, LeaNb = number of leaves, KeWid = kernel width, KeBr = kernel breadth, KeRow = number of rows of kernel, EarWt = ear weight, 1KeWt = weight of 1 kernel, Flo = Number of days to male flowering during the 1991 irrigation cycle (see Table 2).

source for maize landraces, most farmers routinely utilize the seed stocks of other farmers. Although farmers rarely pool seed lots of different varieties, they often mix seed lots considered to be of the same variety to obtain the seed quantities they need (Louette et al., 1997).

Recognition of this practice led Louette (1994) to define a ‘seed lot’ as the physical unit of seeds used to produce the next season’s crop. ‘Variety’ in Cuzalapa refers to a set of farmers’ seed lots that bear the same name. Farmers appear to identify a seed lot as belonging to a variety when it resembles the variety phenotypically. Analyses of phenotypic diversity, both within 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 (Louette et al., 1997).

Third, management of maize planting in Cuzalapa favors the genetic exchange and modest degree of heterosis that naturally occurs through cross-pollination (Louette, 1994; for Chiapas, see Bellon & Brush, 1994). Farmers plant varieties on contiguous plots on different dates, leading to the coincidence of flowering among varieties even when their growing cycles are not the same. These practices could lead to significant changes in the morphological characteristics of varieties and allele frequencies.

Fourth, because the area in each field is limited and several varieties are sown in the same field, the size of the seed lots planted per variety is small. Since the effective population size is regularly reduced in a large proportion of seed lots, rare alleles are lost and the genetic diversity of the populations fluctuates.

Methods

Preliminary information on seed selection practices and farmers’ criteria was obtained through informal interviews and direct observation. In Cuzalapa, seed selection is based exclusively on ear characteristics. 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. Sometimes farmers select their ears for seed immediately before planting, choosing them from the ears remaining after consumption of the previous season’s harvest.

Identifying farmers seed selection criteria

The criteria used by farmers in Cuzalapa to select their maize seed were identified in two experiments. The purpose of the first experiment was to identify farmers' seed selection criteria for the two major varieties of white maize 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. After silking, stalk diameter (StDia), ear height (EarHgt), plant height (PlHgt), and number of leaves above the ear (LeaNb) were measured. The index of dry matter ($DryMat = PlHgt*StDia^2$) and the ratio of the plant height to ear height (EarHgt/PlHgt) were calculated from these descriptors. An $r^2 > 0.85$ between DryMat and dry matter has been reported for maize by Navarro (1984) and Scopel (1994).

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 (EarLgt), length of the ear presenting kernels (FilLgt), ear weight (EarWt), ear diameter (EarDia), number of kernel rows (KeRow), number of kernels per row (Ke/Row), and breadth of the kernel (KeBr). The width of the kernel (KeWid) was obtained by dividing the circumference of the ear by the number of kernel rows. The total number of kernels (KeNb) was calculated from the Ke/Row*KeRow. The alignment or arrangement of the kernels on the row (KeAli) was classified using two categories; the health of the ear (incidence of rots and insects) (EarInf) using three categories; and the quality of the filling (EarFil) using four categories. All descriptors are defined in Table 2.

With respect to traditional practices, each of 25 farmers was asked to select 15 seed ears per variety from the set of 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 all 25 farmers was pooled into one sample. Ears selected by more than one farmer were counted 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 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 (LeaNb, KeRow, EarInf, EarFil, and KeAli) 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.

A second experiment allowed the relationship between selection criteria and varietal characteristics to be generalized for major varieties grown by farmers. For each of the five varieties, sets of 15 to 30 seed ears were selected by 2 to 5 individual farmers and sets of 15 to 30 seed ears were drawn randomly from the farmer's harvest. The selected and random sets of ears were then grouped together by variety and compared. Descriptors included the length, width, and breadth of the kernel (KeLgt, KeWid, KeBr), number of kernel rows (KeRow), cob and ear diameters (CobDia, EarDia), ear, cob and kernel weight (EarWt, CobWt, 1KeWt), and total ear length (EarLgt) (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 test 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 that are difficult to identify otherwise. 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.

