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Evaluating the potential for farmer and plant breeder collaboration: A case study of farmer maize selection in Oaxaca, Mexico

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Summary

Formal plant breeders could contribute much to collaboration with farmers for improving crop varieties for local use. To do so outside researchers must have some understanding of local selection practices and their impact on crop populations in terms of the genetic theory underlying plant breeding. In this research we integrated methods from social and biological sciences to better understand selection and its consequences from farmers' perspectives but based on the concepts used by plant breeders. Among the households we worked with, farmers' selection practices were not always effective yet they understood the reasons for this and had no expectations for response to selection in some traits given the methods available to them. Farmers' statements, practices and genetic perceptions regarding selection and the genetic response of their maize populations to their selection indicate selection objectives different than may be typically assumed, suggesting a role for plant breeder collaboration with farmers.

Abbreviations: CPB – collaborative plant breeding; h^2 – narrow sense heritability; R – response to selection; S – selection differential; V_E – environmental variance; V_G – genetic variance

Introduction

Some researchers have suggested collaborative or participatory plant breeding (CPB) in response to the challenge of making agriculture more sustainable (e.g., Eyzaguirre & Iwanaga, 1996). Collaborative plant breeding includes a range of approaches to local crop improvement that benefit from contributions by both plant breeders and farmers. This approach can potentially result in varieties adapted to the needs of low resource farmers in highly stress-prone environments, and lead to enhanced *in situ* conservation of crop genetic resources (Witcombe et al., 1996). However, as with other applied research and action efforts with farmers, CPB has until recently been dominated by deductive reasoning regarding farmer knowledge and practices and the effects of those on crop populations. While this may sometimes be justified, there are enough differences among many CPB situations, and between CPB contexts and those of conventional plant breeding, that it would be valuable to consider local, empirical evidence and the possibility for inductive reasoning as a basis for subsequent decision-making. In addition, as more research is conducted on farmers' knowledge and practices, the dangers of generalizing from case studies becomes evident. For example, several studies observed that farmers often test new varieties in optimal environments, such as home gardens with adequate moisture and fertile soil, and evaluate them for later planting in more stressful environments, as a way to evaluate certain traits while reducing the risk of losing the variety (Ashby et al., 1995; Soleri & Cleveland, 1993). Yet some farmers frequently plant new varieties on their worst land before any increase in their use of them, which has also been interpreted as a risk aversion strategy (Sthapit et al., 1996; Witcombe, 1998).

Despite the wide range of interpretations of what CPB actually involves in practice, there are recurrent themes in the research literature (Ceccarelli et al., 1997; Weltzien R. et al., 1998). First, a central point of agreement across disciplines is that CPB's value lies in its relatively close attention to adaptation to local sociocultural and biophysical circumstances (e.g., Eyzaguirre & Iwanaga, 1996). Second, CPB entails some sort of interaction between formally trained plant breeders or other researchers and farmers, with the objective of making crop varieties better meet local needs by drawing on some of the insights contributing to the effectiveness of modern plant breeding as well as the knowledge and experience of farmers.

The success of plant breeders' work is due, in part, to the application of knowledge of population and quantitative genetics and statistics to the crop improvement problems they are investigating. One of the simplest and most obvious ways that plant breeders can contribute to CPB is through the use of genetics and statistics to help solve the specific challenges of local crop improvement. However, the application of these without an understanding of the local context is a transfer-of-technology (TOT) approach, and may be fraught with all the problems now seen to be associated with TOT (Chambers et al., 1989). To a great extent, participatory research was developed as a response to these problems, seeking to overcome them through communication, respect for farmers' knowledge and experience, improved understanding of local factors, and collegial collaboration (Ashby, 1997). To facilitate a participatory approach, CPB that seeks improvement of local crop populations by building on farmers' own practices and materials ('farmer-led' CPB, McGuire et al., 1999) will require that plant breeders have some understanding of farmers' selection goals, practices and their local crop populations. To make most effective use of the theory and methods of genetics and statistics, such an understanding will need to be in terms of those theories, ones fundamental to plant breeding. Basing collaboration on untested assumptions extrapolated from experience in conventional breeding contexts – the deductive approach – may not always be appropriate or efficient. In addition, such assumptions neglect one of the aspects of CPB about which there seems to be greatest agreement, the value of specific biological and sociocultural adaptation for achieving crop improvement for low resource agricultural systems.

Even beginning to have such an understanding of farmers' knowledge, practices and their implications can be difficult. While many of the features characteristic of CPB situations make obtaining meaningful empirical data challenging, an increasing number of investigations (e,g., Louette et al., 1997; Weltzien R. et al., 1998), including the one reported here, are trying to do just that. This paper reports the findings of a study of farmers' selection of maize seed in the Central Valleys of Oaxaca, Mexico. Our overall goal was to improve outside researchers' understanding of the local seed selection process so that they could contribute most effectively to collaborative improvement of that process. Specifically, we wanted to understand seed selection from the farmers' perspectives but in terms of the concepts relevant to plant breeders. We based our approach on the biological model of plant breeding used in formal, western plant breeding because the model addresses a fundamental aspect of plant selection. We recognize, however, that the actual application of that model and the outcomes of selection are the result of the biological model combined with contingencies and local manifestations of factors including ones that are individual, social, cultural, economic, geographic, historical and evolutionary (Berlin, 1992; Cleveland et al., 1999).

Methods

Site and sample selection

We worked with eight farm families in Santa Maria (pseudonyms are used throughout for community and individual names), a community in one of the wettest of the three Central Valleys of Oaxaca the Zimatian Valley, and with five families in San Antonio, a community in the Mitla Valley, the driest of the three (Dilley, 1993). Households were initially selected for participation in another component of this research concerning quantitative description of their crop populations (Soleri & Smith, n.d.). Some households were identified through recommendations of fellow community members and municipal authorities as households known to be managing diverse maize varieties or as respected maize farmers (e.g., hardworking, not implying large-scale). Others were chosen during walking tours of the field areas early in the 1996 spring planting season. We attempted to make the sample representative of household types in each of the communities, covering the two most important distinguishing characteristics in those communities: gender of household head and wealth. Interviews were conducted in Spanish with the individuals primarily responsible for agriculture, typically a wife and husband, or mother and son, as well as younger workers who usually deferred to the primary pair. Some of the data reported here, however, refers to only three households from each community whose maize populations were included in the field experiment described in this paper. The small sample size was dictated to a great extent by the nature of this investigation that attempted to integrate accurate social science research with robust biological data that often requires substantial replication. For example, for each of the six households 400 individual maize plants were extensively characterized in the field experiment.

