

E C O N O M I C S

Working Paper 99-10

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Biological Perspective:
Implications for Collaborative
Plant Breeding**

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Abstract: Plant breeding by researchers has become increasingly isolated from the plant breeding of farmers. Collaborative plant breeding (CPB) offers the possibility of bringing these two plant breeding traditions together to increase the usefulness of new crop varieties to farmers, especially small-scale farmers working in stress environments with limited external inputs. This paper presents a framework for plant breeders, social scientists, project personnel, and policy makers to understand farmer plant breeding for improving the long-term well-being of small-scale farmers through CPB. Research questions are proposed based on three components of the basic biological model of plant breeding: genetic variation, environmental variation and its interaction with crop genotypes, and crop plant selection. For each component, the authors review the range of data, conclusions, and assumptions in the research literature about farmers' 1) knowledge, 2) practice, and 3) crop varieties and growing environments. The paper concludes by discussing the general implications of this approach for CPB. The framework described in this paper for understanding farmer plant breeding from a biological perspective can make a significant contribution to the success of CPB. By posing questions such as the ones suggested in this paper, a more systematic picture of farmer plant breeding, both in specific instances and in general, should emerge. Further testing of specific hypotheses based on the questions presented here is needed, especially in the context of CPB projects. This research could help farmers and plant breeders communicate more efficiently with each other, so that breeders can use their knowledge of biological theory, statistical design and analysis, and access to a wide range of genetic diversity, and farmers can use their knowledge of their crops and environments and their techniques for managing them more effectively. This collaboration should yield varieties that better meet farmers' needs and conserve crop genetic diversity *in situ*, thus contributing to sustainable agriculture.

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Summary and Implications for Further Work

Plant breeding (including both choosing among varieties and selecting plants in segregating populations) by modern professional plant breeders has become increasingly isolated from plant breeding by farmers. Collaborative plant breeding (CPB) offers the possibility of bringing these two plant breeding traditions together to increase the usefulness of new crop varieties to farmers, especially to small-scale, limited external input farmers in high stress growing environments. To be effective, CPB requires better information about how farmers understand and use their crop varieties. Our goal in this paper is to present a framework for plant breeders, social scientists, project personnel and policy makers to better understand farmer plant breeding for improving the long-term well-being of small-scale farmers through CPB. We begin with an explanation of the methods used this paper. The major components of the biological model of plant breeding are the topics of the next three sections of the paper: genetic variation, environmental variation and its interaction with genetic variation, and crop plant selection. For each of these components of the biological model we propose key research questions about farmers' 1) knowledge, 2) practice, and 3) crop varieties and growing environments. We then review the range of data, conclusions, and assumptions in the research literature relevant to these questions. We use examples from our own work in Oaxaca, Mexico, especially for those topics where very little other research exists.

We found a range of explicit and implicit answers to the questions we pose in the research literature, answers which are often contradictory. This finding supports our initial impression that generalizations based on experience with specific varieties, environments or farmers may not be valid, and that CPB may be limited by the availability of an appropriate framework for research on farmer plant breeding. However, the research literature does lend support to the idea that farmers' knowledge and practice reflect an intuitive, empirical and theoretical understanding of their crop populations that in many ways is fundamentally similar to the basic understanding of plant breeders as reflected in the biological model we describe. Yet this knowledge and practice is also different, because the details of their experiences (e.g. values, social relations, crops, and growing environments) are different. In other words, the search for generalizations is valid, but we need to be careful about making them at too superficial a level.

We conclude that our framework for understanding farmer plant breeding from a biological perspective can make a significant contribution to the success of CPB. By posing questions, such as the ones we suggest, a more systematic picture of farmer plant breeding, both in specific instances, and in general, should emerge. By examining the assumptions which have often necessarily formed the basis for CPB, this framework could provide a more robust foundation for collaboration. Further testing of specific hypotheses based on the questions presented here is needed, especially in the context of CPB projects. This research could help farmers and plant breeders communicate more efficiently with each other, so that breeders can use their knowledge of biological theory, statistical design and analysis, and access to a wide range of genetic diversity, and farmers can use their knowledge of their crops and environments and their techniques for managing them more effectively. This collaboration should lead to varieties that better meet farmers' needs and conserve crop genetic diversity in situ, thus contributing to sustainable agriculture.

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Farmer Plant Breeding from a Biological Perspective: Implications for Collaborative Plant Breeding

David A. Cleveland, Daniela Soleri, and Steven E. Smith

Introduction

Since the first domestications of wild plants about 12,000 years ago, farmer plant breeders have been responsible for the development of thousands of crop varieties in hundreds of species (Harlan 1992). Professional plant breeding began about 200 years ago in industrial countries (Simmonds 1979). Modern plant breeding developed in the early part of the 20th century, based on Darwin's theory of evolution through selection and the genetic mechanisms of evolution developed by Mendel, Johannsen, East and others, and led to further separation of farmer and professional breeding (Allard 1999; Simmonds 1979) and seed supply systems (Cromwell et al. 1993). The emphasis of professional breeding has typically been on developing modern varieties (MVs) with geographically wide adaptation to optimal, relatively uniform growing environments, and high yield in these environments (Evans 1993; Fischer 1996). This contrasts with farmer breeding and farmers' local varieties (FVs, also referred to as landraces), which are usually assumed to have narrow geographical adaptation to marginal, relatively variable growing environments, and high yield stability in those environments from year to year (Harlan 1992; Zeven 1998).

Collaborative plant breeding (CPB, also referred to as participatory plant breeding¹) is an attempt to reverse this historical trend by bringing farmer plant breeders (hereafter simply farmers) and modern, professional, scientific plant breeders (hereafter simply plant breeders or professional plant breeders²) together in the process of developing new crop varieties. The impetus for CPB comes from recent developments in both modern plant breeding and genetic resources conservation, and in traditionally-based agriculture, as part of achieving more sustainable agriculture (Cleveland et al. 1994).

In modern agriculture, emphasis has recently been placed on local adaptation and on genetic diversity. This has resulted largely from increasing awareness of limits to conventional plant breeding as a result of increasing scarcity and decreasing quality of production resources in the low stress environments of modern agriculture. Awareness that future increases in productivity may depend on increasing yields in high stress environments has also motivated emphasis on specific or narrow adaptation and on genetic diversity (Evans 1997; Fischer 1996; Heisey and Edmeades 1999; Smale 1997). This appears to have provided the impetus among some breeders for advocating CPB (Berg 1996; Smith, M.E. and Paliwal 1997). Additionally, some breeders and genetic resources conservationists

¹ Our use of the term collaborative as opposed to participatory is meant to emphasize the possibility and desirability of farmers and plant breeders working together as colleagues, i.e., without either perspective being privileged. The great majority of the reports under the rubric of participatory plant breeding have described farmers participating in plant breeders' work, and have not included the farmers' perspective (Smale et al. 1998b).

² Often referred to as "formal" breeders in the CPB literature. No term is entirely satisfactory, as to be expected in the early stages of a new interdisciplinary endeavor.

concerned with the availability of genetic variation for future professional breeding work have begun advocating CPB as a means of in situ conservation of FVs (Qualset et al. 1997; Worede 1997).

On the other hand, among farmers and their advocates, there is a recognition that MVs often do not serve the needs of farmers in highly stress-prone growing environments, as well as increasing awareness of inadequate and decreasing yields as a result of increasing population size, environmental degradation, and socioeconomic change (Berg 1996; Cooper, D. et al. 1992). Many advocate CPB to improve the well-being of small-scale farmers, especially those in high stress growing environments (Ceccarelli 1996; van Oosterom et al. 1996).

Despite the wide range of interpretations of what CPB actually implies in practice, there are two common, widely accepted themes in the research literature (e.g. Berg 1996; Ceccarelli et al. 1997; Weltzien R. et al. 1998). First, the value of CPB lies in its attention to adaptation to local sociocultural and biophysical circumstances. Second, CPB entails some sort of interaction between professional plant breeders or other researchers and farmers, with the objective of making local cropping systems better meet local needs.

Yet, while CPB implies that modern professional and farmers' plant breeding can be integrated, very few data are available for comparing similarities and differences in the two types of plant breeding, particularly data from farmers' environments and under farmers' management. The lack of data not only points out a need for research, but also means that current discussion must rely to a large extent on untested theory, or unfounded assumptions. The question remains to be answered, whether a synergistic relationship between farmers and breeders is possible, and if it can occur on a wide enough scale to have a significant impact on the future of agriculture and plant breeding, and the well-being of farmers and society in general. Better understanding of farmer plant breeding is critical for CPB.

The success of plant breeders' work is due, in part, to the application of population and quantitative genetics and statistics to the crop improvement problems they are investigating. Other factors contributing to this success are experience, luck and intuition, the "art" of plant breeding. Though often at least as important as the "science" of plant breeding (Duvick 1996, Simmonds 1979), this "art" is specifically tied to individuals and/or environments, whereas fundamental genetic and statistical principles remain constant across a range of contexts.