The results of both experiments 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

Table 2. Vegetative and ear descriptors

Vegetative descriptors	
PlHgt	Total plant height (from the soil to the last node)
EarHgt	Ear height (from the soil to the upper ear node)
EarHgt/ PlHgt	Ratio of ear height to plant height
StDia	Stalk diameter (biggest diameter measured at 5 cm from the soil, with a caliper)
DryMat	Indices of dry matter (PlHgt*StDia*StDia)
LeaLgt	Ear leaf length (from the ligule to the end of the leaf of the superior ear node)
LeaWid	Ear leaf width (at the middle length of the upper ear leaf)
LeaNb	Number of leaves above the superior ear, including the leaf of the superior ear node
Ear descriptors	
EarLgt	Total ear length (from the base to the tip of the ear)
FilLgt	Length of the ear presenting kernels (from the base of the ear to the last kernels)
EarWt	Ear weight at 15% of humidity
EarDia	Ear diameter (measured at the middle length of the ear with a caliper)
CobWt	Cob weight at 15% of humidity
CobDia	Cob diameter (measured at the middle length of the cob with a caliper)
KeRow	Kernel row number (counted at the middle length of the ear)
Ke/Row	Number of kernels per row (counted over two rows per ear)
KeNb	Total number of kernels (Ke/Row*KeRow)
KeLgt	Kernel length (mean of 3 kernels per ear, measured with a caliper)
KeWid	Kernel width (mean of 10 kernels per ear, measured at the tip of the kernel with a caliper) or Phi*EarDia/KeRow
KeBr	Kernel breadth (mean of 10 kernels per ear, measured at the top of the kernel with a caliper)
1KeWt	1 kernel weight at 15% of humidity (mean of 3 samples of 100 kernels/100)
KeAli	Alignment of kernels on the row
	0 = kernels not aligned; 1 = kernels aligned
Ear Inf	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 = ear not affected
EarFil	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

(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.

Determining the influence of selection over the genetic structure of varieties

A third experiment was conducted to determine the effects of farmer seed selection criteria on the maintenance of variety characteristics, 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 2 kernels per ear (S0, initial selected seed sample; R0, initial random seed sample). Each sample was sown in a 20 m × 20 m area within a farmer's field in Cuzalapa. In the first season, the surrounding field was planted to the Amarillo Ancho variety, which is referred to as the 'contaminating variety, cycle 1' (Figure 1). At the end of the first cycle, a set of 100 ears was drawn at random from the plot sown with R0. From the plot sown with S0, the same farmer selected a set of 100 ears. 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

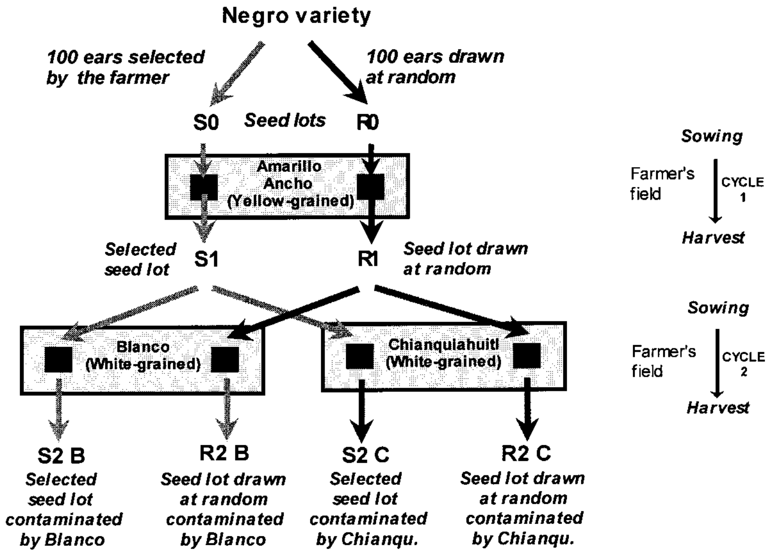

Figure 1. Method for determining the influence of selection on geneflow.

variety in the second season and the experiment was subdivided. In cycle 2, one pair of seed lots selected by farmers (S1) and at random (R1) were contaminated by the Blanco variety, while another pair was submitted to contamination by the Chianquiahuitl variety. Both pairs were sown with the same arrangement as the R0 and S0 seed lots. The Blanco variety 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 in plots) was established at the INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas, y Pecuarias) Experimental Station at La Huerta near Cuzalapa. The initial population of the Negro variety (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: EarHgt, PlHgt, StDia, LeaLgt, LeaWid, LeaNb, KeLgt, KeWid, KeBr, EarDia, CobDia, EarLgt, KeRow, EarWt, CobWt, 1KeWt (see Table 2 for abbreviations and methods of measurement). 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.