Selection

Our discussion concerns intrapopulation selection and does not address the other form of selection practiced by farmers and formal plant breeders, that of choosing between populations, lines or varieties. Here we talk about selection of planting seed (in maize also referred to as grain or kernels).

In broad terms, there are two ways in which scientific plant breeding can contribute to low resource agricultural systems: a) through the development and delivery of plant materials that perform better for farmers than what they are currently growing (e.g., Joshi & Witcombe, 1996; Maurya et al., 1988), and b) by introducing methods by which households, communities, or other local entities can improve the results of their own selection (e.g., Gomez et al., 1995). The former is the most common approach. In either case, where seed is maintained from year to year by households, the crop populations will ultimately be managed and selected by the households cultivating them and, therefore, their selection practices and the implications for the crop populations will be critical information for planning any plant breeding activities, collaborative or otherwise.

Many farmers practice selection, yet this process has rarely been documented and understood, particularly beyond descriptions of selection criteria (for an exception see Louette & Smale, 1998). At the intrapopulation level, farmers typically practice visual mass selection. In addition, their crop populations are subject to ongoing natural selection, also essentially mass selection, for fitness during each growing and storage season.

Plant breeding is commonly assumed to involve directional selection with the objective of changing mean trait values (Simmonds, 1979:99), although there are exceptions to this including breeding to increase horizontal resistance to pests or disease (Simmonds, 1991). Directional selection is also assumed in most discussions of CPB, including this one. Consistent with this is that response to selection in plant breeding is typically measured as a change in means and such measurements may not detect or adequately characterize the changes resulting from other forms such as stabilizing or disruptive selection. However, the occurrence or value of these other forms of selection should not be dismissed in the CPB context where the attributes of these may be desirable.

To better understand farmers' selection we tried to examine farmer knowledge and practice in terms of a fundamental equation used by plant breeders to characterize response to directional selection (e.g., Simmonds, 1979: 100 ff., 191 ff.). This equation provides a biological framework for identifying what information about farmer selection might be valuable in preparing plant breeders for collaboration. Simply put, this equation states that response to selection (R) is the product of two different factors, h^2 and S.

$$R = h^2 S$$

where h^2 = narrow sense heritability and S, the selection differential, the difference between the mean of the whole population and the mean of the selected group. Expression of S in standard deviation units, the standardized selection differential (Falconer, 1989: 192), permits comparison of selections among populations with different amounts or types of variation. Response itself, the difference between the mean of the whole population from which the parents were selected and the mean of the next generation that is produced by planting those selected seeds under the same conditions, will increase as S and/or h^2 increases.

The research reported here is a beginning step in understanding farmer selection and its impact on crop populations. It was conducted both as a case study and as an exploration of methods useful for improving that understanding. In each of the following four sections we report the results of our research in terms of answers to four sets of research questions about the response equation, using a variety of methods and materials described in each of the sections.

Concerning S we asked:

1. What are farmers' explicit criteria for seed selection?
2. What are the criteria of farmer selection as reflected in the ear phenotypes they select? What are the standardized S values for these criteria? What do these patterns suggest about the type of selection farmers are attempting?

Concerning h^2 we asked the following questions in another part of this research project reported in more detail elsewhere (Soleri & Cleveland, forthcoming):

3. What are farmers' genetic perceptions regarding h^2? How do these perceptions define their expectations for R?

Concerning R we asked:

4. Is there a R to farmers' selection in their crop populations as measured by a significant difference between phenotypic means of the selected individuals and the whole population?

Farmers' explicit selection criteria

Research question

What are farmers' explicit criteria for seed selection?

Materials and methods

Informal discussions and participant observation were conducted with eight collaborating households in Santa Maria and four in San Antonio from June-November 1996. Formal interviews in Spanish were applied during December of that year with the same households. Open-ended questions were used to elicit farmer selection criteria, with reference to the maize ears used in the selection exercise.

Findings

Farmers in this region of Oaxaca, as in most other areas of Mexico, select maize seed for planting entirely post harvest, typically as whole ears (Aguilar, 1982; SEP, 1982). Farmers' selection criteria as reported to us can be divided into three categories. The first of these concerns criteria relating to viability of planting seeds, ears with evidence of pest or disease damage are usually set aside for use as animal feed without further consideration of other characteristics. This was most evident in participant observation, and we hypothesize that it may be so fundamental as to often be omitted in verbal descriptions of selection criteria not accompanied by discussion of actual selection of ears; 50% and 25% of households stated freedom from pest/disease damage to the grain and ear respectively, as important in the open-ended questions. However, when specifically asked, all households stated that this is their first concern. The next category includes traits that contribute to large and heavy ears and kernels; ear length, weight, diameter, kernel size, and weight and weight/volume of shelled kernels. The final category encompasses a number of traits that define a varietal type or subtype and in our sample includes traits like grain type (e.g., crystalline vs. starchy), grain form (round vs. flat, i.e., *'bolita' v. 'cuadrado'*, see Soleri & Cleveland, forthcoming), cob and husk color. Although criteria in the third category varied between households and communities, the first two categories were universal and primary.

Selected phenotypes and kind of selection attempted

Research questions

What are the criteria for farmer selection as reflected in the ear phenotypes they select? What are the standardized S values for these criteria? What do these patterns suggest about the type of selection farmers are attempting?