Thus, one of the simplest and most obvious ways that plant breeders and other outside researchers can contribute to CPB is through the use of genetics and statistics to help solve the specific challenges of local crop improvement. However, to do this plant breeders must be able to describe or understand farmers' selection goals and their local crop populations in terms of the fundamental concepts used in plant breeding. Without such an understanding, or the methods necessary to achieve it, outside researchers may be entering into collaboration with farmers with unfounded assumptions that may jeopardize the success of the project. Basing collaboration on untested assumptions extrapolated from experience in

conventional breeding contexts—the deductive approach—may not always be appropriate. In addition, such assumptions may defeat one of the aspects of CPB about which there seems to be greatest agreement, which is the value of local biological and sociocultural adaptation for achieving crop improvement for low-resource agricultural systems.

Implicit in collaboration is respect by outsiders, who may have more control over farmers' plant breeding system than farmers themselves. However, collaboration can occur at different levels, the ultimate goal being improvement of farmers' well-being and the well-being of society in general. A biological intervention such as the introduction of a new variety, or new alleles via introgression, could have great benefits, but may not involve any change in farmers' practice. Yet, under CPB such a change would not be implemented unilaterally by outsiders without understanding local plant breeding, including farmers' goals and interests, and without reaching a mutual agreement. On the other hand, working with a small number of farmers or a farming community as a whole, either in varietal choice or plant selection, may mean significant changes in farmer practice and perhaps in knowledge. It will undoubtedly require substantial changes in the approaches of plant breeders as well. CPB should not mean that farmers need to be involved at all levels of professional plant breeding, or that plant breeders need to be involved in all levels of farmer plant breeding. The key is that there be mutual respect and agreed upon goals.

Our goal in this paper is to present a framework for plant breeders, social scientists, project personnel and policy makers to better understand farmer plant breeding for improving the long-term well-being of small-scale farmers through CPB. We begin with an explanation of the methods used in this paper. The major components of the biological model of plant breeding are the topics of the next three sections of the paper: genetic variation, environmental variation and its interaction with genetic variation, and crop plant selection. For each of these components of the biological model, we propose key research questions about farmers' 1) knowledge, 2) practice, and 3) crop varieties and growing environments. We then review the range of data, conclusions, and assumptions in the research literature relevant to these questions. We use examples from our own work in Oaxaca, Mexico, especially for those topics where very little other research exists. We conclude with general implications of this approach for CPB.

Methods

We define the major components of the plant breeding system of both farmers and professional plant breeders as *knowledge* (including values, intuition, empirical data, and theory, and other mental constructs), behavior or *practice* (what they do, including decision making and management), and the *biophysical environment* (viz. the crop varieties and growing environments) they interact with, including the results of farmer practice (Figure 1). We then review the range of assumptions and conclusions in the research literature,³ including examples from our work in Oaxaca, Mexico, about farmer plant breeding in comparison to professional, scientific breeding, in terms of the basic biological model on which professional plant breeding is based.

³ Not intended to be a comprehensive literature review.

Local Knowledge, Scientific Knowledge and Sustainable Agriculture

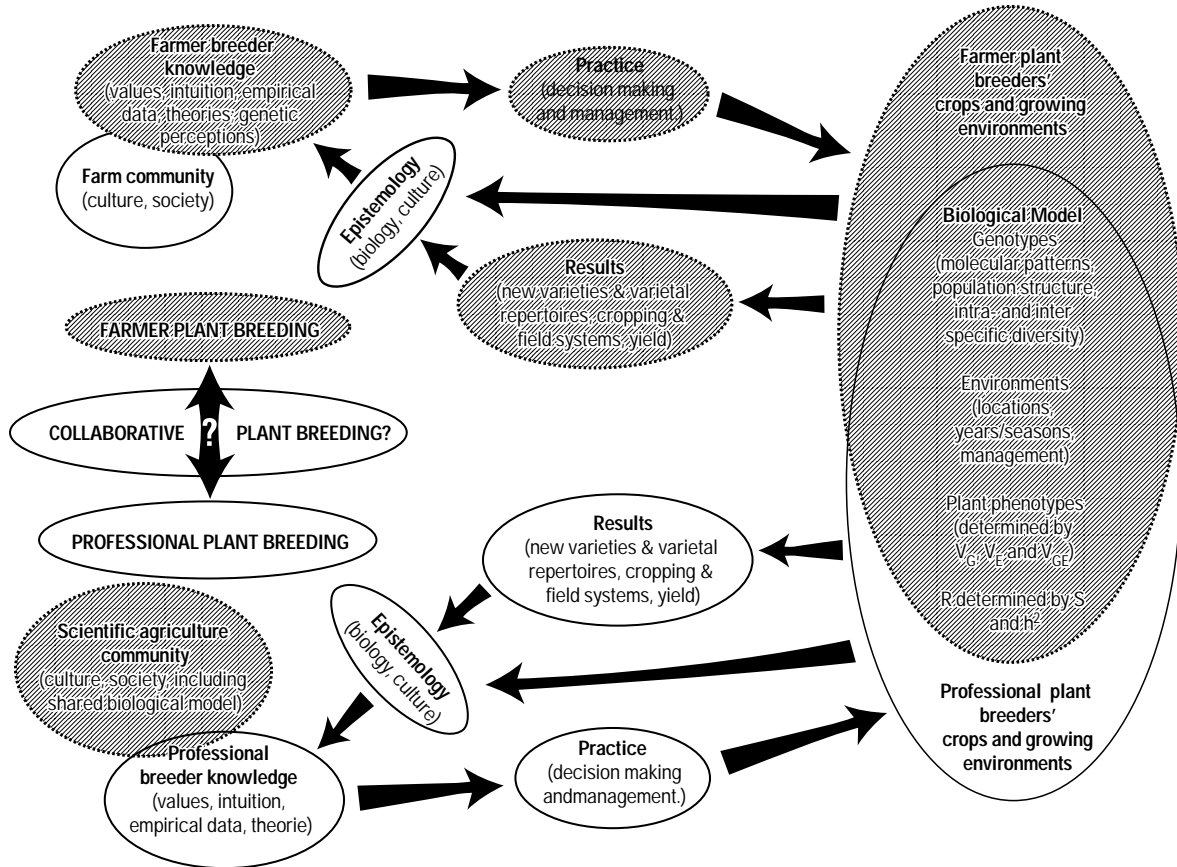


Figure 1. Plant breeding systems. Shaded areas are the focus of this paper.

Plant Breeding System Components

We define plant breeding broadly to include both 1) the *choice* of populations and varieties and other farmer practices that determine the genetic diversity of their crops, the choices plant breeders make between varieties and populations, especially in the initial stages when choosing germplasm for making crosses, and in the final stages when choosing among populations/varieties for further testing or release (Hallauer and Miranda 1988), and 2) the development of new varieties through plant *selection* (both conscious and unconscious) which changes the genetic make up of a plant population. This definition also follows a common practice in the CPB literature (e.g. Witcombe et al. 1996), although the terms “choice” and “selection” may be used interchangeably (e.g. Weltzien R. et al. 1998).

We assume that the goal of plant breeding, by farmer or professional plant breeders, is a combination of populations and growing environments that results in phenotypes that provides the optimal net benefit to the farmer. In other words, intuitive, empirical and theoretical understanding of the determinants of plant phenotype that support successful plant breeding. While a great deal is known about these aspects of professional breeding (mostly the empirical), very little is known by comparison (at least by outsiders) about these aspects of farmer breeding. The role of theory in both scientific and local knowledge systems is controversial (Hull 1999).

We assume that farmers' knowledge about their crop varieties and growing environments is a complex result of both the interaction of inherent cognitive structures and objective patterns of biological and ecological diversity (Boster 1996), as well as of historical, sociocultural and environmental contingencies (Ellen 1996), and that the relationship between knowledge and behavior or practice is also complex (Ellen 1999). Social scientists have long recognized variation in distribution of cultural knowledge as the result of factors including age, sex, social status and affiliation, kinship, personal experience, and intelligence (Berlin 1992). The ethnobiological knowledge that has been documented supports the hypothesis that there are "common cultural patterns in the application of names for plants and animals in systems of ethnobiological knowledge" (Berlin 1992:230). Distribution of knowledge about FVs is often distributed unevenly, with gender and age being a common determinant. For example, Aguaruna women's knowledge of manioc (*Manihot esculenta*) varieties is much greater than that of Aguaruna men (Boster 1985; Berlin 1992), and older Hopi farmers have greater knowledge of maize varieties than younger farmers, probably due to loss of traditional knowledge (Soleri and Cleveland 1993).⁴

Our goal in terms of the knowledge component is better understanding of how farmers perceive phenotypes as a result of the genotype and the environment, what we refer to as *genetic perceptions*. The way in which farmers value and understand their crop varieties affects their plant breeding practice. Therefore, comprehending farmers' subjective knowledge of their crop varieties and growing environments is important in part because it shapes their behavior and affects their crop varieties and farming systems in ways that can be measured objectively, for example in selection differentials. It therefore seems likely that understanding farmers' genetic perceptions can contribute to the success of CPB.

