A BIOLOGICAL FRAMEWORK FOR UNDERSTANDING FARMERS' PLANT BREEDING[1]

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Cleveland, David A. *(Department of Anthropology and the Environmental Studies Program, University of California, Santa Barbara 93106-3210, USA, clevelan@lifesci.ucsb.edu),* **Daniela Soleri** *(Office of Arid Lands Studies, University of Arizona, 1955 E 6th St, Tucson, AZ 85719, USA; current address, Center for People, Food and Environment, 340 Arboleda, Santa Barbara, CA 93110, USA, and Institute for Social Behavioral and Economic Research, University of California, Santa Barbara, CA, 93106, USA, dsoleri@isber.ucsb.edu),* **and Steven E. Smith** *(School of Renewable Natural Resources, University of Arizona, 301 Biological Sciences East, Tucson, AZ 85721, USA, azalfalf@ag.arizona.edu).* A BIOLOGICAL FRAMEWORK FOR UNDERSTANDING FARMERS' PLANT BREEDING. *Economic Botany 54(3):377–394, 2000. We present a framework for understanding farmer plant breeding (including both choice of varieties and populations and plant selection) in terms of the basic biological model of scientific plant breeding, focusing on three key components of that model: 1) genetic variation, 2) environmental variation and variation of genotype-by-environment interaction, and 3) plant selection. For each of these concepts we suggest questions for research on farmers' plant breeding (farmers' knowledge, practice, and crop varieties and growing environments). A sample of recent research shows a range of explicit and implicit answers to these questions which are often contradictory, suggesting that generalizations based on experience with specific varieties, environments or farmers may not be valid. They also suggest that farmers' practice reflects an understanding of their crop varieties and populations that is in many ways fundamentally similar to that of plant breeders; yet, is also different, in part because the details of their experiences are different. Further research based on this framework should be valuable for participatory or collaborative plant breeding that is currently being proposed to reunite farmer and scientific plant breeding.*

UN MARCO BIOLÓGICO PARA ENTENDER EL FITOMEJORAMIENTO DE LOS AGRICULTORES. *Se presenta un marco teórico para un mas claro entendimiento del fitomejoramiento de los agricultores (se incluye tanto la selección o identificacion de variedades, poblaciones, o plantas individuales) desde la óptica de un modelo biológico básico. Dicho modelo trata 1) la variación genética 2) la variación ambiental, la variación de la interación genotipo-ambiente y 3) la selección de plantas. Para cada uno de los conceptos anteriormente expresados se sugieren preguntas para investigar el fitomejoramiento de los agricultores (conocimiento de los agricultores, práctica, variedades de cultivo y sus ambientes). Una muestra de la reciente investigación demostró un rango de implicitas y explicitas respuestas para las preguntas formuladas, las cuales son en ocasiones contradictorias, lo que sugiere que la generalización de las experiencias basada con específicas variedades, ambientes o agricultores pudieran no ser válida. Se plantea que las prácticas de los campesinos reflejan un entendimiento de sus variedades y poblaciones que tienen en parte cierta similitud con los fitomejoreadores convencionales, aunque en parte es tambien diferente ya que los detalles de las experiencias de agricultores y fitomejoradores convencionales son distintas. Otras investigaciones basados en este marco pudieran contribuir al fitomejoramiento colaborativo o participativo, lo cual actualmente ha sido propuesto para reunificar a los agricultores y los científicos del fitomejoramiento de plantas.*

Key Words: collaborative plant breeding; farmer plant breeding; farmer crop varieties; genetic variation; genotype-by-environment interaction; landraces; plant selection.

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). Plant breeding as a specialized activity began about 200 years ago in in-

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dustrial countries (Simmonds 1979). Modern professional 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, Nilsson-Ehle, East, and others (Allard 1999; Simmonds 1979). Plant breeding by modern, scientific, professional plant breeders (hereafter simply plant breeders) has become increasingly separated from plant breeding by farmers, especially small-scale farmers in high-stress growing environments with limited access to external inputs (hereafter simply farmers) (Berg 1996). This separation is also true of professional and farmer seed-supply systems (Cromwell, Wiggins, and Wentzel 1993). As Simmonds succinctly stated, "the current stage of crop evolution is rapidly passing into the hands of professional plant breeders, a trend which has been at least locally apparent for 200 years" (Simmonds 1979:11). At the same time, many plant breeders consider farmers also to be capable of plant breeding. According to Allard, "The consensus is that even the earliest farmers were competent biologists who carefully selected as parents those individuals . . . with the ability to live and reproduce in the local environment, as well as with superior usefulness to local consumers" (1999:29). Stoskopf et al. wrote that in the period before scientific plant breeding there was "considerable progress in plant improvement" that "can by definition, be said to be plant breeding" (1993:1).