Materials and methods

Because stated information such as selection criteria may not always accurately reflect actual or implicit practice, or may be misunderstood in verbal descriptions (Bernard, 1994), this part of our research attempted to identify selection criteria based directly on the phenotypes of ears farmers select. We conducted a simple selection exercise with 13 farming households using a random sample of 100 ears of maize from farmers' fields and for which plant morphophenological and ear traits were documented (see Soleri & Smith, n.d.). In the first year (1996) each household selected from a 100 ear sample from their own field. Because of the poor rainfall in 1997 and subsequent

Table 1. Selection exercise maize populations, households and scientists in this study

Community[a]	Selection exercise identification number (ID#)	Household (F)/ Scientist (S)	Maize population[b]	Year of harvest
Santa Maria (A)	11A	1 F	401	1996
	12A	2 F	402	1996
	13A	3 F	403	1996
	14A	4 F	404	1996
	15A	5 F	405	1996
	16A	6 F	406	1996
	20A	6 F	501	1997
	21A	1 F	502	1997
	22A	2 F	502	1997
	23A	3 F	502	1997
	24A	4 F	502	1997
	25A	5 F	502	1997
	26A	6 F	502	1997
	27A	7 F	502	1997
	28A	8 F	502	1997
	29A	9[c] S	502	1997
San Antonio (B)	11B	10 F	601	1996
	12B	11 F	602	1996
	21B	10 F	701	1997
	22B	11 F	701	1997
	23B	12 F	701	1997
	24B	13 F	701	1997
	25B	14 F	701	1997
	26B	10 F	702	1997
	27B	9[c] S	702	1997
	28B	15[d] S	702	1997
	29B	16[e] S	702	1997

[a] Community that is source of maize population used and also home of household making the selections.

[b] The following populations are successive generations of the same seed grown in 1996 and 1997, respectively; 401 & 502, 406 & 501, 601 & 702, 602 & 701.

[c] Regional maize breeder with national agricultural research institute.

[d] International maize genetic resources expert.

[e] US maize breeder working in the sub tropics and tropics of Latin America.

crop failure in many fields, only four maize populations were used for the selection exercise that year, two from Santa Maria (501, 502) and two from San Antonio (701, 702) (see Table 1). Households selected only on the population from their own community, in Santa Maria this was from population 502 and in San Antonio from population 701, with one exception in each community. Households were asked to select their choice of the best ten ears for use as planting seed. Differences between trait means of the total 100 ear samples and 10% selections were evaluated using t-tests with statistical significance set at $p \leqslant 0.05$.

In part as an initial exploration of the assumption of directional selection, we also asked three outside researchers to perform the same selection exercise with population 702, and one of those researchers also selected on population 502. The researchers included a Oaxaca-based regional maize breeder for the national agricultural research institute, a maize genetic resources expert from an international research institute in Mexico City, and a US maize breeder who has been working in the sub tropics and tropics of Latin America for the past 15 years. We hypothesized that those researchers' presumed interest in directional selection might provide a contrast with farmers' selections in the form of their respective standardized S values from the same 100 ear sample.

Findings

Within the two populations for which data regarding pest or disease damage were systematically collected (502 and 701) the proportion of affected ears was 12 and 36%, respectively. Among all farmer selections on these two populations (n = 13), three from San Antonio (23B, 24B, 25B) – all on population 701 – each included one affected ear. Each of these ears had lengths and weights over one standard deviation greater than the mean for that 100 ear sample and their inclusion may reflect their desirable phenotypes and the frequent comment that with some care 'good' (clean) seed could be obtained even from some ears with pest or disease damage, should that be necessary. Beyond the primary discrimination between ears with and without evidence of pest and disease damage, these data do not allow identification of a hierarchy of selection criteria. This is due to the significant, positive phenotypic correlations among many of the ear characteristics measured in this study and of interest to farmers. Still, the results of this selection exercise appear informative both in this specific case, as well as a source of insights for further investigation of farmer selection.

Although standards have been outlined (e.g., Hallauer & Miranda, 1988), plant breeders recognize that S is neither a simple nor normative constant but rather will change depending on other variables such as who is selecting, their goals, and the material on which they are selecting (h^2 and population size) (Sim-

Table 2. Comparisons in this study to discern influences on farmers' S values

Level	Relevant comparison and data	Selection exercise ID numbers for relevant comparisons in this study
Across communities	Overall, all farmer selection data	11A–28A and 11B–26B
Between communities	Farmer selections aggregated by community	11A–28B v. 11B–26B
Within communities	a) Maize populations, with same household selecting on different populations grown in same year	Sta. Maria: 20A v. 26A, S. Antonio: 21B v. 26B
	b) Years, with same household selecting on same populations grown in different years	Sta. Maria: 11A v. 21A, 6A v. 20A S. Antonio: 11B v. 26B, 12B v. 22B
	c) Households, different households selecting on same maize population grown in same year	Sta. Maria: 21A–28A S. Antonio: 21B–25B

monds, 1979: 102). In the context of CPB it may be useful to recognize several levels at which variation might influence S. Levels represented in this study are across, between, and within communities. Possible intracommunity comparisons here are based on factors such as phenotypic differences between crop populations (population), differences in these populations due to annual variations in growing seasons (year), and inter household variations (household) (Table 2). Intra household variation, for example in selection criteria and practices, and agronomic or seed storage practices, may be another significant source of differences but were not thoroughly addressed in this study.

Looking across both communities at farmer selections by trait indicates that of the pest and disease free ears, those that were longer and heavier, often with larger 100 grain weights and ear diameters as compared to the 100 ear samples, were the favored phenotypes sought in these selections (Table 3). Disaggregation of the data by community suggests that ear diameter is of greater interest to households in San Antonio than in Santa Maria as indicated by the proportion of significant t-tests in each (Tables 4 and 5).

For all three of the intra community factors (populations, years, households), comparisons between selections showed variation present in at least one community in either the number of significant t-tests or the magnitude of standardized S for significant t-tests. For example, selection differentials for some traits varied substantially among households in the same community selecting on the same maize population (Table 4, 21A–28A and Table 5, 11B–25B). Whether this is a difference in selection criteria, ability or desire cannot be discerned by our data. Still, this finding is consistent with much social science research that documents the importance of inter and intra household variation in terms of knowledge, decision-making, resource use and other factors (Berlin, 1992; Friis-Hansen, 1996).