We use a framework for understanding farmer plant breeder knowledge, practice and crop varieties and growing environments that is based on the basic biological model of plant breeding (discussed in the next section). The components of the plant breeding system we focus on are highlighted in Figure 1. However, we do not assume that when there are differences between farmers and breeders, that the farmer is always "wrong", or that outsiders have not been diligent enough in rationalizing farmer knowledge and practice in their own terms (see Scoones and Thompson 1993; Uphoff 1992).

We recognize that in the elaboration and application of the basic model of plant breeding there are also many differences among plant breeders (Cleveland n.d.). For example, regression diagrams used in the analysis of yield stability have become "the plant breeder's icons, ubiquitous but with a variety of styles to support a variety of dogmas" (Evans 1993:163). Therefore, while beyond the scope of this paper, we assume that another essential element for successful CPB is increased understanding of professional plant breeding, for example, the basis for variation in plant breeders' knowledge and practice in relationship to the genotypes and environments they work with, and how their knowledge and practice change in the context of CPB.

⁴ It is important to remember, however, that declarations of socially differentiated knowledge may be used to justify unequal access to resources, rather than reflect actually knowledge distribution (Cleveland and Murray 1997; Fairhead and Leach 1994).

We also recognize that successful plant breeding by either farmers or plant breeders does not depend on a complete understanding of the biological mechanisms involved. Despite the increased power that modern genetics and statistics, and the promise of the new biotechnologies, bring to plant breeding, the genetic basis of important biological phenomena such as heterosis, yield and yield stability, are still unknown, and art and experience are key to successful plant breeding (Duvick 1996). Our assumption is, however, that better understanding of the relationship between knowledge, practice and plants can improve the outcome of collaborative efforts between farmer and professional breeders.

While we focus in this paper on the biological and sociocultural components of farmer plant breeding, greater understanding of economic variables is also essential for support of CPB (see Smale et al. 1998b). The goal should be an analysis of subjective and objective benefit-cost ratios, marginal utilities, and risk, integrated with biological and sociocultural analysis for all aspects of the plant breeding system.

The Biological Model

We use as a framework for assessing farmer knowledge the understanding of plant biology and genetics as developed in modern plant breeding over the last 200 years, and universally accepted by plant breeders (see e.g. Falconer 1989; Simmonds 1979). We define plant breeding broadly to include both choosing among varieties and selecting plants in segregating populations. The goal of plant breeding, whether by farmers or breeders, is to develop a plant population composed of phenotypes that meet farmers' criteria, and that farmers will, therefore, adopt and maintain. Phenotypes include traits of production (yield, yield stability, postharvest traits, etc.), storage, food quality (processing, cooking, taste), and aesthetics (color, shape and texture of seed and other plant parts). We begin, therefore, with the basic framework that breeders use for understanding variation in plant phenotype (V_P) as a function of genetic variation (V_G), environmental variation (V_E), and genotype-by-environment interaction (GxE) variation ($V_{G \times E}$): $V_P = V_G + V_E + V_{G \times E}$. While agronomists focus on changing V_E , breeders focus on changing V_G , but they must control experimentally and statistically for V_E and $V_{G \times E}$ in order to do so efficiently (Cooper, M. and Hammer 1996b). Under the typical assumption of directional selection, the effectiveness with which breeders make changes in the phenotype through selection is measured by genetic gain (R). We discuss variation, environmental variation and genotype-by-environment interaction, and plant selection in the three major sections of this paper.

Genetic variation is the basis for genetic improvement both at the plant level through plant selection, and at the varietal level through varietal choice. Environmental variation and GxE determine the expression of the genotypes in the form of the phenotypes, on which selection is made; and plant selection results in new varieties or maintains old ones, and varietal choice determines farmers' varietal repertoires. Genetic variation can be attributed to particular types of gene action $V_G = V_A + V_D + V_I$ (V_A = variance due to additive effects of alleles, V_D = variance due to dominance among alleles at a locus, and V_I = variance due to interaction between loci). This may be represented as a proportion of phenotypic variance, which produces the genetic measures of broad sense ($H = V_G / V_P$) or narrow sense heritability ($h^2 = V_A / V_P$). Heritability is a critical indicator of the possibility for successful selection in plant breeding. Environmental variation can be partitioned into several

components: $V_E = V_L + V_T + V_M$ (V_L = variance due to location; V_T = variance due to time, e.g., season or year; and V_M = variance due to breeder or farmer management). $V_{G \times E}$ represents the degree to which genotypes behave consistently across a number of environments.

The success of plant selection in meeting the goals of the farmer or plant breeder is often measured by the response to directional selection (R). R is the product of two different factors, h^2 and S : $R = h^2 S$. The selection differential (S) is simply a measure of how the individuals that are selected differ from the rest of the population from which they were selected. The standardized S is the difference between the phenotypic mean of the whole population and the mean of the plants selected, expressed in standard deviation units, permitting comparisons between populations with different levels of V_G and/or experiencing different selection pressures. R then is a measure of the extent to which phenotypic differentials measured by S are heritable, i.e., genetically based. In other words, R is the difference between the phenotypic 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. R will increase as S increases and/or as h^2 increases. The results of selecting for a given trait improve as the proportion of phenotypic variability contributed by genetic variance increases. That is, selection among genotypes is based on phenotype, but response to selection is a function of genetic variability and h^2 (DeLacy et al. 1996).

This points to two major potential contributions of breeders to CPB: increasing h^2 through experimental design to increase the proportion of V_P due to V_G , and, where necessary, increasing V_G by introduction of germplasm or hybridization techniques not available to farmers.

The Oaxaca Case Study

We report here some results from our work with farmers in the southern Mexican state of Oaxaca (1996-1998). To date we have worked with a small number ($n=13$) of farm households and their maize varieties in two communities (Santa Maria and San Antonio, pseudonyms) in the Central Valleys of Oaxaca. Santa Maria is a Mestizo community of approximately 3000 people at 1490 masl (meters above sea level), with an average of 750 mm of annual precipitation, rated as an area of medium agricultural potential by the Mexican National Agricultural Research Institute's (INIFAP) production standards. San Antonio is a Zapotec community with approximately 3000 inhabitants at 1780 masl, with 470 mm of average annual precipitation, and rated as predominantly an area of low or no agricultural potential. The opportunistic samples of eight and five households in Santa Maria and San Antonio, respectively, have been participants in a detailed study of genetic structure of farmer managed crop populations (Soleri and Smith n.d.).

In these communities some of the collaborators were identified through recommendations of fellow community members and municipal authorities as households known to be managing diverse maize varieties or to be respected maize farmers (e.g., hardworking, knowledgeable, but not large scale). Others were chosen at random during walking tours of the field areas in the 1996 spring planting season. We attempted to make the sample

representative of household types in each of the communities, and it covered the two most important distinguishing characteristics in those communities: gender of household head and wealth. Interviews were conducted 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. The small sample size was dictated to a great extent by the nature of this investigation which attempted to integrate in-depth understanding of farmer knowledge and practice with robust biological data that often require substantial replication. For example, for each of the households 500-1000 individual maize plants and ears were intensively documented in plots in farmers' fields, detailed measurements were taken on ears in seed selection experiments, and for some households replicated experiments were carried out in which hundreds of plants and ears from experimental plots were measured.

A series of formal interviews and open-ended discussion questions with the farm households (usually the primary female and male farming members as a minimum) were carried out. The goal of this aspect of the research is to develop a methodology for understanding farmers' genetic perceptions. The interviews include a series of hypothetical scenarios about farmers' maize populations, often using maize ears or photographs of plants to help depict the scenario and to stimulate subsequent discussion. The scenarios focused on the expression of traits with both high and low h^2 , in both a variable, high-stress environment typical of the region (normal field) and a hypothetical uniform, low-stress (optimal) field that in no way limited the plants' growth potential. They were designed to understand how farmers perceive concepts such as heritability in their maize varieties. The scenarios built on farmers' experience but also presented some situations that are unfamiliar to them, for example a uniform field lacking nothing needed for optimal production. The interviews were supplemented through informal discussions and participant observation.

Genetic Diversity

The first major component of farmers' plant breeding we will discuss is genetic diversity (variation). The basis of genetic diversity is different versions (alleles) of genes due to differences in kind and/or order of their molecules. Allelic diversity exists at the plant, population, variety, and species levels, all of which are important for plant breeding and are defined and discussed in this section. Defining the units of genetic organization in crops is critical to discussing genetic variation.

Genetic variation can be defined as a measure of both richness (number of alleles) and evenness (their relative proportions) for a single locus, a population, or several populations of a variety or species (Silvertown and Doust 1993; Frankel et al. 1995). Variation increases as the number of alleles increases and as the evenness of their frequencies in the population increases. In addition, the distribution of alleles in populations also contributes to variation in terms of the arrangement of alleles in plant genomes (level of heterozygosity), including their physical linkage. Species' mating systems affect genetic structure with cross-

pollinating species generally assumed to maintain more allelic diversity within as compared to between populations, with the opposite being true of self-pollinating species (Hamrick and Godt 1997).

Like all taxonomic categories, the terms used to describe crops are to some degree inherently subjective and thus ambiguous, and there are differences in definitions among farmers and plant breeders, and between the two groups. The definitions we use are given below.