The emphasis of professional plant breeding typically has been on developing modern varieties (MVs) with geographically wide adaptation to optimal (relatively low stress and uniform) growing environments, and high yield in these environments (Evans 1993; Fischer 1996). Although there has also been attention to breeding for stress tolerance, this attention has focused on relatively large-scale environments and commercial farmers who can afford to purchase seed, not on the farmers who are the topic of this paper (Bänziger, Edmeades, and Lafitte 1999; Ceccarelli et al. 1994; Heisey and Edmeades 1999) This contrasts with farmer breeding and farmers' local varieties (FVs, which include landraces, locally adapted MVs, and progeny from crosses between landraces and MVs), which are usually assumed to have more narrow geographical adaptation to marginal (relatively high stress, and variable) growing environments, and high yield stability (low variance across environments including years and locations) and moderate yield in those environments (Harlan 1992; Zeven 1998). Landraces are often defined as "geographically or ecologically distinctive populations which are conspicuously diverse in their genetic composition both between populations and within them" (Brown 1978:145).

Collaborative or participatory plant breeding (CPB) is an attempt to bring farmers and plant breeders together to develop new crop varieties to meet farmers' needs (Hardon 1996; Smale et al. 1998; Witcombe et al. 1996). An important impetus for CPB comes from increasing awareness among plant breeders of the need to increase the sustainability of agriculture in the face of environmental deterioration and growing demand for production, by placing greater emphasis on

(1) increasing yields and yield stability in marginal environments, both (a) those that have been high yielding, but where inputs are being reduced to reduce production costs and negative environmental impacts, and (b) those of many of the world's farmers who have not adopted MVs, but whose FVs have inadequate yields, and
(2) conserving the base of genetic diversity on which all plant breeding depends, and which is threatened by the loss of FVs as the area planted to FVs and the number of farmers growing them declines (Callaway and Francis 1993; Ceccarelli 1996; Cooper and Byth 1996; Evans 1997; Fischer 1996; Heisey and Edmeades 1999; Sleper, Barker, and Bramel-Cox 1991).

CPB is based on the assumption that modern, scientific plant breeding can be adapted to local sociocultural and biophysical conditions and can be integrated with farmer plant breeding. However, few data are available for comparing the two systems, particularly in farmers' environments and with farmers' practices. Most of the research with farmers has been done by social scientists who have not used a plant-breeding framework for analysis, and most research on the biological aspects of farmers' plant-breeding systems has been done by plant breeders or biologists who have not systematically investigated farmers' knowledge or practice, if at all. The result is that plant breeders in CPB projects may be forced to rely on assumptions about farmers' knowledge, practices, and crop varieties that have not been tested and may not be valid for the situation they are working in.

We agree with Cooper and Byth's suggestion that plant breeders' work on-farm "needs to be firmly incorporated into the overall paradigm of crop improvement, and not allowed to develop as an independent thrust," yet adapting plant breeding to farmers' conditions may require new developments in theory and method, for example, in moving from wide to specific adaptation as a breeding goal (Cooper and Byth 1996:18, 20). Thus, adapting professional plant breeding for CPB may require plant breeders to better understand farmer plant breeding and crop management. In addition, to the extent that CPB entails a change in the knowledge or practices of farmers, successful change may require that farmers understand the reasons for change in terms of professional plant breeding. This paper suggests a framework for carrying out research to enhance this mutual understanding.

METHODS

DEFINING PLANT BREEDING

CPB involves farmers and plant breeders working together in some part of the plant breeding system to develop crop varieties that meet farmers' needs. We define this system to include not only the crop varieties and growing environments, and the behavior or practice that changes them, but also individual and group knowledge, which includes values, empirical data, and theories. We assume that the primary goal of CPB is varieties which, in combination with specified growing environments, will optimize benefit to the farmer.