The data were compared using an ANOVA procedure with two factors: (1) contamination (no contamination 0, contamination by Blanco 2B, and contamination by Chianquiahuitl 2C), and (2) selection (selected by farmer S or selected at random R). 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 9 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 Dehydrogenase (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 Dehydrogenase (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, PGI-I, PGM-I and 2, and SDH-1. The techniques used were those recommended by Stuber et al. (1988). Based on the allele frequencies for the 9 polymorphic alleles, pairwise X-squared distances were calculated between R0 (Negro variety) 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 asked questions from a checklist and responses were discussed. Questions were clustered into three themes: (1) the characteristics on which farmers focus when selecting seed ears, (2) farmers' beliefs regarding the purpose of selection, and (3) farmers' beliefs about what can be accomplished through seed selection. The questions elicited their opinions about seed selection and its potential for improving their maize landraces. In the second set of more structured interviews, questions were reduced to those shown in Table 8. To reduce confusion over interpretation, the Spanish phrases used by farmers are reported with English translations.

Results

Seed selection practices

Farmers in Cuzalapa do not control pollen sources or consider the vegetative and agronomic characteristics of the plants that produce the ears from which they select seed. 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). Plant selection is used by farmers in other traditional agricultural systems, however. Berg (1993), Sandmeier et al. (1986), and Mushita (1992) have described selection methods based on plant characteristics for sorghum and pearl millet in Africa. The stock of ears on which selection is based includes ears harvested in the entire field – those in the center and those on the borders of the field, which are more likely to be contaminated by adjacent maize fields.

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

	Blanco		Chianquiahuitl	
	% var[c]	Significance of the difference[d]	% var	Significance of the difference
Vegetative[a]				
PlHgt	+10.9	***	+7.5	***
EarHgt	+13.5	***	+5.7	***
EarHgt/PlHgt	+1.8	*	0.0	NS
StDia	+20.7	***	+20.7	***
DryMat	+57.6	***	+46.5	***
LeaNb[b]	+41.8 (6)[e]	***	+78.4 (7)	***
Ear[a]				
EarLgt	+22.9	***	+14.7	***
FilLgt	+30.4	***	+19.7	***
EarWt	+68.3	***	+44.1	***
EarDia	+10.3	***	+8.5	***
KeRow[b]	+4.1 (8)	***	+45 (12)	***
KeNb	+42.8	***	+33.3	***
KeWid	+9.9	***	+3.5	***
KeBr	–7.5	***	–2.6	**
KeAli[b]	+23.7 (1)	***	+26.1 (1)	***
EarInf[b]	+47.1 (2)	***	+0.5 (2)	***
EarFil[b]	+154.4 (3)	***	+54.7 (3)	***

[a] PlHgt = plant height, EarHgt = ear height, EarHgt/PlHgt, StDia = stalk diameter, DryMat = dry matter indices, LeaNb = number of leaves, EarLgt = ear length, FilLgt = length of ear presenting kernels, EarWt = ear weight, EarDia = ear diameter, KeRow = number of rows of kernel, KeNb = total number of kernels, KeWid = kernel width, KeBr = kernel breadth, KeAli = alignment of the kernels on the row, EarInf = infection of the ear, EarFil = filling of the ear (Table 2).
[b] Data were transformed in ranges to apply the ANOVA test, and % of var was calculated for the main classes.
[c] % var = (mean value in the selected set – mean value in the population)/mean value in the population.
[d] Significant differences at 5% (*), 1% (**), 0.1% (***); non-significant differences at 5% (NS).
[e] Class for which the % of variation was more important, % variation for this class.
Note: Since selection occurs only based on the ear characteristics, differences in vegetative characteristics are the result of indirect selection.

Farmers' selection criteria

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 (EarHgt/PlHgt) and the breadth of the kernel (KeBr), had a significantly higher level in the

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

Ear descriptors	Plant descriptors									
	Chianquiahuitl					Blanco				
	EarHgt	PlHgt	StDia	DryMat	LeaNb	EarHgt	PlHgt	StDia	DryMat	LeaNb
EarLgt	0.3	0.4	0.6	0.6	0.2	0.4	0.5	0.5	0.6	0.3
FilLgt	0.3	0.4	0.6	0.6	0.2	0.4	0.5	0.6	0.6	0.3
EarDia	0.3	0.3	0.5	0.5	0.2	0.3	0.4	0.5	0.5	0.3
KeRow	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.2	0.2	0.1
KeWid	0.1	0.2	0.2	0.2	0.0	0.2	0.3	0.3	0.3	0.2
KeBr	0.1	0.2	0.1	0.1	0.1	–0.1	–0.1	–0.1	–0.1	–0.1
KeNb	0.1	0.2	0.5	0.4	0.1	0.4	0.4	0.5	0.5	0.3
EarWt	0.3	0.4	0.6	0.6	0.2	0.4	0.5	0.6	0.6	0.3