Finally, selections made by outside scientists (29A, 27–29B) provide another comparison with those made by farmers. This comparison is best characterized by the relatively higher standardized S values in the scientists' selections on population 702 (Table 5). The larger average standardized S values of scientists' selections make them more effective for accomplishing directional selection if that is the selection goal. However, in the one comparison available with population 502 the scientist's selections were for the most part insignificant (Table 4). This may be an indication of variation in scientist criteria, specifically it may reflect this breeder's interest in qualities he identifies with the *bolita* racial group that predominates in this region (Wellhausen et al., 1952: 185–188) not accounted for in the traits measured here. Having devoted most of his

Table 3. Mean standardized selection differentials[a] for cases where 10% selections significantly different than 100 ear samples[b] and proportion of significant selections. Summary of both communities, farmer selections only

	Ear diameter	Ear length	Ear weight	Kernel row number	100 grain weight	Shelling ratio (grain wt/ear wt)
Mean standardized S and SE for cases with significant *t*-tests	0.95 ± 0.07	0.88 ± 0.05	1.14 ± 0.07	0.63 ± 0.16	0.85 ± 0.04	na
Proportion of significant *t*-tests (%)	48	91	87	9	53	4

[a] Standardized selection differential = (mean of selection – mean of 100 ears)/SD of 100 ears (Falconer 1989: 192).

[b] $p \leqslant 0.05$, significant *t*-tests represent 10% selection with mean different than 100 ear sample.

Table 4. Standardized selection differentials (S)[a] for 10% selections significantly different than 100 ear samples[b], Santa Maria

Selection exercise ID#	Ear diameter	Ear length	Ear weight	Kernel row number	100 grain weight	Shelling ratio (grain wt/ear wt)
11A		0.95	0.91		0.68	
12A	0.96	0.65	0.94		–	
13A						
14A	0.83	1.20	1.58		–	
15A		0.48		–0.47	0.86	
16A	1.29	1.33	1.81		–	
20A	0.78	0.43	1.58	0.78	0.77	
21A		0.75	0.91		1.02	
22A	0.74	0.88	1.35		0.88	
23A		0.67	0.75		0.95	
24A		1.03	1.04			
25A		0.65				
26A		0.83	0.73			
27A		0.95	1.16		0.78	
28A			0.90			0.72
Mean S ± SE	0.92 ± 0.10	0.83 ± 0.07	1.14 ± 0.10	0.63 ± 0.16	0.85 ± 0.04	na
Significant *t*-tests (%)	33	87	80	13	58	7
Scientist						
29A			0.40			

[a] S = (mean of selection – mean of 100 ears)/SD of 100 ears (Falconer, 1989: 192).

[b] $p \leqslant 0.05$, significant *t*-tests represent 10% selection mean larger than 100 ear sample unless otherwise indicated.

– Data not collected.

Table 5. Standardized selection differentials (S)[a] for 10% selections significantly different than 100 ear samples[b], San Antonio

Selection exercise ID#	Ear diameter	Ear length	Ear weight	Kernel row number	100 grain weight	Shelling ratio (grain wt/ear wt)
11B						
12B	0.87	0.86	0.86		–	
21B	0.69	1.06	1.15			
22B	1.29	0.99	1.25			
23B	1.02	1.09	1.40		0.97	
24B	1.22	1.15	1.60		0.87	
25B		0.87	0.84			
26B	0.71	0.74	0.99		0.68	
Mean S ± SE	0.97 ± 0.10	0.97 ± 0.06	1.16 ± 0.11	na	0.84 ± 0.09	na
Significant t-tests (%)	75	91	91	0	42	0
Scientists						
27B	1.28	1.28	1.70		0.86	
28B	1.12	1.37	1.61		0.82	
29B	1.12	1.31	1.71	0.98	0.91	
Mean S ± SE	1.17 ± 0.05	1.32 ± 0.03	1.67 ± 0.03	na	0.86 ± 0.03	na
Significant t-tests (%)	100	100	100	33	100	0

[a] S = (mean of selection – mean of 100 ears)/SD of 100 ears (Falconer, 1989: 192).

[b] $p \leqslant 0.05$, significant t-tests represent 10% selection mean larger than 100 ear sample unless otherwise indicated.

– Data not collected.

professional career to development of improved bolita varieties may explain this interest.

Variation in the results at both the intra and interpopulation levels suggests that farmers' selection, as measured by standardized S values, is a complex dependent variable influenced by a number of factors. Depending upon the context, it appears that the interplay of these factors can lead to different criteria and thus selections. These preliminary data suggest that it may not be correct to assume homogenous selection criteria at these levels though that hypothesis will need to be tested with larger sample sizes and over time. Discerning levels of broad agreement from those in which there is substantial variation may help CPB projects identify methods to adequately address homogeneity of criteria at one level and heterogeneity of criteria at others. In addition, taking significant heterogeneity into account may ensure inclusion of a more diverse group of participants, another factor hypothesized to make CPB projects more effective (Ashby, 1997; McGuire et al., 1999).

Traits. In this study the consistent direction of selection and high proportion of significant t-tests for the correlated traits of increased ear length and weight, and to a lesser extent ear diameter and 100 grain weight across households, maize populations, years and communities suggests the importance of those traits to these farming households. This can be contrasted with less sought after traits such as kernel row number. Thus their explicit selection criteria accurately reflect the traits that farmers actually seek when selecting seed for planting.

Selection differentials. For those t-tests that were significant, farmers' selections resulted in standardized S values ranging between 0.43–1.33 and 0.73–1.81 for ear length and ear weight, respectively (Tables 4 and 5). This compares with a standardized S for a 10% selection typically sought by breeders of 1.4 to 1.8 (Fountain & Hallauer, 1996: 166; Hallauer & Miranda, 1988), though not always achieved.

Kind of selection. For those ear size traits of greatest apparent interest to farmers with significant *t*-tests, it would appear that farmers are attempting directional selection, choosing individual phenotypes that fall within one end of the population distribution (Figure 1). This can be contrasted with a trait that is not a selection criterion for farmers in this area (kernel row number) (Figure 2), with distributions of selected phenotypes suggesting random selection.