Plant breeding practice includes both:

(1) The development of new varieties through artificial selection of plants by farmers and breeders within segregating plant populations, which changes the genetic make up of the population. Artificial selection is both indirect, a result of the environments created in farmers' fields and plant breeders' plots, and direct, a result of human selection of planting material. Direct artificial selection can be both conscious (based on explicit criteria), the result of decisions to select for certain traits, or unconscious (based on implicit criteria), when no conscious decision is made about the trait selected for, as when large seeds are automatically selected because they are easier to handle. (There is some confusion over terms in the literature. Indirect artificial selection is sometimes defined as (a) "natural" selection (Simmonds 1979:14–15), (b) the same as conscious selection (Allard 1999: 19, 26), or (c) entirely "unconscious" selection (Poehlman and Sleper 1995:9).)

(2) The choice of germplasm that determines the genetic diversity available within a crop as a basis for selection. Farmers and plant breeders make choices between varieties and populations, especially in the initial stages of the selection process when choosing germplasm for making crosses, and in the final stages when choosing among populations/varieties (Hallauer and Miranda 1988) for further testing, or for planting (farmers) or release (plant breeders). Farmers' choices when saving seed for planting, in seed procurement, and in allocating different varieties to different growing environments affects the genetic diversity of the crops they plant, and determines the diversity on which future selection will be based.

THE BIOLOGICAL MODEL

As a framework for evaluating farmer breeding we use the elementary biological model on which plant breeding is based, as it is presented in standard texts (e.g., Falconer 1989; Simmonds 1979). First, variation in population phenotype (V_P) on which choice and selection are based is determined by genetic variation (V_G), environmental variation (V_E), and variation in genotype-by-environment interaction (V_{GxE}) $V_P = V_G + V_E + V_{GxE}$. Broad sense heritability (H) is the proportion of V_P due to genetic variance (V_G/V_P), whereas narrow sense heritability (h^2) is the proportion of V_P due to additive genetic variance (V_A), that is, the proportion of V_G directly transmissible to offspring (V_A/V_P), and therefore of primary interest to breeders.

Second, response to selection (R) is the difference for the traits measured between the mean of the whole population from which the parents were selected and the mean of the next generation that is produced by planting those selected seeds under the same conditions. R is the product of two different factors ($R = h^2S$), where S is the selection differential, the difference between the mean of the selected group and the mean of whole original population selected from. Expression of S in standard deviation units (the standardized selection differential, Falconer, 1989:192), permits comparison of selections among populations with different amounts or types of variation. The results of selecting for a given trait improve as the proportion of V_P contributed by V_G (especially V_A) increases.

The biological relationships described in these simple equations underlie plant breeders' understanding of even the most complex phenomena they encounter (Cooper and Hammer 1996; DeLacy et al. 1996). For example, two highly respected plant breeding texts state that the relationship between genotype and phenotype is "perhaps the most basic concept of genetics and plant breeding" (Allard 1999:48), and of $R = h^2S$, that "If there were such a thing as a fundamental equation in plant breeding this would be it . . ." (Simmonds 1979:100).

ASSUMPTIONS

Although we use a framework based on the basic biological model of plant breeding, we do not assume that when there are differences between farmers and breeders, that the farmer is wrong, nor do we assume 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 acknowledge that successful plant breeding by either farmers or professional breeders does not depend on a complete empirical or theoretical understanding of the biological mechanisms involved (Duvick 1996; Simmonds 1979).

We assume that an essential element for successful CPB is increased understanding of professional plant breeding. We recognize that in the elaboration and application of the basic model of plant breeding there are many differences among plant breeders, and this may be especially true when extending conventional breeding to farmers' environments, such as envisioned by CPB (see e.g., Ceccarelli, Grando, and Impiglia 1998). Another essential element for successful CPB may be increased understanding of the basis for variation in plant breeders' knowledge and practice in terms of the genotypes and environments they work with, and of their sociocultural environment, and how these change in the context of CPB (Cleveland n.d.).

Better understanding of farmers' plant breeding in terms of the biological principles on which scientific plant breeding is based should increase the success of CPB by facilitating collaboration in the use of scientific plant breeding's emphasis on data collection and dissemination, theoretical and analytical tools, and global access to genetic resources, and by facilitating the use of farmers' understanding of their complex farming systems within which they practice plant breeding. This is especially likely when CPB involves changes in farmers' knowledge or practice, but not as likely when it doesn't, e.g., when a new variety is introduced that is similar to existing farmers' varieties, and which they can adopt without changes in selection, choice, or production practices.