[a] EarHgt = ear height, PlHgt = plant height, StDia = stalk diameter, DryMat = dry matter indices, LeaNb = number of leaves, EarLgt = EAR length, FilLgt = length of ear presenting kernels, EarDia = ear diameter, KeRow = number of rows of kernel, KeWid = kernel width, KeBr = kernel breadth, KeNb = total number of kernels, EarWt = ear weight (Table 2).
[b] Coefficient superior to 0.10, statistically different from 0 for $\alpha = 0.001$.

selected set of ears than in the population. The breadth of the kernel (KeBr) was the only characteristic with a significantly lower value on seed ears (Table 3).

'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, 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 (EarWt), ear length (EarLgt), length of the ear presenting kernels (FilLgt), total number of kernels (KeNb), and kernel filling (EarFil). The alignment of kernels on the rows (KeAli) appeared also to have some importance.

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 (DryMat) and stalk diameter (StDia), which are correlated. For other vegetative descriptors, however, differences between the set of plants from which ears were selected and the entire set of plants were less than the differences observed for ear characteristics (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.

Some descriptors were affected differently according to the characteristics of the variety. Selection increased the proportion of ears with 8 rows and the width of the kernels in the Blanco variety. In the Chianquiahuitl variety, selection increased the proportion of ears with more than 12 rows, inducing little change in width of kernel (Table 3). For the number of rows of kernel, the change in the Blanco variety was less pronounced than in the Chianquiahuitl variety, because more than two-thirds of the Blanco ears in the population had 8 rows. The percent of Chianquiahuitl ears with more than 12 rows rose from 41.7% to 58.3%. Row number distinguishes one variety from another and is a trait on which farmers can select directly. The results suggest a link between the selection pressures of farmers and variety ideotypes.

Other characteristics were affected differently because of field conditions where the crop was cultivated. For example, in comparing the Blanco variety to Chianquiahuitl, selection greatly reduced the proportion of ears affected by fungi or insects and the proportion of badly filled ears. Because of better field conditions or lower susceptibility, the Chianquiahuitl variety produced a smaller proportion of rotten ears (3.5% for the classes 0 and 1 of EarInf) and baddly filled ears (26.2% for the class 1 and 2 of EarFil) than the Blanco variety (36.2% and 82% respectively).

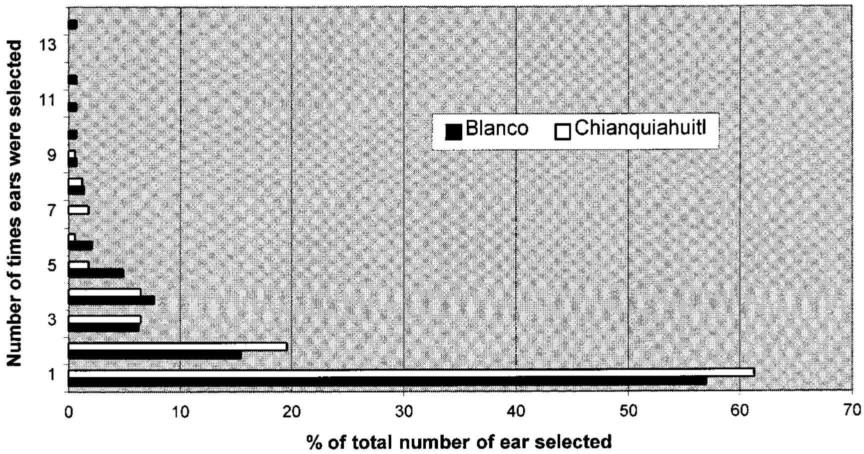

Figure 2. Farmer consensus on seed selection criteria. Percent of the total number of ears selected by one or more farmers. Note: Blanco 142 ears selected from 1233, Chianquiahuitl 168 ears selected from 1125.