Perhaps the greatest potential source of bias inherent in this exercise relates to how accurately it represents the proportion of the population being selected. Louette & Smale (1998) used a 1% selection of 15 ears in their simulations, based on calculations of the number of ears necessary to produce sufficient seed to sow the field size from which the ears were harvested. A 10% selection seemed more appropriate for the Oaxaca study because we wished to simulate as closely as possible the type of comparisons these farmers were using to make their choices. In participant observation and informal and formal discussions it was clear that selections are not made from a global comparison among all ears harvested but rather as an iterative process during food processing and just before planting on the ears remaining, and continued only long enough to provide sufficient seed for the area to be planted. Ears are husked and selected ones put aside for seed only until this amount is obtained, no household reported or was observed husking all ears and selecting among them. As the husks are the primary protection against post harvest pest infestation in this area recognized by both farmers and outside scientists (D. Bergvinson, CIMMYT entomologist, personal communication October 1997), husking all ears for selection is not desirable.

In addition, depending on factors including precipitation during the growing season and the quality of the fields available to the household, seed for several fields may be selected from the harvest of the ‘best’ field, resulting in a higher proportion of ears being used than was envisioned under the situation Louette & Smale (1998) report.

Farmers genetic perceptions and expectations for response to selection

Research questions

What are farmers’ genetic perceptions regarding h^2? How do these define their expectations for R?

Materials and methods

To understand their selection practices and expectations, we asked farmers a series of questions to elucidate their genetic perceptions, e.g., perceptions of the role of genetic variation (V_G) and h^2 in selection. We used hypothetical scenarios regarding the expression of traits with high or low average heritabilities in a variable, stress-prone field typical of the region and a hypothetical uniform, optimal field, one that in no way limits plants’ growth potential. These scenarios built on farmers’ experience, but also presented some situations unfamiliar to them, for example a uniform, optimal field. Our questions about the expression of traits in typical and optimal environments were designed to provide outside researchers with a methodological approach for understanding farmers’ theory, specifically, how they perceive of abstract concepts such as heritability in their maize varieties and environments.

These scenarios were presented in Spanish as a part of formal interviews with the 13 farming households in August and November 1997 and August 1998. A variable sample of maize ears and individual photographs of different tassel colors, all from local fields were used to ‘demonstrate’ the scenarios, and were useful to both interviewers and respondents.

Findings

Farmers distinguished between traits of high and low average heritability (see Soleri & Cleveland, forthcoming for details of findings) and their expectations for response to selection reflected these distinctions. It appears that for traits with low average heritability, farmers generally did not hope to change varieties through selection. Nevertheless, farmers’ answers indicated an awareness of selection and the ability to use it when they felt it desirable and possible even though they typically have very low expectations regarding traits that comprise their seed selection criteria. In part, both the lack of expectations for change and the concern with maintenance of current traits appear to

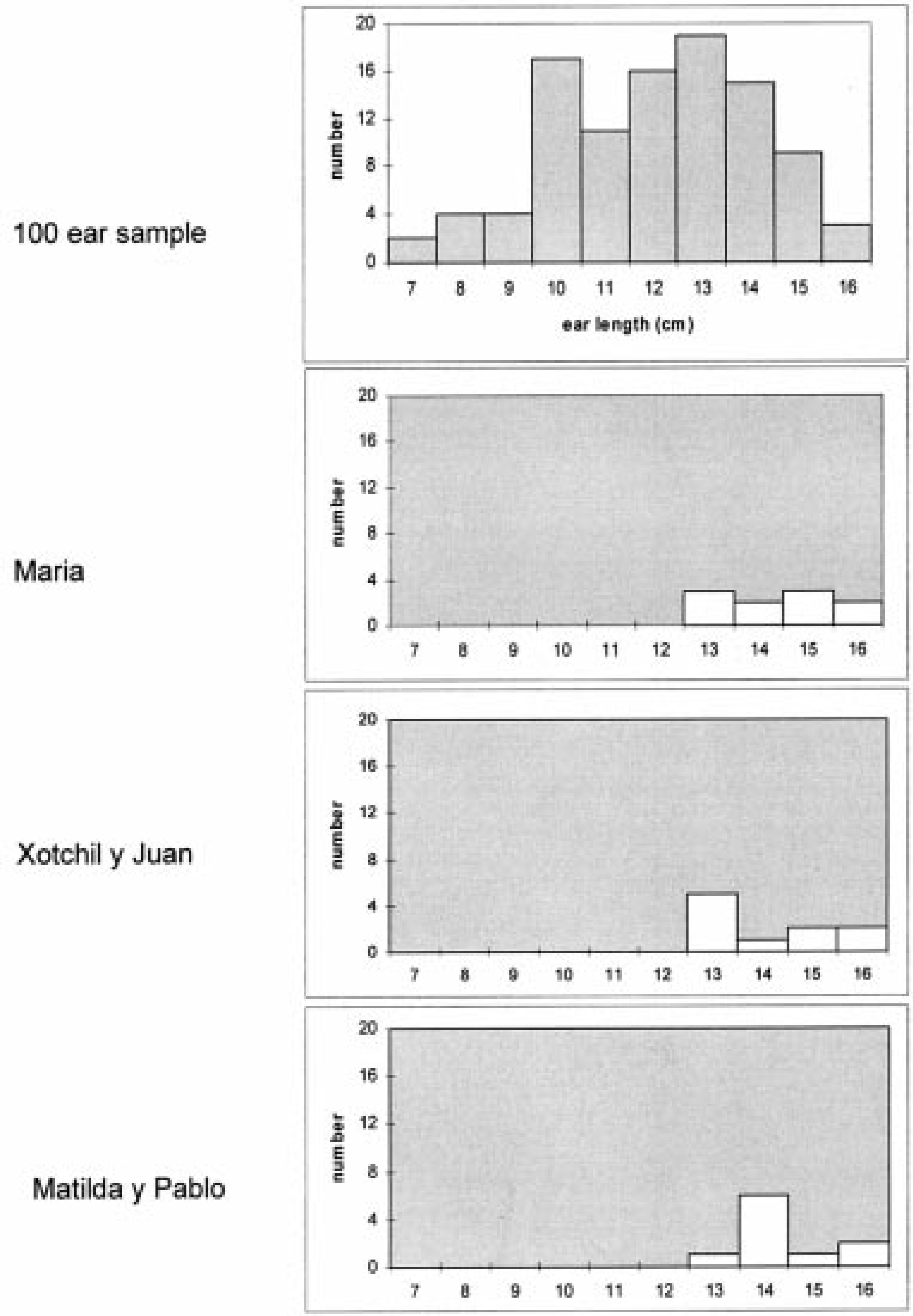

Figure 1. Examples of San Antonio 10% selections: ear length.