The next three sections are on three central aspects of farmer plant breeding from the viewpoint of the biological model: genetic variation, environmental and genotype-by-environment variation, and plant selection. For each of these, we propose key research questions about farmers' knowledge, practices, and crop varieties and growing environments. To explore answers to these questions, we use examples from the research literature and, for those topics where little other research exists, from our own work in Oaxaca, Mexico.

GENETIC VARIATION

Genetic variability (often referred to generally as genetic diversity) is the basis for genetic improvement of farmers' crop varieties and crop repertoires through plant selection or varietal choice.

FARMER KNOWLEDGE

How are Farmers' Criteria for Crop Classification Related to Perceptions of V_G?

A major controversy within ethnobiology has been whether classification is the result of the universal structure in nature that imposes itself on the human mind, perhaps facilitated by universals in human cognition (the intellectualist view), or whether it is the result of culture-dependent differences in goals, values, and theories (the utilitarian view) (Medin and Atran 1999). Boster's work with Aguaruna farmers in the Amazon supports the first view: cassava

(*Manihot esculenta* Crantz) classification reflects a tendency to create and classify the smallest distinct taxonomic unit, in patterns similar to those of scientists (Boster 1985, 1996). This theory is supported by data on Ari observation, classification, and selection of ensete (*Ensete ventricosum* [Welw.] Cheeseman) in Ethiopia, in which primary importance is placed on morphological traits not directly related to practical use (Shigeta 1996).

Support for the utilitarian view is a more common research finding. For example, for the Mende of Sierra Leone, growth duration is a major criterion for classifying rice (*Oryza glaberrima* Steudel and *O. sativa* L.) varieties, with a mixture of varieties of different durations managed and planted to avoid labor bottlenecks and interharvest 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 can be similar to scientific classification. Farmers in Cuzalapa, Mexico classified their maize FVs using traits such as plant height and weight and diameter of cob, in the same pattern as did statistical trait analysis of ear characteristics (Louette, Charrier, and Berthaud 1997). There is also evidence suggesting that farmers may be aware of the value of the genetic potential of hybrids, such as seeds harvested from the edges of plots, where hybridization is more likely to occur, both for self-pollinated (rice in Sierra Leone, Richards 1986), and cross-pollinated crops (maize in Mexico, Louette and Smale 1998).

Differences in conclusions about the basis for classification systems may be due not only to the bias of the initial orientation of the researchers, but to differences in the nature of the crops and environments involved. For example, the pattern of phenotypic expression of qualitative traits in a clonally propagated crop (cassava, ensete) is much different than for quantitative traits in sexually propagated crops (rice), especially cross-pollinated ones (maize). Farmers may simply enjoy "playing" with diversity (Berg 1996), yet their perceptions of genetic variation (to the extent revealed in plant phenotypes and across environments) depends on their physical ability to observe it, determined in turn by the scale at which it occurs, the extent to which it is hidden by V_E, and also on how important it is to them. Farmers' recognition of V_G between maize (*Zea mays* L.) FVs and between and within maize populations in Oaxaca, Mexico, is influenced by the relative contributions of V_G and V_E to V_P, that is the heritability of the particular trait (Soleri, Smith, and Cleveland n.d.).

There is also significant variation in distribution of farmer knowledge about V_G as the result of social factors including age, gender, social status and affiliation, kinship, personal experience, and intelligence (Berlin 1992), accompanied by variation in the way farmers conceive of their intellectual ownership of these resources (Cleveland and Murray 1997). There may also be a range in the consistency of classification schemes within communities; for example, potato variety (*Solanum tuberosum* L.) classification in the Andes appears to be consistent (Zimmerer 1996), whereas cassava variety names among the Amuesha of Peru have a high level of inconsistency, with the same common name applied to different phenotypes (Salick, Cellinese, and Knap 1997).

FARMER PRACTICE

Farmers can affect genetic variation in two major ways: at the intraspecific level by adding and deleting varieties, and at the intravarietal level by consciously and unconsciously encouraging genetic recombination through hybridization.