Population. We use population to refer to a group of individuals of a given variety that are maintained as a group under particular conditions, e.g. Juanita's white maize. Populations of farmer varieties can be genetically very open. For self-pollinating crops a FV population usually consists of several or many homozygous lines (Weltzien 1989), although these "lines" can be heterozygous, depending on the rate of outcrossing (Erskine 1997). A **seed lot** is a population defined more narrowly as the seed of a given variety that one farmer sows at a specific time (Louette et al. 1997).

Variety. A variety is defined by breeders as a subunit of a species that is "distinct" from other varieties of the same species. In practice, it is perhaps one of the most difficult units to define, with boundaries in time and space being especially arbitrary (Soleri and Cleveland 1993). For self-pollinating species it depends to some extent on how the farmer manages her seed. If different lines are grown together, and managed as a unit, then they would be considered a variety. But if any of these components are managed at some other time or place as a separate unit, then they would be considered separate varieties. **Farmers' varieties** (FVs) are phenotypically distinct units named by farmers and considered by farmers to be "local" varieties, and they can include indigenous varieties, imported varieties (including MVs), and hybrids between indigenous and imported varieties.

Species. A biological or genetic species is a group of actually or potentially interbreeding populations that are reproductively isolated from other species (Hartl and Clark 1989).

Race. A group of related varieties within a species sharing specific, constant traits that characterize the race. For example, maize FVs in Mexico have been grouped into races (Wellhausen et al. 1952).

Germplasm. This is a general term that can refer to any of the above units, or a subset of them.

Genome. The total genetic makeup of any one of the units above.

Genetic variation of farmer varieties

What is the level of V_G in farmers' populations and varieties?

Is V_G "optimal" for the farmers' environments?

What is the effect of farmer practice on gene flow, and thus on V_G ?

In general, in those areas where farmers still grow FVs, it is often assumed that there is a large amount of genetic variation both between and within these varieties (Frankel and Soulé 1981; Frankel et al. 1995; Harlan 1992). A number of studies have documented the

genetic variation of FVs at the varietal and population levels (Alika et al. 1993; Bekele 1983; Belay et al. 1993; Ceccarelli et al. 1987; Dennis 1987; Weltzien 1989) These studies suggest that FVs have a large amount of allelic variation at the varietal and population levels, and that this variation appears to buffer V_P under stress, and provide genetic potential for selection of superior material (Frankel et al. 1995). For example, one study of maize FVs in the US Southwest showed significant morphological and phenological differences between two varieties studied (Soleri and Smith 1995). An Ethiopian study found that a mixture of maize cultivars with different durations increased yield and stability in experiments under variable rainfall and drought (Tilahun 1995). However, the variation within FVs is not always optimal for the farmers who are using them in a given environment, for example when resistance to an important stress factor is absent (e.g. Trutmann and Pyndji 1994).

In spite of popular conceptions to the contrary, FVs seem to be very dynamic, with genetic diversity constantly affected by gene flow. For example, there is evidence for introgression of maize MVs into FVs in Mexico (Castillo-González and Goodman 1997). A study of one community in the Cuzalapa watershed in Jalisco, Mexico, found a 1-2% level of gene flow between different varieties in adjacent maize plots, which probably has a significant effect on genetic composition over several crop cycles (Louette 1997). The extent of gene flow over time is evidenced by the morphological and genetic continuum across the four major local varieties, suggesting that traits from a variety introduced 40 years ago have introgressed into the other varieties.

Genetic diversity may also be locally reduced genetic drift as a result of small seed lots. For example, when too few ears (less than 40) form the basis of a seed lot, alleles at a frequency of less than 3% may be lost, and heterozygosity reduced by 1% (Crossa and Vencovsky 1994). In the Cuzalapa case study 32% of the seed lots were composed from less than 40 ears (Louette 1997).

Farmer practice

Does farmer practice result in hybridization (which increases V_G)? If so, how?

What farmer practices affect varietal and population repertoires (and thus V_G) through time?

How do community level variables affect varietal and population repertoires?

The genetic diversity of farmers' crop varieties is in part a deliberate or inadvertent consequence of their practice, including the creation of genetic diversity and the choice of varieties. While most research has focused on the level of the individual farmer or farm household, social interactions at the community level may also be important for genetic diversity.

Creation of genetic variation

Farmers can affect genetic variation through conscious and unconscious hybridization, and its incidence appears to vary widely between individual farmers and between communities. Hybridization can occur between species, varieties, and populations, but not between entities that are biologically, spatially or temporally isolated reproductively.

Hybridization between species. There are reports in the literature of encouraged or tolerated hybridization between species, e.g., wild squash (*Cucurbita argyrosperma* ssp. *sororia*) with cultivated species (*C. argyrosperma* ssp. *argyrosperma* and *C. moschata* a.) (McKnight Foundation 1998). One of the most well-known examples is of teosinte (*Zea mays mexicana*) hybridizing with maize (*Zea mays mays*) (Benz et al. 1990; Wilkes 1989), although the extent and significance of this has been challenged (e.g., Kato Y 1997). In Sierra Leone, there is strong circumstantial evidence for spontaneous hybridization between indigenous African rice (*Oryza glaberrima*) and Asian rice (*O. sativa*), and for farmers selecting new varieties from the segregating generations that result (Richards 1996). Hybridization between species is probably responsible for a very small, although potentially important, portion of genetic variation in FVs, in part because it is infrequent, and also because it is likely often managed as introgression. (In other words, in segregating generations following hybridization, farmers look for plants whose phenotype is dominantly that of commonly used species, but that have a key trait or traits introgressed from the more exotic/wild species, with subsequent backcrosses to the common species.)

Hybridization between varieties and populations of a species. Distinguishing hybridization between varieties and between populations of a variety can be difficult, especially for self-pollinating species. As with interspecific hybridization, intervarietal hybridization may be managed by farmers primarily as introgression, although probably less so because of the smaller genetic distance involved.

In West Africa, opportunities for spontaneous hybridization between rice varieties are provided when a single farmer plants different varieties of the same duration class in adjacent plots, when adjacent plots contain rice varieties of different farmers of the same duration class, and when farmers use a large plot communally (Richards 1986; Richards 1996). For vegetatively propagated crops, seed may be produced from occasional hybridization between varieties, and Amuesha farmers in Peru routinely select new varieties of cassava from vegetative propagules produced by volunteer seedlings, including seedlings from abandoned plots where seed may have laid dormant for long periods (Salick et al. 1997). Some Quechua farmers in the Andes search their potato fields for the plants produced by the seed resulting from the occasional hybridization via cross-pollination (Zimmerer 1996). In a CPB project in Rajasthan, India with pearl millet (a cross-pollinated crop), farmers frequently planted seed of foreign varieties saved from variety trials with their own FVs, which resulted in increased variability in the next generation, and intense discussion by farmers about selection (Weltzien R. et al. 1998).

Varietal repertoires through time

In general, it appears that farmers add or delete a variety when changes in the local biophysical or sociocultural environment alter the importance of varietal traits for adaptation to those environments, with varietal replacement, or abandonment, determined by the availability of seed of new varieties (including MVs) that are similar to FVs, or the availability of alternatives to products made with FVs (Soleri and Cleveland 1993; see also Louette et al. 1997; Bellon 1991; Bellon 1996; Dennis 1987; Richards 1986). The interaction between these factors in determining the fate of a particular FV may be complex, as in the

case of changing Hopi blue maize varieties where several varieties seem to be collapsing into one as a result of decreased amount of time available for maintaining varieties, increased availability of non-Hopi varieties and food products that fill similar needs, and because of changing social conditions that reduce the importance of unique characteristics (e.g. the introduction of machine grinding reduced the importance of the softer blue corn variety) (Soleri and Cleveland 1993). In contrast, however, some groups of Andean farmers select varietal mixtures of potato en masse, only rarely or never selecting individual FVs as components (Zimmerer 1996).

It is often assumed that the adoption of MVs decreases on-farm genetic diversity, and this is supported by a number of studies. For example, data collected in two communities in one valley in Peru in 1985 indicate that expansion of area planted to potato MVs for one community in the early stages of MV adoption has a significant effect on the number of farmer-named potato FVs grown. This community had an average of 2.1 hectares and 10.1 FVs per farm in 1985, and analysis suggested that an increase of 1 hectare in area planted to MVs was associated with a decrease of 5 FVs per farm (Brush et al. 1992). That is, as the proportion of land in a household's farm devoted to MVs increases, the number of FVs being grown drops. For another community in the advanced stages of MV production, there was no association between area planted in MVs and number of FVs grown. However, in this community, while the average area planted to FVs was smaller, the average number of FVs was greater, which suggests the difficulty of making conclusions about changing diversity, especially in the absence of any genetic data.

In some cases, adoption of new varieties, including MVs, resulting in partial replacement of FVs, may increase yield while maintaining or even increasing genetic diversity. For example farmers in one community in Chiapas, Mexico maintain both MVs and FVs of maize to reduce overall variability in yield at the farm level in flat and sloping field plots respectively (Bellon 1991). Maize FVs were most reliable for the rocky, drier and less fertile soils of the slope fields, while MVs were favored for their greater productivity in the improved growing environments of the flat field sites.