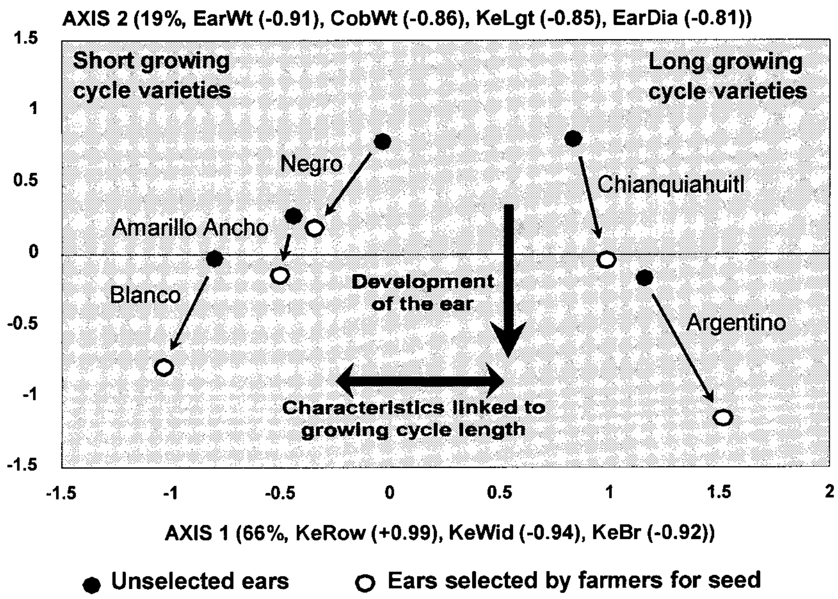

Figure 3. Seed selection criteria for five of the main varieties grown by farmers in Cuzalapa. Based on Factorial Discriminant Analysis of ears descriptors for ears selected at random and by farmers for three short cycle varieties and two long cycle varieties.
Note: Percent following axis number indicates the proportion of the total variation explained by the axis. Descriptors refer to those most correlated with the axis, and number in parenthesis indicates direction of correlation.
EarWt and CobWt = ear and cob weight, EarDia = ear diameter, KeRow = kernel rows number, KeLgt, KeWid and KeBr = kernel length, width and breadth (Table 2).

The consensus test revealed the consistency of seed selection criteria among farmers (Figure 2). Out of the ears selected for the Blanco variety, 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 6 ears were selected by seven different farmers. The total number of ears selected more than once represents no more than 5–6% of all of the ears displayed by either variety.

Criteria and variety ideotype

The findings of the first experiment are generalized by the second. Results confirm that seed selection: (1) is oriented to heavier, bigger, and better-developed ears,

Table 5. Comparison between the set of selected ears and the set of ears drawn at random for 5 varieties[a]

Variety	Number of ears per set	EarWt[b] g	CobWt g	EarDia cm	CobDia cm	EarLgt cm	KeRow	KeLgt cm	KeWid cm	KeBr cm
Blanco	90 Random	110 ± 31	15 ± 6	3.8 ± 0.3	2.1 ± 0.3	16 ± 3	8.7 ± 1.1	0.95 ± 0.13	1.06 ± 0.09	0.38 ± 0.04
	103 Selected	149 ± 25	21 ± 5	4.0 ± 0.2	2.1 ± 0.2	19 ± 2	8.6 ± 1.0	1.04 ± 0.08	1.23 ± 0.08	0.40 ± 0.03
		***	***	***	NS	***	NS	***	***	**
Amarillo ancho	140 Random	106 ± 29	17 ± 5	3.7 ± 0.3	2.2 ± 0.3	16 ± 2	9.3 ± 1.3	0.92 ± 0.10	1.00 ± 0.09	0.38 ± 0.04
	100 Selected	130 ± 28	19 ± 5	3.9 ± 0.3	2.2 ± 0.3	18 ± 2	9.3 ± 1.3	0.94 ± 0.09	1.02 ± 0.08	0.38 ± 0.04
		***	***	***	*	***	NS	NS	*	NS
Negro	60 Random	81 ± 32	12 ± 4	3.6 ± 0.3	2.0 ± 0.3	14 ± 3	9.3 ± 1.3	0.82 ± 0.09	0.94 ± 0.09	0.35 ± 0.04
	60 Selected	120 ± 26	18 ± 5	3.7 ± 0.3	2.1 ± 0.2	17 ± 2	9.3 ± 1.3	0.90 ± 0.08	0.99 ± 0.08	0.36 ± 0.04
		***	***	**	NS	***	NS	***	**	NS
Chian-quiahuitl	71 Random	98 ± 38	15 ± 7	3.7 ± 0.4	2.0 ± 0.3	15 ± 3	11.4 ± 1.4	0.94 ± 0.12	0.82 ± 0.08	0.34 ± 0.04
	79 Selected	146 ± 29	20 ± 6	4.0 ± 0.3	2.1 ± 0.2	17 ± 2	12.0 ± 1.5	1.01 ± 0.09	0.83 ± 0.07	0.34 ± 0.03
		***	***	***	*	***	*	***	*	NS
Argentino	60 Random	130 ± 60	21 ± 10	4.2 ± 0.5	2.3 ± 0.3	15 ± 3	12.3 ± 1.7	0.99 ± 0.12	0.88 ± 0.07	0.33 ± 0.05
	60 Selected	187 ± 66	29 ± 12	4.6 ± 0.4	2.5 ± 0.2	16 ± 3	13.1 ± 1.4	1.07 ± 0.12	0.90 ± 0.08	0.34 ± 0.03
		***	***	***	**	**	**	**	NS	NS