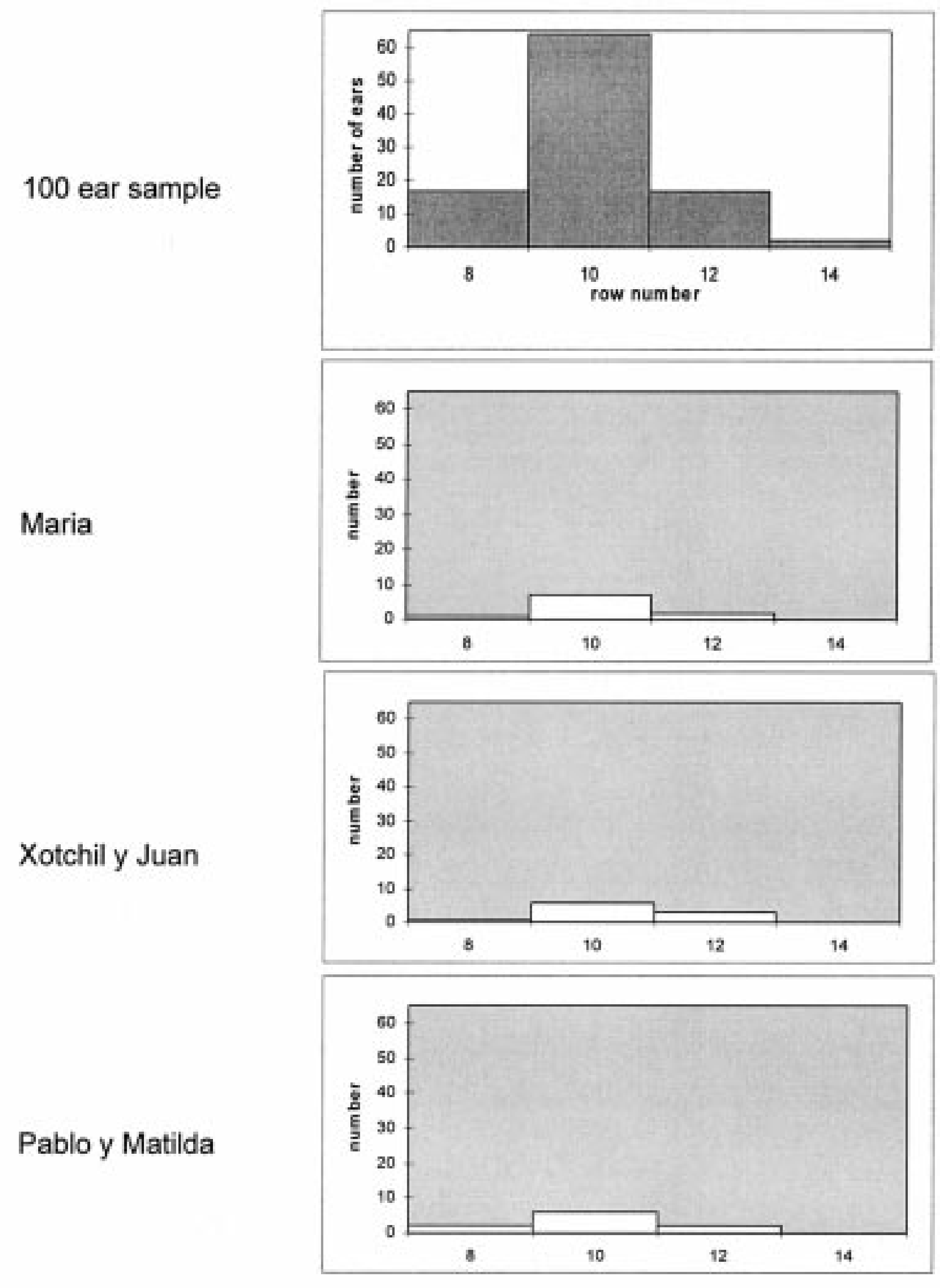

Figure 2. Examples of San Antonio 10% selections: kernel row number.

be a pragmatic recognition of the substantial environmental variation (V_E) and/or large amounts of gene flow via cross-pollination that must occur under local conditions: areas of vast, in some cases year-round, maize cultivation, often in fields as narrow as 11 m. Indeed, farmers explicitly attributed their low expectations to cross-pollination and their understanding of the influence of V_E on plant phenotypes in their fields (i.e., the h^2 of those traits). As such, their expectations appear parallel to two basic observations by formal researchers. First, the lack of control over pollen sources (extensive cross-pollination) effectively reduces h^2 of phenotypes by as much as one half in comparison to its level under biparental control. Second, in cases of a medium to low h^2 ($\leqslant 0.5$), progeny of selected individuals will tend to reflect more the mean of the entire population from which the parents were selected than the mean of the selected parents alone (Simmonds, 1979: 100). In addition, farmers' expectations may also reflect a primary concern with objectives other than changing their populations, as discussed below.

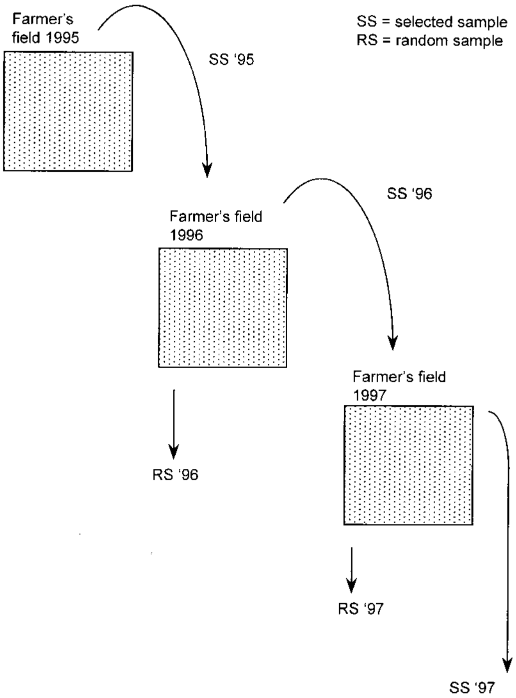

Figure 3. Response to selection field trial: year and type of seed used for each population.