What Farmers' Practices can Affect Intraspecific V_G?

Farmers' annual choices about what varieties they will plant in which locations and at which times, including the abandonment of varieties and the acquisition of new ones, affects V_G at the intraspecific level. 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 (Soleri and Cleveland 1993; see also Bellon 1996; Louette, Charrier, and Berthaud 1997; 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 the 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).

Most research has focused on individual farmers making decisions about individual varieties. However, this may lead to assumptions that are not justified. First, it is obvious that individual decisions are made within a sociocultural context, and networks affecting farmers' access to seeds are not experienced equally by all. For example, a study in Rwanda found that seed networks were socially limited, with poorer households having the most limited access (Sperling and Loevinsohn 1993). A common observation is that there are individuals in a community known for the number of varieties that they maintain, e.g., male shamans and some women farmers in the Peruvian Amazon (Salick, Cellinese, and Knap 1997). There has been almost no analysis until recently of the effect on a farmer's varietal repertoire of his/her decisions based on perceptions of other farmers' management of their varietal repertoires and his/her access to them. Initial findings suggest that farmers' perceptions of changes in the maize varietal diversity in their communities can affect the number of varieties they maintain (Smale, Bellon, and Aguirre Gomez 1999).

Second, researchers may have focused unjustifiably on individual varieties. For example, contrary to the assumptions of other researchers in the area, Zimmerer found that some groups of Andean farmers choose varietal mixtures of potato for planting en masse, only rarely or never selecting individual FVs as components (Zimmerer 1996).

What Farmers' Practices can Affect Intravarietal V_G

Hybridization, the crossing of two distinct genotypes (species, varieties, or populations), is probably the main way in which farmers' choice affects the V_G of FVs. Hybridization can result from activities that unconsciously affect the level of reproductive isolation, such as allocation of planting material (cropping patterns), or farmers may have hybridization as a conscious goal.

There are reports in the literature of encouraged or tolerated hybridization between species, e.g., wild squash (*Cucurbita argyrosperma* C. Huber subsp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates) with cultivated species (*C. argyrosperma* subsp. *argyrosperma* and *C. moschata*) (McKnight Foundation 1998). One of the most well-known examples is of teosinte (*Zea mays* L. subsp. *mexicana*) hybridizing with maize (*Zea mays* subsp. *mays*) (Benz, Sanchez-Velasquez, and Santana Michel 1990; Wilkes 1989), although the extent and significance of this has been challenged (e.g., Kato Y 1997). Hybridization between species is probably responsible for a 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.

Reports of hybridization between varieties or populations of a species are more common. Farmers may also manage this level of hybridization primarily as introgression, although this is probably less likely because of the smaller genetic distance involved. In vegetatively propagated crops, seed may be produced from occasional spontaneous hybridization between varieties and sought out by farmers, e.g., by Amuesha cassava farmers in Peru (Salick, Cellinese, and Knap 1997), and Quechua potato farmers in the Andes (Zimmerer 1996).

In self-pollinating species, e.g., rice, the possibility for cross pollination between varieties may be increased when a farmer plants different varieties of the same duration class in adjacent plots, when adjacent plots contain different farmers' varieties of the same duration class, and when farmers use a large plot communally, as with rice in Sierra Leone (Richards 1986, 1996). In cross-pollinating crops the levels of hybridization potentially are much higher. In a CPB project in Rajasthan, India with pearl millet (*Pennisetum glaucum* (L.) R. Br.), 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).

GENETIC VARIATION OF FARMERS' VARIETIES

What is the lLvel of V_G in FVs?

Most of the evidence and discussion regarding V_G in FVs refers specifically to landrace populations. Evidence suggests that since domestication there has been increasing intraspecific diversity in the form of landraces until modern plant breeding "drastically restricted . . . the intraspecific diversity of crop species" (Frankel and Soulé 1981:179). The genetic diversity of landraces is probably one of the most researched components of farmers' plant breeding, although this has rarely taken the broader population structure of what are now recognized as open genetic systems into account (e.g., Louette et al. 1997). A number of studies suggest that landraces have a large amount of allelic variation (Frankel, Brown, and Burdon 1995). Species' mating systems affect the structure of genetic variation, with cross-pollinating species having more allelic diversity within as compared to between populations, with the opposite being true of self-pollinating species (Hamrick and Godt 1997). Yet there is significant overlap, for example, about 19% of loci are polymorphic in lentil, which may be typical of self-pollinating species (Erskine 1997). Significant intravarietal variation in morphology and phenology has also been documented for cross-pollinating species, for example, in two Hopi maize FVs (Soleri and Smith 1995).