[a] Mean and standard deviation. Significant differences at 5% (*), 1% (**), 0.1% (***); Non-significant differences at 5% (NS).
[b] EarWt = ear weight, CobWt = cob weight, EarDia = car diameter, CobDia = cob diameter, EarLgt = ear length, KeRow = number of rows of kernel, KeLgt = kernel length, KeWid = kernel width, KeBr = kernel breadth (Table 2).

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 (KeRow, KeWid, and KeBr), while those linked to the second axis are related to ear development (EarWt, EarDia, or KeLgt).

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 drawn at random for the descriptors that define that axis (Table 5).

As shown by the relative position of the selected and random samples on axis 1 (Figure 3), selection causes divergence in number of rows and kernel width among the varieties of different growing cycle length. 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 6). 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

Table 6. Comparison of ear and plant descriptors for R0, S2B, R2B, S2C, and R2C

Factor considered	PlHgt[a]	EarHgt	StDia	LeaNb	KeRow	KeWid	KeBr	1KeWt
Contamination								
Significance[b]	NS	**	**	NS	*	NS	NS	NS
Newman Keuls		0 a	0 a		0 a			
groups[c]		2B a	2B a		2B b			
		2C b	2C b		2C ab			
Selection								
Significance	NS	NS	NS	NS	**	NS	*	NS
Newman Keuls					R a		R a	
groups					S b		S b	
Contamination × selection								
Significance	NS	*	NS	NS	*	*	NS	NS
Newman Keuls		R0 ab			R0 a	R0 ab		
groups		S0 ab			S0 a	S0 ab		
		R2B a			R2B a	R2B ab		
		S2B abc			S2B b	S2B ab		
		R2C bc			R2C a	R2C a		
		S2C bc			S2C b	S2C b		

[a] PlHgt = plant height, EarHgt = ear height, StDia = stalk diameter, LeaNb = number of leaves, KeRow = number of rows of kernels, KeWid = kernel width, KeBr = kernel breadth, 1KeWt = weight of 1 kernel (Table 2).
[b] Significant differences at 5% (*) and 1% (**); Non-significant differences at 5% (NS).
[c] Two treatments with identical letters indicates that both samples are part of the same group, based on the Newman-Keuls test.

same order as the values for the three varieties Blanco, Chianquiahuitl, and Negro, except for kernel breadth. 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 patterns graphically (Figure 4). The plane defined by the two first axis 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 (PlHgt, EarHgt, LeaNb, and StDia), while those more strongly linked to axis 2 are ear characteristics (1KeWt, KeBr, KeRow, and KeWid).

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 variety by the Blanco variety, which is phenotypically similar to the Negro variety, has little effect on plant and ear descriptors. By contrast, contamination by the Chianquiahuitl variety, which is phenotypically different from Negro, induces changes related to the characteristics of the Chianquiahuitl variety. R2C has greater vegetative growth than R0, as expressed by the plant height (PlHgt), ear height (EarHgt), number of leaves (LeaNb), and stalk diameter (StDia) on the first axis of the FDA. R2C also presents smaller kernels arranged on more rows (weight of 1 kernel 1KeWt, width of the kernel KeWid, and number of kernel rows KeRow), as indicated by the second axis. The values are statistically different for StDia only (Table 6).

Seed selection appears to have had the same effect on contaminated populations for both contaminating varieties. The selected seed (52C, 52B) has better plant growth than the initial population. 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 EarHgt, StDia, and DryMat, which are characteristics of the Chianquiahuitl variety.