Genetic response to farmer selection

Research question

Assuming directional selection, is there significant R to farmers' selection in their maize populations as measured by a significant difference between phenotypic means of the selected individuals and the whole population?

Materials and methods

Populations from three collaborating households in each of the two study communities were used for this field experiment. Three generations of farmer-selected samples (SS) and two generations of corresponding random (non selected) samples (RS) from the same populations were obtained from each household (Figure 3). These were sown in a completely randomized block design using split plots with main plots representing households and the generation/type (random or selected) of population occurring as sub plots. Eight replications were sown in a farmer's field in Santa Maria in April 1998 with two rows of border on all sides. All field preparation and management were typical of local practices. Data were collected on a maximum of 10 plants in each subplot, first and last hills were excluded. Plant morphological (plant and ear heights, stalk diameter, ear leaf dimensions, number of primary tassel branches), reproductive phenology (days to anthesis, anthesis-silking interval), and post harvest ear traits (ear length, diameter and weight, kernel row number, grain yield and 100 grain weight) were measured. Reproductive phenology was documented at two levels; a) on the individual level for five or fewer plants in each subplot, and b) at the population level for each subplot, including all viable plants in determining the date at which 50% had initiated silk emergence and date at which 50% had initiated anthesis. Analyses were accomplished using GLM procedures (SAS version 6.12) with all effects considered random and number of plants per hill and plant spacing (width [sum of half interrow distance on either side of plant] × length [sum of half intrarow distance on either side of plant]) as covariates. Generation and type means for populations within households were compared using orthogonal contrasts with significance set at $p \leqslant 0.05$, and response to directional selection represented by significant contrasts.

Findings

Three comparisons of means are reported here; between random and selected samples from the same year for two crop years (RS'96 v. SS'96 and RS'97 v.

Table 6. Standardized means[a] for significant orthogonal contrasts[b] of three comparisons made between random (RS) and farmer selected (SS) populations

Household	Trait[c]	Population standardized means for significant contrasts					
		RS ’96 v. SS ’96		RS ’97 v. SS ’97		RS ’95 v. SS ’97	
1	–						
2	Primary tassel branches	94.6	100.5				
3	–						
4	Kernel row number					100.0	103.8
5	Stalk diameter					100.0	107.0
	Ear leaf width					100.0	106.0
	Primary tassel branches					100.0	107.8
	Ear diameter					100.0	106.8
6	Ear height	102.4	91.6				
	Primary tassel branches	102.2	95.7				
	ASI (population)[d]					100.0	87.5
	Days to anthesis (population)[e]			102.1	99.6		
	Kernel row number					100.0	103.8

[a] Population mean as a proportion of the mean of SS ’95 by population and trait, calculated from LS means.

[b] Orthogonal contrast significant at $p \leqslant 0.05$.

[c] Traits documented (n = 13): ear height, plant height, stalk diameter, ear leaf width, number of primary tassel branches, population ASI, individual plant days to anthesis, population days to anthesis, ear diameter, ear weight, kernel row number, grain yield, 100 grain weight.

[d] Date of 50% plants silking–date of 50% plants in anthesis, using all plants/population/replication.

[e] Days to anthesis of 50% of plants/population/replication.

SS’97), and between the first and last selected samples in this experiment (SS’95 v. SS’97) (Table 6). For the traits measured and across all of the populations there were few significant differences evident between the means of the whole population and selected samples derived from these as represented by their progeny generations (n = 4).

Few significant differences were observed between selected samples of the same population over three generations (SS’95 v. SS’97). Despite the low number, this was the comparison having the greatest number of significant contrasts (n = 7). This is not surprising as it is the comparison including the greatest number of generations and thus the greatest opportunity for inclusion of an identifiable change, or accumulation of minor changes that may only become significant over generations. Contrasts between random and selected samples from the same year are the most obvious test of the hypothesis that farmer selection is resulting in change. Of those, only four were significant. Indeed, even the total of 11 significant results (Table 6) across all of the contrasts reported here may be an inflation of the actual number because with $p \leqslant 0.05$ and with 234 contrasts performed (13 traits × 3 contrasts × 6 populations), approximately 12 type 1 errors might be expected.

These findings suggest that with their current selection strategy and over the generations included in this study the additive genetic variance for farmers’ selection criteria is very low relative to V_E, resulting in no statistically significant response. That is, despite adequate selection differentials for traits of interest, under this selection method h^2 appears to be so low that there is no significant response to selection. As such, the ultimate impact of farmer selection appears comparable to random selection, leaving the population means relatively unchanged from year to year. Still, this finding requires qualification for two reasons; First, it is based on a very small number of cycles and therefore incapable of detecting longer term trends that may be significant when measured over a greater time period. Even under experimental conditions formally-trained plant breeders often obtain low responses to mass selection that may not be easily detected in a few cycles (Hallauer & Miranda, 1988). Second, the field experiment was conducted in only one location and year that could not represent the range of environments these populations experience. As such, phenotypic expression within and across populations may have been differentially influenced by genotype × environment interactions as well as by natural selection in the experimental environment.

Given farmers' low expectations for response to selection, substantiated by the results of this field trial, why do they persist in selection for large ears and seeds and pay a premium for large-sized grain for planting seed in the market, when they could purchase more small-sized seed for the same amount of money? When asked this question, three of the 13 households suggested that larger seeds may provide an advantage in terms of emergence and seedling vigor, especially under stress, such as drought (Soleri & Cleveland, forthcoming). This would shift selection for size into the first category for seed selection described earlier, traits concerning seed viability and seedling vigor and not inheritance per se, making the low expectations for response irrelevant in determining how and why selection is conducted (see Louette & Smale, 1998 for similar findings regarding seed viability). Another household, while acknowledging having no expectations for positive, directional change, expressed concern that without this selection for large seeds there might be a change for the worse in the maize populations over time. This implies recognition of the possibility that selecting large seed size maintains this characteristic in a population and therefore is a heritable trait. The remaining majority of households (n = 9) stated that this is a habit that persists despite widespread recognition that it has no consequences in terms of population traits.