There are also many examples of farmers not adopting MVs even though they are familiar with them. In four communities in central Mexico for example, farmers retained their maize FVs despite proximity to national and international research centers and market integration (Perales et al. 1998). Researchers attributed this retention to household cultural values as well as FVs' superior or comparable agronomic performance relative to MVs. No net economic or yield advantages were discerned for MVs as compared to FVs, while the latter had other qualities desirable to local households.

Data from most case studies have inferred the effects of farmer practice on genetic diversity based the number of farmer-named varieties, and there are few genetic data on the effect of changing varietal repertoires on genetic diversity, and very few data are available at the regional or species level.

Community practice

There is some evidence that household activities affecting crop varietal repertoires are affected by variables at the community or higher levels of social organization. The pool of genetic variation that farmers use in their decision making about seed acquisition and planting patterns (e.g., proportion of land planted to different populations or varieties) is determined by biophysical factors but also social networks that provide access to seeds (and other agricultural resources). These networks may be important influences on decisions affecting varietal repertoires.

For example, a study in Rwanda found that seed networks were socially limited, with poorer households having most limited access (Sperling and Loevinsohn 1993). A number of studies have identified individuals in the community who are known for the number of varieties that they maintain, and their skill at managing them. In the Peruvian Amazon male shamans and some women farmers are known for maintaining large numbers of cassava varieties (Salick et al. 1997). One of the collaborating farmers in our Oaxaca study has been growing a “foreign” maize variety (from a village in another valley) for the past 12 years (Soleri and Cleveland n.d.). It seems that her high social status, farming expertise, and economic advantage may be contributing to the spread of this variety through the community as more and more people seek to purchase planting seed of this type from her.

Farmer Knowledge

Do farmers perceive V_G , and if so, at what biological levels?

What are farmers’ criteria for classification and choice of crop populations and varieties, and how are they related to V_G ?

Farmers’ perception of genetic variation (as revealed in plant phenotypes) depends on how they value it and on their physical ability to observe it. This is determined in turn by the scale on which it occurs and the extent to which it is hidden by environmental variation. Value attributed to genetic variation may be the result of variation in agronomic, postharvest, or aesthetic characters.

V_G between varieties

It has been suggested, based on work with cassava classification by Aguaruna farmers in the Amazon, that humans have an innate tendency to create and classify the smallest distinct taxonomic unit (Boster 1985; Boster 1996). This theory is supported by data on Ari observation, classification and selection of ensete in Ethiopia, for whom primary importance is placed on morphological traits *not* directly related to practical use (Shigeta 1996). These conclusions are based on asexually propagated crops, and may apply less to sexually propagated crops, especially cross-pollinated ones where there are high levels of heterozygosity. They support the general hypothesis that farmers may simply enjoy “playing” with diversity (Berg 1996; Richards 1986), and even the selection of varieties may be the result of an innate human tendency to create and classify the smallest distinct taxonomic unit (Boster 1985). An appreciation for diversity may be an evolutionarily selected universal in humans (Wilson 1984).

However, a more common research finding is the importance of utilitarian criteria for farmers. For the Mende of Sierra Leone, growth duration is a major criterion for classifying rice varieties, with a mixture of duration types managed and planted in order to avoid labor bottlenecks and inter-harvest food shortages (Richards 1996). Farmers also classify and choose varieties based on ceremonial and religious values, as Hopi (Soleri and Cleveland 1993) and Quechua (Zimmerer 1996) farmers do with maize. Farmer classification of utilitarian traits for varieties of cross-pollinated crops can also parallel Western scientific classification for such traits as plant height, and weight and diameter of cob. Statistical analysis of ear traits classified farmers' maize varieties in the same pattern as did farmers (Louette et al. 1997).

Our work in the Central Valleys of Oaxaca, Mexico, suggests that for understanding farmers' genetic perceptions and classification it is important to differentiate traits of relatively low and high h^2 . Farmers attribute obvious phenotypic traits with high average h^2 , e.g., kernel color or texture, to "natural" (genetic) differences between FVs, e.g., *cuadrado* vs. *bolita* grain type (Soleri and Cleveland n.d.). Some traits that have lower average h^2 are also important for farmer discrimination between varieties, for example plant height and yield under specific conditions. Preliminary analysis suggests the hypothesis that for some traits farmers identify the extreme classes—e.g., typical average total plant height on-farm (155 vs. 218 cm), average days to anthesis (40 vs. 70)—and then partition intermediate phenotypes into those extreme classes, practicing a "lumping" as opposed to "splitting" classification strategy. Determining if this lumping is in a sense an implicit recognition of the polygenic nature of such traits requires further research. This suggests a very different process than the one suggested by Boster for Aguaruna cassava varietal classification of qualitative traits in a clonally propagated crop (Boster 1985).

There is also a range in the consistency of varietal classification schemes. For example, classification of potato varieties in the Andes of South America appears to be very consistent within communities (Zimmerer 1996), whereas the Amuesha of Peru have a high level of inconsistency in varietal names for cassava with the same common name applied to different phenotypes (Salick et al. 1997).

V_G between populations of a given variety

Comparatively little research has been done on farmer perceptions of V_G within varieties. Some qualitative observations suggest that farmers are aware of genetic variation (for example, they are aware of the value of the genetic potential of seeds harvested from the edges of plots, where hybridization is more likely to occur, as with rice in Sierra Leone) (Richards 1986). Indeed, if farmers select successfully within segregating populations this implies that they can perceive genetically based differences between and within populations (see "Plant Selection," p. 20).

Findings from our Oaxaca case study suggest that farmers perceive differences between populations of the same variety, for example for reproductive phenology, plant height or predominant kernel texture (Soleri and Cleveland n.d.). Despite recognition of different populations, farmers are not necessarily motivated to seek them out. This is especially true in Santa Maria, and may be due in part to peoples' observation of population mixing in the

field, resulting from cross-pollination. However, it is different for some traits of interest to farmers that have relatively higher mean h^2 . One farmer in San Antonio sought out and planted a population of *bolita amarillo* (yellow-kerneled maize) that has purple tassels because he enjoys looking at them while in the field, and doesn't otherwise value this population more than the yellow-kernel populations with yellow tassels. While other farmers say that they like the color that the purple husk of some white- and yellow-seeded individuals gives to *tamales*, they rarely select for it.

V_G within populations

Farmers in our Oaxaca case study generally state that they only perceive V_G within maize populations for relatively high h^2 traits such as tassel color, and gross ear and grain phenotype (color and shape) observed postharvest (Soleri and Cleveland n.d.). The majority do not claim to observe genetic variation within a population for many low h^2 traits expressed prior to harvest that are typically of interest to breeders (e.g., response to stress). This is true even when asked about the expression of such traits in a hypothetically optimum, uniform environment. This implies that they believe the h^2 of these traits in their maize populations is zero. There are three possible explanations of their statements. The most likely and first mentioned by all households is that their growing environments are exceedingly variable, and the proportional effect of environmental variability on many traits is substantial, resulting in heritabilities so low that, even if present, V_G is invisible, and therefore inaccessible to farmers in their selection. Secondly, it could be that their conceptualization of all individuals in a population being "the same" includes a certain permissible within-population variation. Despite the tremendous V_E in their growing environments, two of the farmers in our sample pointed out that even under controlled conditions there are always "natural" differences between individuals in a population. Still their practice and selection strategies do not differ from those of other collaborating households, suggesting that whether farmers see h^2 as being low or zero, they believe that the variation they observe is primarily the product of V_E . Theoretically h^2 may be zero if no V_G is present; however, given that Oaxaca lies in the center of diversification for maize, and that farmers' seed networks and planting practices allow ample opportunity for gene flow, this explanation seems improbable.

Environmental Diversity and Genotype-by-Environment Interaction

The second major component of farmers' plant breeding we will discuss is environmental diversity and genotype-by-environment interaction. Evaluating variability in performance of varieties across different environments is a key plant breeding activity that is the subject of much research and methodological development (DeLacy et al. 1996). Components of growing environments as described by plant breeders include spatial or location variables (L, temporally stable or repeatable variables, e.g., soil characteristics, latitude), temporal variables (T, temporally unstable or non-repeatable variables, e.g., seasonal or annual variation in elements of the growing environment such as rainfall, temperature, wind, pests and pathogens), and often management variables (M, e.g., fertilizer application, irrigation).

Whether variation in management would be a repeatable element or not will depend on if it is subject to change from year to year. For example, if the use of fertilizer or irrigation will only occur in years when migrant remittances are good, then it would be a nonrepeatable element.

The degree to which the performance of a set of genotypes (e.g., varieties, populations) changes with these environmental factors can be described by the genotype-by-environment (GxE) interaction (Simmonds 1979), and may often account for a significant proportion of total V_p .