For ear characteristics, seed selection appears to have reduced the contaminating effect of the Chianquiahuitl population on the Negro variety. Relative to R0, R2C is located in a positive direction on the

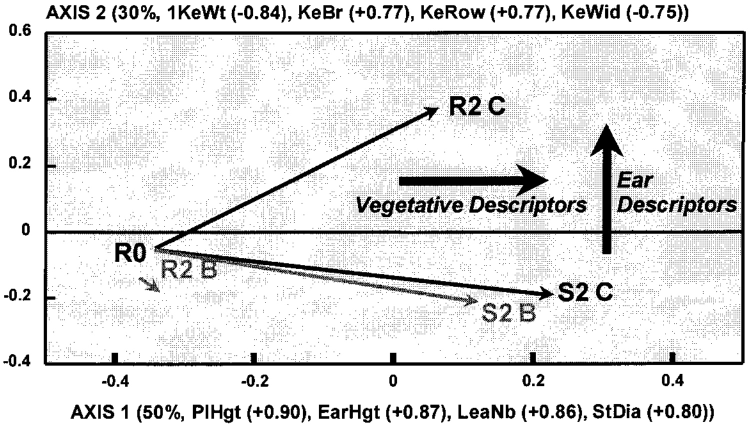

Figure 4. Effect of seed selection on contamination of Negro variety by the Blanco and Chianquiahuitl varieties. Based on Factorial Discriminant Analysis for ear and plant descriptors measured on initial and subsequent Negro populations, selected by a farmer and at random.

R0 initial population of Negro Variety.
S2B second generation contaminated by the Blanco variety, selected by farmers.
R2B second generation contaminated by the Blanco variety, selected at random.
S2C second generation contaminated by the Chianquiahuitl variety, selected by farmers.
R2C second generation contaminated by the Chianquiahuitl variety, selected at random.

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 parenthesis indicates direction of correlation.

PlHgt = plant height, EarHgt = ear height, LeaNb = Number of leaves above upper ear, StDia = Stalk diameter, 1KeWt = 1 kernel weight, KeBr = kernel breadth, KeRow = kernel rows numbers, KeWid = kernel width (Table 2).

Table 7. χ^2 distances between Negro, Blanco and Chianquiahuitl varieties and between R0 and S2B, R2B, S2C, and R2C[a]

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

[a] 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.

second axis, while S2C is at the same level or lower, indicating the effect of selection over the descriptors that define the second axis. The values are statistically different between R2C and S2C for the width of the kernel KeWid and for the number of rows of kernel KeRow, 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 variety 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% (statistically different at 5%, chi-square test) 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 they select for 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-squared distance calculated from the allele frequency of the 9 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 7 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

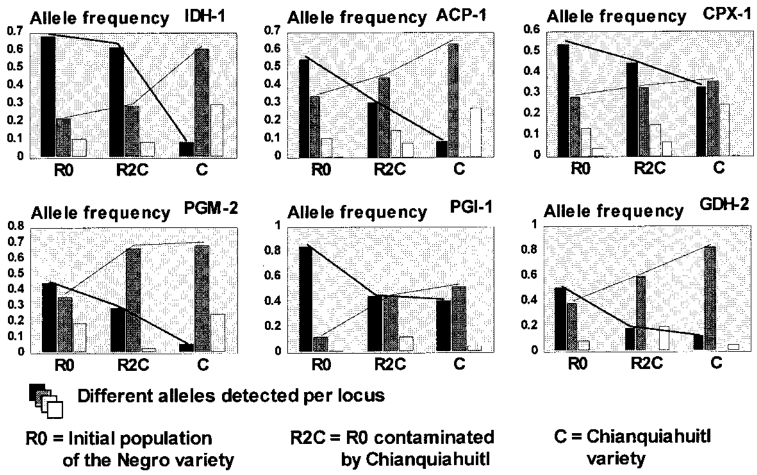

Figure 5. Effect on allele frequencies of contamination of Negro variety by Chianquiahuitl variety. Allele frequencies of IDH-1, ACP-1, CPX-1, PGM-2, PGI-1 and GDH-2.
Note: For each locus, a color bar represents the frequency of one allele. For each of the six loci represented here, 3 to 4 alleles were detected. Lines join the bars that represent the same allele in the three samples (R0, R2B, C), for the two more frequent alleles per locus in R0.

of contamination by the Chianquiahuitl variety were observable at 6 of the 9 polymorphic loci examined. For the population without farmer selection (R2C), the frequencies of the 2 most frequent 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 pattern could be identified (graphics not shown). However, the χ-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, 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 are shown in Table 8, in decreasing order of frequency. When asked to describe their own selection criteria, all 25 farmers interviewed stated that they select ears that are well-filled with 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 & 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.