Whether preference for large seed size is based largely on unarticulated recognition of the physiological superiority of large seeds, or is based on custom or aesthetics, cannot be ascertained without further investigation including regarding the effect of seed size on seed and plant performance. Even then, determining the original motivation for a contemporary 'custom' would be difficult but should not preclude the possibility that a concern for seed viability and seedling vigor was a factor. Overall these findings do suggest that alternatives to a hypothesis of directional selection should be investigated.

Summary and conclusions

Returning to the response to selection equation, the findings of this small case study suggest the following answers to our research questions:

1. Farmers' explicit selection criteria focus on grain and ear qualities that concern seed viability, ear and grain size and traits identified with specific varieties.
2. In the selection exercise a majority of farmers sought ears that were significantly longer and heavier as compared to the entire sample from which they selected. For these two traits farmers achieve substantial standardized S values with their selection, often close or equal to values typically sought by formal plant breeders. Comparison between communities showed differences in frequency of significantly different selections for ear diameter.
3. The pattern of selection for the primary criteria appears directional, frequently selecting only phenotypes above a particular threshold value.
4. For the same population selected on by many farmers (701), researchers were able to achieve apparently higher mean standardized S values for all traits as compared to farmers suggesting that either their skills or objectives were different. In other words, while farmers selected phenotypes above a certain threshold value for a particular trait, compared to researchers they did not always select the phenotypes farthest above that threshold.
5. Disaggregation of the data within communities by household, maize population or year in which the population was grown, revealed variation in significant selections at all of these levels suggesting these variables as some of those that may contribute to definition of heterogeneous and distinct selection criteria and practices, with potential implications for CPB efforts.
6. Despite 2 and 3 above, all households expressed a theoretical perspective regarding the potential for response to selection in which S and directional selection are largely irrelevant. Among the same traits for which they achieve substantial standardized S values and appear to exercise directional selection they have no expectations for response to their selection.
7. Using their current selection methods, h^2 of farmers' primary selection criteria is low, as they themselves are also very quick to point out. For many but not all households, this may be accompanied

by the belief that there simply is no V_G for a trait, or perhaps more accurately, that there might as well not be given the way they experience it. This perception could easily occur due to the swamping of V_G by V_E in the environments in which they are working. In fact, many breeders may have the same problem in perceiving the effects of extreme V_E on V_P due to the limited range of V_E they have experienced or include in their research relative to that experienced by many low-resource farmers (see Ceccarelli, 1989).

8. Actual response to farmer selection was approximately zero in this study, consistent with farmers' own expectations and their comments regarding h^2 of traits.

Conclusions

The purpose of this study was to begin evaluation of the potential for formally trained plant breeders and farmer plant breeders to work together in CPB, using a biological model as a framework for the qualitative and quantitative investigation of farmer seed selection. The empirical data while informative about this specific case study, is not intended to be conclusive, and is most appropriately used as a basis for discussion and an indicator for issues requiring a more thorough understanding. What do these findings imply in terms of plant breeders and farmers working together to improve varieties to better meet local needs? Given extant environments and selection strategies, breeder development of 'improved' varieties must include either fixation for critical traits and provisions to maintain those despite cross-pollination and low h^2 for those traits in local environments, or plant breeders must be prepared to continually replace those varieties as they degenerate under local conditions. Collaboration to make farmer selection more effective will likely be more economical and result in more stable production by minimizing dependence on external infrastructures for varieties and seed.

Farmers' genetic perceptions and observations describe attributes of the populations or environments they work with, and give plant breeders valuable insights regarding farmers' theory and the sorts of environments farmers are working in that might otherwise require extensive experimental work, or simply be left to deductive assumptions. These insights place farmers' actions in a very different light than do the assumptions commonly made by outsiders that those actions are naïve at best (e.g., Aquino, 1998: 249). The findings reported here indicate that the farmers we worked with have a good understanding of why their selection functions as it does. Most of them distinguish easily between traits with high and low average heritabilities, as well as having an awareness of V_G and an ability to use it for selection where they feel heritabilities permit. While farmers seem to have no problem identifying desirable ear phenotypes and achieving adequate selection differentials for these, the genetic perceptions provide insights into how this selection is best interpreted. That is, the assumption that these selection differentials represent explicit attempts at directional selection requires reconsideration. As such, differences between scientists' and farmers' standardized S values may not reflect differences in skill so much as differences in objectives.

The results suggest farmers' overriding concern in seed selection may be seed viability and seedling vigor, although there is variation as to their articulation or explicit awareness of this issue. It is difficult to discern whether this concern is strengthened by the opinion that with the methods available to them they cannot hope for greater response to selection, an opinion supported by our field experiment. Given observed selection differentials, h^2 for simple mass selection of documented farmer selection criteria may be insufficient to result in a response (Soleri & Smith, n.d.) especially with uniparental selection. Although low V_G could theoretically be the reason for low h^2, even simple visual inspection of local fields implies that great intra field variability (V_E) could easily explain this lack of h^2.

These findings suggest two contributions that plant breeders and other researchers could make to CPB efforts in this area: a) improvements in seed viability and seedling vigor including screening for genetic components of these and for post harvest pest resistance in local environments (husk coverage), as well as viable methods of post harvest pest control; and b) collaboration with farmers to make simple changes in their selection strategies that will reduce intrafield V_E, thereby increasing h^2 of some potentially valuable traits. For the latter, investigation of the potential of techniques such as in-field selection based on environmental stratification is an obvious first step (Gardner, 1961; Hallauer & Miranda, 1988: 169). Improving the effectiveness of selection may encourage farmers' interest in selection criteria that they do not currently consider in terms of intra population improvement. However, to make a lasting contribution, the increased

h^2 and the associated increase in response must be sufficient to reward and reinforce the amended selection approach from the perspective of the farmers using it.

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