However, much plant breeding has been empirically rather than theoretically based, with breeders working with “a large number of unknown genotypes in ill-defined environments resulting in little understanding of GxE” (Souza et al. 1993:197). To increase the efficiency of breeding for target environments, plant breeders are increasingly employing sophisticated experimental design and statistical analysis to estimate the components of V_p , especially $V_{G \times E}$, including its biological basis (Cooper, M. and Hammer 1996a; Kang and Gauch 1996; Nyquist 1991; Yan and Hunt 1998).

GxE is often graphically represented by regressing the performance of varieties in a trial over the environments they were grown in, where each environment is defined by the mean performance of all genotypes grown there, and environments are ordered from lowest to highest mean yield. Stability can be quantified by the slope of the regression line. The mean of all genotypes will have a slope = 1.0 and stability of individual varieties is indicated by comparison. Those with a slope \approx 1.0 have average stability, with slope increasing above 1.0 decreasing stability, and with slope decreasing below 1.0 increasing stability, with a variety having a regression slope = 0 defined as the most stable (Eberhart and Russell 1966; Lin et al. 1986; Souza et al. 1993).⁵ Because the environments in which CPB is conducted are likely to be variable, and because farmers may place a premium on stability rather than maximization of performance, consideration of GxE is critical within the context of CPB.

An important distinction is made between quantitative and qualitative GxE. A variety with *quantitative GxE* may be stable (relatively low GxE) or unstable (relatively high GxE), but does not change rank across environments compared with other varieties. *Qualitative GxE* between two or more varieties is often referred to as a “crossover” because the regression lines for yield (or another trait) cross over at some point.

Farmers’ varieties and growing environments

Are the varieties farmers plant, including FVs, adapted to a narrow or wide range of environments, regionally and on-farm?

Are varieties more adapted to variable (time-related) aspects of the environment, stable aspects (location-related), or farmer management aspects?

Is there quantitative or qualitative GxE for different FVs, or FVs and MVs?

⁵ Among plant breeders there is disagreement over the definition of yield stability, which may depend on “how the scientist wishes to look at the problem” (Lin et al. 1986:894), and many define responsive varieties with slopes \geq 1 as the most stable (see Cleveland n.d.).

Commonly used definitions of FVs include that they are adapted to a narrow range of environments (Frankel et al. 1995; Zeven 1998). However, discussions of whether a particular variety is narrowly or widely adapted are often confused by failure to distinguish *temporal*, *locational* and *management* aspects of the environment, and sometimes conflate these with *geographical* extent of adaptation (Souza et al. 1993). This is especially true when discussing farmers' systems (Bjørnstad 1997).

Specific adaptation

Some FVs are adapted to specific environments for which they show high GxE, a frequent example being phenological adaptation to climate patterns, e.g., with drought patterns and pearl millet in Rajasthan (van Oosterom et al. 1996). One study in Ethiopia found that 13 wheat FVs showed qualitative GxE for four locations where they are grown but low correlations between yield and stability measures (Tesemma et al. 1998). At the regional level, varieties of lentil appear to have specific adaptation to locations, temporal patterns, and management levels (Erskine 1997).

Similarly, MVs that are “widely” adapted geographically may be narrowly adapted to the relatively low stress conditions of locations and management environments where they outyield FVs, but are outyielded by FVs in stress environments typical of those of many Third World farmers, i.e., they exhibit qualitative GxE with FVs (e.g. Ayeh 1988 for common bean; Flinn and Garrity 1986 for rice; Kelley et al. 1996 for pearl millet; Weltzien and Fischbeck 1990 for barley; Evans 1993:165 and Ceccarelli 1996 summarize other studies).

Broad locational adaptation

On the other hand, some FVs may be widely adapted geographically and planted across a range of locations by individual farmers and within and between communities. The widespread exchange of crop varieties by farmers suggests such wide adaptation (Wood and Lenné 1997), although the degree of genetic differentiation between FV populations grown by different groups is largely unknown. In southwestern North America maize varieties have been frequently shared between tribes, even though each tribe usually considers a given variety to be its own unique FV and has its own name for it (Soleri and Cleveland 1993). In Cuizalapa, Jalisco, Mexico, farmers' FV seedlots may often contain seeds from locations outside of the local community (Louette et al. 1997).

Similarly, MVs may also be widely adapted to a range of locations, including not only low-stress locations but also high-stress one where they outyield FVs. For example, the CIMMYT experience in wheat breeding using large numbers of crosses, international testing of advanced lines, and continuous alternating selection cycles in environments that differ but allow expression of high yield (shuttle breeding) have led to wheat MVs that appear widely adapted and are higher yielding than local varieties in stressful environments, such as Western Australia (Romagosa and Fox 1993). In Zimbabwe, maize hybrid MVs have had high adoption rates among limited-resource farmers in more marginal environments (Heisey et al. 1998).

Farmer practice

What variables in farmers' growing environments (temporal, locational, management) are correlated with farmers' classification and choice of varieties?

What is the range (narrow v. wide) of the variables that define these environments?

What environments do farmers choose for testing new material, and how are they related to their target environments?

Farmers allocate their crops, varieties and populations to the limited land available to them as part of their planting decisions, but very little research has been done on the pattern or on the social, environmental and genotypic determinants of these decisions. Some FVs appear to be managed for narrowly defined environments. For example, in the Great Lakes region of East Africa farmers plant different varietal mixtures of common bean with varying resistances to multiple diseases in specific locations and often maintain them separately, a strategy which may be the most effective for optimizing yield stability (Trutmann 1996). On the other hand, some varieties appear to be managed for a wide range of environments. In Cuzalapa, Jalisco, Mexico, farmers' FV seedlots may contain seeds from a wide range of locations (Louette et al. 1997). The common assumption that the large number of potato varieties maintained by Andean farmers is managed by allocating each variety to specific fields or within field environments is contradicted by the finding that some farmers harvest and plant these varieties as bulk mixtures across all growing environments (Zimmerer 1996).

There is evidence that some farmers may carry out initial screening and selection in optimal environments, for example in gardens with more adequate moisture (Soleri and Cleveland 1993) or soil fertility (Ashby et al. 1995) than fields. The great majority of farmers in one survey sample in Rwanda experimented with new bean varieties that they usually obtained from markets or from family and friends (Voss 1992). They first planted the new varieties in pure stands in plots near the house, and if one proved worthy it was then tried under various field conditions, and eventually incorporated into the appropriate mixture or mixtures. Practices like these are often interpreted as a risk aversion strategy to avoid losing new varieties before understanding in what environments they will perform best, or what desirable traits they can offer.

In contrast, rice farmers in Nepal often plant new varieties on their worst land, which has also been interpreted as a "risk aversion strategy" (Sthapit et al. 1996), and it has been suggested that this is a common practice (Witcombe 1998). This implies that farmers are looking for varieties adapted across a wide range of locations.

Farmer knowledge

How do farmers perceive and evaluate GxE for yield over time v. over locations?

How do farmers' perceptions of qualitative GxE affect their decision to have one or more than one variety for a set of environments?

How do farmers' perceptions of quantitative GxE affect their choice of a variety for an environment?

GxE for time v. GxE for location

Yield stability over locations (sometimes referred to as adaptability) has often been considered to be much less important to farmers than yield stability over time (e.g. Barah et al. 1981; Souza et al. 1993). Ashby et al. suggest that farmers' experiments involve replication through time rather than across locations, i.e., the check may be "in the farmer's head" (Ashby et al. 1995; see also Sperling 1996).

This assumption has rarely been tested, yet available data suggest that GxE for location on-farm is often perceived by farmers to be significant and depends on the specific situation. Individual farmers in Sierra Leone explain their maintenance of a large number of rice varieties in part because of their adaptation to different locations on their farms (Richards 1986). There are also differences between farmers within a community. For example, in Rajasthan, India those with good land or more land said they wanted seed stocks useful for a broad range of planting conditions, including variations in soil fertility as well as in rainfall, and frequently purchase seed, whereas farmers with very poor land chose only one type, one rejected by the former group, and are proud of saving their own seed for 100 years (Weltzien R. et al. 1998). In contrast, wide locational adaptation is implied by farmers' classification of maize varieties in a community in Jalisco, Mexico, based on morphology and phenology, rather than "geographic origin, adaptation to some limiting factor, or ritual function," and farmers appear to give no value to saving their own seed (Louette et al. 1997:33).

Qualitative GxE

If farmers do not perceive qualitative GxE (crossovers) in performance for varieties between environments there may be no reason for them to grow different varieties in these environments. When farmers do perceive crossovers between varieties in two environments, then they may have to decide if they will grow one variety in both environments, or if they will grow different varieties in the two environments.

A number of researchers conclude that farmers do perceive qualitative GxE. For example, one sample of Rwandan farmers selected among professional breeders' varieties of common bean for home testing based on performance under bananas, on poorer soils, and in heavy rain, in addition to high yield. Researchers judged those farmers to be well aware of the responses of different genotypes in different environments, though no in-depth interviews with farmers were reported (Sperling et al. 1993). Rajasthani millet farmers, realizing that there is a trade-off between panicle size and tillering ability, prefer larger panicles in the least stressful environment, and high tillering in the most stressful (Weltzien R. et al. 1998).