What are farmers' perceptions of the purpose of seed selection and its potential for crop improvement? For the majority of farmers surveyed in Cuzalapa, the

Table 8. Farmers' perceptions of seed selection and its purpose, Cuzalapa[a]

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?[b]	By changing the planting date, applying fertilizer, or planting the variety next to a different variety, but not by selecting seed

[a] Most frequent responses among 25 farmers, in order of decreasing frequency.
[b] Two examples were discussed: growing cycle length (plant characteristics) and number of rows of kernel (ear characteristics).

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. Another purpose mentioned by the farmers is to maintain the purity or ideotype of the variety ('*para que sea legítimo*'). This point was already made by Hernandez X. in 1985. 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 germinates ('*toda semilla sana nace*').

When asked if they could modify the characteristics of a variety, the first reaction of most farmers was astonishment ('*no se puede . . . ¿como?*'). Farmers proposed instead an exchange of seed for the same variety with another farmer or a change of variety. When asked specifically how they might change the time to silking *with the same seed*, they suggested 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, but detected very evident changes, such as kernel color or row number, rather than changes in characteristics such as plant height or length of growing cycle. Only one farmer mentioned the possibility of using seed selection to change variety characteristics. 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*').

The farmers interviewed in Cuzalapa do not perceive seed selection as a means of modifying a variety. 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 genetic exchange. 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 modifying its characteristics through seed selection.

Discussion

Farmers in Cuzalapa, and in most regions of Mexico, select maize seed exclusively on ear characteristics. Since maize is an open-pollinated crop, they select solely on the female plant. Selection includes male characteristics only in the case of characteristics presenting xenia effects, such as kernel color and kernel texture. This practice could contribute to the maintenance of diversity because the pollen source is not controlled (Sandmeier et al., 1986).

Farmers' seed selection in Cuzalapa exerts two types of pressures. The first is for production. By choosing well-developed ears with healthy kernels, they ensure good germination and favor the more productive genotypes for the region's growing conditions. The second protects ideotypes by reinforcing the characteristics of the variety as defined by farmers. The farmer selects the ear that resembles the ear he wants to harvest. Farmers use ear characteristics to distinguish their variety because these vary less with growing conditions than plant characteristics. 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. Double selection of this type has been reported by Johannessen (1982) for Guatemala and was recommended for Mexican farmers at the beginning of this century (Chavez, 1913). 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?

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 against off-types can lead to the maintenance of a phenotypic polymorphism among varieties planted in adjacent areas (Dickinson & Antonovics, 1973). This finding could explain the continued coexistence of so many distinct varieties in Cuzalapa despite the planting practices that favor genetic exchange among them.

Since their maize farming system is based on two cultivation cycles with distinct growing conditions, Cuzalapa farmers need to ensure that their early and late-maturing varieties maintain their characteristics and that they can be clearly differentiated. Boster (1985) has 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 may 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 but raise questions about the likelihood of achieving genetic gains through 'improving' methods of mass selection.

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 greater seed selection pressure could be exerted. 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 in-field stratification is used. Third, even though many farmers complain about the plant characteristics of the varieties they cultivate, such as plant height and stalk diameter, they do not select directly for plant characteristics. Intensifying selection pressure could improve the agronomic characteristics of varieties without significantly modifying their diversity since gene flow between fields would continue.

However, some features of seed management in Cuzalapa raise questions about the genetic gains that may be achieved, and therefore the economic benefits that may be realized, by attempting to render more effective farmers' mass selection practices. Effective mass selection depends on retaining seed over successive generations. Few farmers in Cuzalapa follow the practice of saving seed from their own harvest (Louette et al., 1997). Similar findings are reported for other regions of Mexico (Aguirre, 1999; Rice et al., 1998; Smale et al., 1999). Farmers interviewed in these studies exchange, pool, or replace seed for several reasons, including seed loss due to poor harvests or insect damage in storage. A principal reason, however, is the belief that the same seed should not be planted in the same plot over successive seasons because its yield will decline. This concept of a 'tired' variety and the need to 'renew' through exchange has been reported for other crops and regions (Almekinders et al., 1994; Lij & Wu, 1996; Sequeira et al., 1993; Sperling et al., 1996; Wood & Lenné, 1997).

Finally, farmers may not perceive that seed selection is a viable way of modifying a variety or improving it. The farmers we interviewed in Cuzalapa would change varieties or replace the seed for a variety before attempting to modify its characteristics through seed selection. 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. 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. In that case, providing innovative farmers with new tools may still serve an unforeseen purpose.

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