However, farmers' perception of qualitative GxE appears to depend on the range of environments and/or genotypes they are referring to. In our study in Oaxaca, farmers in Santa Maria do not maintain distinct types of white maize identified for allocation to specific environments (e.g., soil type, elevation, precipitation) and instead identify two types based on ear and kernel phenotypes with no apparent relationship to in-field performance. In contrast, San Antonio farmers classify and maintain *violento* (short growth duration) and *tardón* (long growth duration) classes of white maize. Whether or not these two duration classes are kept separate or combined appears to depend on the importance to

farmers of duration for managing drought. In San Antonio, V_E between location-year combinations is seen as being greater than in Santa Maria, and farmers believe that *violento* performs better in years with late season drought, and *tardon* in years with early season drought (Soleri and Cleveland n.d.). These findings suggest that V_E between fields is perceived as greater by farmers in San Antonio and that, therefore, they allocate distinct sets of V_G to those environments.

Quantitative GxE

When farmers intend to grow only one variety, for example in one location under a constant management strategy, then the choice of variety may depend in part on the stability of performance as temporal (e.g., rainfall) or management (e.g., fertilizer application) components of the environment vary. If variety A has larger mean yield and lower variance (i.e., greater stability, e.g., for yield) than variety B through time in this location, then the choice would be A. If variety A has larger mean yield but also a larger variance, then the choice will depend on the farmer's attitude toward risk.

Some data suggest that farmers' analysis of GxE is important in making allocation and adoption decisions in maize. For example, data from Malawi suggest that the ratio of coefficients of variation in MVs compared to that of FVs, based on farmers' subjective yield estimates, is negatively related to allocation of land and fertilizer to MVs (Smale et al. 1995). In other words, as farmers perceive that yields of MVs are more unstable, fewer resources are allocated to them. Cambodian rice farmers' criteria for varietal choice differs according to environmental stress, so that yield stability (drought and flood tolerance) was more important in choosing early- and late-maturing varieties grown in higher stress environments, and yield and eating quality were more important for medium-maturing varieties grown in lower stress environments (Lando and Mak 1994).

Plant Selection

It is typically assumed that farmers practice *mass selection*. This is the identification of superior individuals in the form of plants, and/or propagules, from a population, and in the case of crops like maize, the bulking of seed to form the seed stock for the next generation (Welsh 1981). It requires only a single season, and relatively little effort compared with other selection methods. If practiced season after season with the same seed stock, mass selection has the potential to maintain or even improve a crop population, depending upon the heritability of the selected traits, GxE for the trait, the proportion of the population selected, and gene flow in the form of pollen or seeds into the population.

Although mass selection has clearly been effective over time for some traits, gain from selection year to year can be very small because heritabilities are low. In others words, much of the phenotype that the farmer bases selection on may be determined by the environment and not the genotype. Response to selection for traits with higher heritability than yield, such as days to anthesis, will be greater. Additionally, in cross-pollinating species like maize, where the genetic contribution of the pollen-donor is unknown for most

traits, selection response can be low. In these cases selection is exerted only on the maternal parents unless it occurs prior to fertilization, for example, by the removal of unselected plants before flowering. Response to mass selection will also depend on the approach to selection used, as there are a number of variations on this strategy such as stratified mass selection, biparental mass selection and selection aided by the use of a constant genotype (Hallauer and Miranda 1988).

Stratified mass selection is a technique for improving the heritability of selection criteria in mass selection. It involves partitioning fields into sub-plots, which reduces the within-plot V_E , especially for repeatable elements such as soil type, thereby increasing the proportion of total V_P within those plots that is genetic. An equal proportion of individual plants are then selected from each plot.

Due to the typically variable growing environments of most low-resource farmers it is probable that some form of stratification should be used to help reduce the effect of environmental variation in the selection process. Stratified mass selection may be particularly useful for CPB because it requires only a small additional labor investment compared with simple mass selection, while improving heritability in variable farmers' fields. Because of the many variables involved it seems critical that an attempt be made at estimating the efficacy of possible modifications to local mass selection at a site and with a particular crop population before those modifications are promoted to farmers. If farmers do not already practice in-field selection the increased time and effort required will need to be weighed against benefits derived from any increase in gain from selection achieved, and against benefits that could be derived from alternative uses of the same resources.

Another group of selection techniques often used by breeders is based on *progeny selection* at the family level. Half-sib (a family sharing one common parent) or full-sib (a family consisting of individuals all sharing both of the same parents) selection is based on family means, not individual phenotypes. By averaging the within-family phenotypic values it is hoped that V_E will be reduced, thus increasing h^2 (Falconer 1989). For example, selection for grain yield in a composite maize population based only on one parent gave a response of +1.7%/yr, whereas when both parents were selected the response increased to 7.0%/yr (Hallauer and Miranda 1988:213). Replication is used to further reduce the repeatable environmental component of V_P and increase h^2 . Multi-year and/or location replications can help reduce non-repeatable elements of environmental variation. A disadvantage of progeny selection is that it may involve controlled matings and require at least two growing seasons and substantial labor to organize and execute the field trials.

In terms of population genetics, selection can be classified according to the effect on the genetic structure of a population, which may be explicit goals of the plant breeder (Silvertown and Doust 1993). *Directional selection* moves the mean of the population for a trait or traits in one direction, for example, increasing plant height or ear size. Directional selection has been the goal of most modern plant breeding, although stabilizing selection to maintain gains has also been important (Simmonds 1979). *Disruptive selection* creates a bimodal population distribution for a trait as it favors phenotypes at the two extremes of

the distribution. *Stabilizing selection* favors phenotypes in the center of the distribution, eliminating the extremes, thereby reducing the variance of the distribution. The genetic results are similar to those of directional selection from a constantly retreating starting point, at least over the short run, although the goals are quite different. *Random selection* results in no overall change in the population distribution or variance for a trait over time unless a small population size results in genetic drift. It is important to note that these various types of selection can be the result of natural (non-human) selection as well as, or in addition to, artificial (human) selection. The combination of natural and artificial selection operating on farmers' crop populations can have a complex effect on the structure of those populations.

Farmers' varieties

What is the heritability of farmers' varieties in farmers' selection environments?
Is heritability large enough for farmers to make acceptable gains in selection?

A few studies have been done on heritability of FVs in experimental plots. In Ethiopia, for example, research with wheat FVs found intermediate to high heritabilities for many traits, including for grain yield (Belay et al. 1993). Assessments of heritabilities in farmers' selection environments are even more rare but may be critical for estimating the potential for gain through improved farmer selection in those environments. One example of such estimates is our study in the Central Valleys of Oaxaca, Mexico (Soleri and Smith n.d.), using a new method for estimating broad sense heritability (H) in farmers' fields (Smith, S.E. et al. 1998). Although less precise than conventional methods, this approach appears to provide a useful initial orientation to H and thus selection potential in areas and with populations for which estimates are rare. Overall, H estimates calculated in this study indicate that response to mass selection as practiced by farmers and as advocated by some CPB projects (see Rice et al. 1997) will be negligible or low. However, the analysis also suggests a number of traits of interest to farmers with H values showing potential for significant response if mass selection were improved, for example through in-field selection with stratification (average H = 0.65 for days to anthesis, 0.74 for ear height, and 0.63 for ear length).

Farmer practice

At what stages in the life cycle (e.g. in-field v. postharvest) do farmers carry out selection, what proportion of the population do they select, and how?
To what extent does farmer choice of growing environments, including management strategies, result in unintentional or automatic selection?
What are S and R for farmers' selection practices?
What would be the change in R with a change from postharvest to in-field selection?
What would be the change in R from mass selection to stratified or progeny selection?
How do results of farmer selection compare with their implicit selection criteria?

In some crops, for example small-seeded crops like rice, farmers are more likely to carry out selection on plants in-field, including criteria for a variety of traits (Richards 1986; Sthapit et al. 1996), although major selection criteria may also include postharvest traits (Sthapit et al. 1996). In other crops, for example large-seeded crop like maize, selection may be almost entirely postharvest, as with maize in Mexico (Aguilar 1982; SEP 1982; cited in Louette and Smale 1998).

Farmer seed selection may often be complex, however, and vary among households and among household members. In a study in Columbia, 31% of farmers began selection of bean seed in-field by selecting areas where plants had abundant foliage and low disease incidence, while the remaining farmers selected entirely postharvest (Janssen et al. 1992). In Mexico, most researchers have reported that seed selection is done by men, but new findings suggest that this conclusion may be the result of the methods employed (Smale et al. 1998b). In the Sierra Santa Marta, detailed and repeated interviews with both men and women in the same farm household showed that selection occurs in four or five stages, in most of which women participate (Rice et al. 1998). In the Central Valleys, selection is done on ears entirely postharvest, including a small proportion selected by women between harvest and sowing, as ears are husked for food preparation (Soleri et al. n.d.). Just before sowing, the previously selected seed will be screened again, especially for pest damage during storage, and the remaining majority of the seed will be acquired by husking and shelling additional ears as needed from the stored harvest, frequently done by both men and women. The primary criteria are cleanness (lack of insect damage or mold), color according to color class, and large ear and grain size. Secondary criteria are grain shape (e.g., round for *bolita*) and shape and color of cobs and husks.

The assumption is often made that in-field mass selection will increase R compared with post-harvest seed selection. CPB projects have been designed based on this assumption, with no supporting empirical evidence for the particular farmers and varieties involved (Rice et al. 1998 described one example). However, this is true only if the heritability of the traits of interest is raised by in-field selection, for example, by stratification, and if whole plant traits are relevant to farmers' selection goals. In addition, if only in-field selection is used, it is important to know if the overall gain in both pre- and postharvest traits will be greater than for postharvest selection and the impact on participation and control by different household members (Smale et al. 1998a).

The biological effect of farmer selection has seldom been measured. A study in Cuzalapa, Jalisco, Mexico using morphological and isozyme data found that farmers' selection maintains the phenotype of their varieties (the ideotype) in the face of high levels of gene flow (Louette and Smale 1998). Thus, ear traits and linked phenological traits were maintained even though other characteristics may continue to evolve genetically.

In Oaxaca, Mexico we carried out selection exercises with farmers on maize ears, in which farmers selected the top 10% of ears (based primarily on large ear and seed size and freedom from pests and diseases) from a random sample of 100 ears taken from plots in their own fields (Soleri et al. n.d.). Ear traits such as kernel row number and shelling ratio showed no significant difference between the 100 ears and the selected sample of 10, across households and communities. There were occasional but no consistent significant differences for some plant morphological and phenological traits. For those comparisons that were statistically significant, farmers' selections resulted in standardized selection differentials (or selection intensities: $S/\text{standard deviation of 100 ear sample}$) of 0.48-1.33 and 0.73-1.81 for ear length and grain weight, respectively. This compares with an intensity value for directional selection of a 10% sample typically sought by breeders of 1.8 (Hallauer and Miranda 1988).

The results of farmer selection may be different than their implicit goals for several reasons. For example, farmers may intend to perform directional or stabilizing selection for a particular trait based on the phenotypes in a population, but if the intrapopulation V_p on which they are selecting is predominantly the product of V_E , then the result may be random selection, i.e., $R=0$. This may be the case for farmers in our Oaxaca case study since there were no significant differences between the means of the whole random population and selected samples derived from these as represented by their progeny generations (Soleri et al. n.d.). Similarly, significant differences were not observed between random samples of the same population over generations.

These findings suggest that with their current selection strategy the additive genetic variance for farmers' selection criteria is very low, resulting in no statistically significant response. The ultimate impact of farmer selection appears comparable to random selection for some traits, leaving the populations relatively unchanged from year to year. A more accurate interpretation, however, may be that farmers perceive traits such as ear weight and length as part of a group of direct and indirect selection criteria relevant to seed quality and seedling performance. As such, their interest in these traits may not be in terms of their inheritance per se, and S values would reflect the weighing of these various criteria in farmers' selection, and not goals of directional selection as so frequently assumed.

Farmer knowledge

What are farmers' explicit selection criteria?

What are farmers' implicit selection criteria, inferred from the material selected for planting?

What are farmers' explicit goals in selection?

What is farmers' knowledge of the effects of their selection practices?

As in most studies, in our case study stated selection criteria of Oaxacan farmers are complex (Soleri et al. n.d.). The most important criteria appear to be those related to seed viability – all ears with evidence of pest or disease damage to the seed or cob are usually discarded. The next category includes traits that contribute to large ears and large kernels, especially ear length and weight. The final category encompasses a number of traits that define a varietal type and in our sample included traits like grain type (e.g., flinty v. starchy), grain form (round v. flat), cob and husk color. Although criteria in the third category varied between households and communities, the first two categories were universally most important. Explicit criteria were similar in the Cuzalapa case study (Louette and Smale 1998).

Farmers' implicit selection criteria can be ascertained by comparing values of phenotypic traits in selected material with those in nonselected material, but this has rarely been done. In Oaxaca, Mexico we compared the 10% of selected ears and the total 100-ear sample in a series of selection exercises (Soleri et al. n.d.). Farmers from both communities consistently selected for increased ear size from among pest- and disease-free ears. Compared to the 100-ear sample, the ears selected by farmers were longer and heavier overall, with those selected by farmers in San Antonio having larger ear diameters as well. Ear row number

showed no significant difference between the 100 ears and sample of 10 across households and communities. Thus their explicit selection criteria accurately reflect the traits that farmers actually seek when selecting seed for planting.

Weltzien et al. (1998) note that surprisingly little research has been done on selection goals, considering their importance for the selection process, especially for marginal environments, and this applies especially to farmers. In informal interviews in Cuizalapa, Jalisco, Mexico, farmers indicated that they do not see seed selection as a way of changing or improving their maize varieties, but of protecting the “legitimacy” of a variety, i.e., of maintaining varietal ideotypes (Louette and Smale 1998).

Results of our study in Oaxaca suggest that for traits with low heritability, farmers generally did not hope to change a variety (Soleri et al. n.d.). Both the lack of expectations for change and the concern with maintenance of current traits appear to be a pragmatic recognition of the substantial V_E and 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. Nevertheless, their answers indicated an awareness of selection and the ability to use it when they felt it desirable and possible. Farmers typically have very low expectations for change regarding traits that comprise their seed selection criteria. In this study farmers attributed their low expectations to cross-pollination and their understanding of the influence of V_E on plant phenotypes in their fields (h^2 of those traits). Interpreted as such, their expectations appear to reflect two observations made by researchers: 1) 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, and 2) a medium to low h^2 (<0.5), which means that 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 parents (Simmonds 1979).

Conclusions

In this paper we have proposed questions about farmer plant breeding (knowledge, practice, and crop varieties and growing environments) based on the basic biological model of professional plant breeding. While there has not been much research on most of these questions, we found a range of explicit and implicit answers in the existing literature, answers which are often contradictory. This finding supports our initial impression that generalizations based on experience with specific varieties, environments or farmers may not be valid, and that CPB may be limited by the availability of an appropriate framework for research on farmer plant breeding.

However, the research literature does lend support to the idea that farmers’ knowledge and practice reflect an intuitive, empirical and theoretical understanding of their crop populations that in many ways is fundamentally similar to the basic understanding of plant breeders as reflected in the biological model we described. Yet this knowledge and practice is also different, because the details of farmers’ experiences (e.g., values, social relations, crops and growing environments) are different. In other words, the search for

generalizations is valid, but we need to be careful about making them at too superficial a level. Therefore, the success of CPB will depend on analyzing and assessing farmers' knowledge, practice, and crop populations in ways that are informative for outside collaborators. Doing so will require the application of existing methods from conventional plant breeding, population genetics, and statistics, as well as the development of new, cost-effective methods, for example to understand farmers' genetic perceptions or to estimate H on-farm. Once oriented, outside scientists will be better able to use their own knowledge and experiences to contribute to CPB.

It is important to repeat that while the framework presented in this paper is focused on understanding farmers' knowledge, practice, and crop varieties and environments in terms of the biological model of professional plant breeding, the ultimate utility of this approach for CPB will depend on the addition of socioeconomic, including benefit/cost, analyses. For example, in our Oaxacan case study farmers may be choosing to shift their time and energy away from crop selection, because emigration rates of both men and women to other areas of Mexico and to the USA to find wage labor are high and increasing. In San Antonio especially, extensive emigration from some households may subsidize increasingly economically marginal maize production. Migrant remittances and the loss of migrants' labor could act as disincentives for investment in population improvement and varietal change and lead to loss of interest in and knowledge of seed saving and varietal choice.

It is also worth repeating that successful CPB may ultimately depend on including professional breeding within the same scope of analysis as farmer breeding (Figure 1). That is, farmer and professional plant breeding should be evaluated on the same basis, without assuming that either is "better" than the other. Therefore, research on professional plant breeding is needed to understand more about 1) the combination of values, intuition, empirical data and theories that make up plant breeders' knowledge, including differences among plant breeders, 2) the relationship between plant breeders' knowledge and practice, 3) the extent to which elaboration and application of the basic biological model in conventional breeding may be inappropriate for the often very different biophysical and sociocultural environments of small-scale farmers, and 4) the validity of generalizations about farmer breeding based on unique experience with a limited sample of farmers.

We conclude that our framework for understanding farmer plant breeding from a biological perspective can make a significant contribution to the success of CPB. By posing questions such as the ones we have suggested, a more systematic picture of farmer plant breeding, both in specific instances and in general, should emerge. By examining the assumptions which have often necessarily formed the basis for CPB, this framework could provide a more robust foundation for collaboration. Further testing of specific hypotheses based on the questions presented here is needed, especially in the context of CPB projects. This research could lead to more effective use by breeders of their knowledge, statistical design and analysis and access to a wide range of genetic diversity, and by farmers of their knowledge of their crops and environments, and their techniques for managing them. In turn, this can support more efficient communication and collaboration between farmers and plant breeders, leading to varieties that better meet farmers' needs, conserve crop genetic diversity in situ, and thus contribute to sustainable agriculture.

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