How is V_G Affected by Farmer Practice?

The net effect of the adoption and abandonment of varieties may either increase or decrease V_G, because there are "infinite combinations between the variability of existing crops and the new variability of cultivars that partially or completely replace them" (Witcombe et al. 1996: 456). Although adoption of MVs due to their superior performance has been documented to decrease on-farm genetic diversity through the loss of FVs, there may be a limit to this loss in the later stages of adoption (e.g., for potato in Peru, Brush, Taylor, and Bellon 1992). However, there are few genetic data on the effect of changing varietal repertoires (including MV adoption) on allelic diversity (number and evenness) at the farm, community, or regional levels.

Similarly, although it is known that farmer practices can increase hybridization, there are few data on its genetic effect. In Cuzalapa, Jalisco, Mexico, farmers regularly mix maize populations together by classifying seed obtained from widespread, diverse sources in the same variety (Louette, Charrier, and Berthaud 1997). This practice, together with the planting patterns, leads to a 1–2% level of gene flow between adjacent maize plots during one crop cycle, which probably has a significant effect on genetic composition over several crop cycles (Louette 1997). Evidence of a morphological and genetic continuum across the four major local varieties suggests that traits from a variety introduced 40 years ago have introgressed into the other varieties. Several studies have documented introgression of maize MVs into FVs in Mexico (Castillo-Gonzáles and Goodman 1997). Although evidence from the Cuzalapa study suggests that gene flow "probably leads to a modest degree of heterosis among all cultivar types," this may not always be the case. In fact, whether gene flow increases or decreases V_G, and what effects this may have on adaptation is unknown for FVs. In conservation biology gene flow is often considered beneficial because it can prevent inbreeding depression and loss of V_G in small populations, but it can also reduce V_G, leading to outbreeding depression and reduced adaptedness, and the effect may depend critically on population size (Ellstrand and Elam 1993).

Is V_G "Optimal" for Farmers' Environments?

Much of the research on genetic diversity in FVs has been done with the aim of assessing its potential for MV breeding programs (e.g., Ouendeba et al. 1995), not in terms of adaptation to farmers' growing environments. Available data suggest that the genetic variation of FVs appears to buffer the effects of variable, high-stress environments, and provide genetic potential for selection of superior material (Frankel, Brown, and Burdon 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 (Trutmann and Pyndji 1994). One reason for low or less than optimal V_G within a FV is genetic drift due to a founder effect (Barrett and Husband 1989), and this may be most likely when crops are introduced outside of their areas of origin and/or diversity.

V_G among varieties is also important. A number of studies illustrate the greater stability and productivity of mixtures of populations (lines) for self-pollinated crops. For example in the Great Lakes region of East Africa farmers plant mixtures of many varieties of common bean (*Phaseolus vulgaris* L.) that are site specific, with varying resistances to multiple diseases, a strategy that may be the most effective for optimizing yield stability. A similar situation can occur for cross-pollinated crops, and 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).

ENVIRONMENTAL DIVERSITY AND GENOTYPE-BY-ENVIRONMENT INTERACTION

Environmental diversity or variation can be partitioned into several components: $V_E = V_L + V_T + V_M$ (V_L = variance due to location, e.g., soil and climatic variables; V_T = variance due to time, e.g., season or year; and V_M = variance due to breeder or farmer management). V_{GxE} represents the degree to which genotypes behave consistently across a number of environments. Low quantitative GxE means relatively little change in performance over environments. High quantitative GxE is characterized by marked changes in performance with changes in environmental factors and is associated with reduced stability of performance (defined as variance across environments) of an individual genotype. Qualitative GxE between two or more varieties means that they change rank across environments, and this is often referred to as a crossover because the regression lines for yield (or other traits) cross over at some point.

FARMER KNOWLEDGE

How do Farmers Perceive GxE in Relation to Their Choice of a Variety for a Given Location?

The choice of a variety (A) with higher mean yield but larger regression slope (lower yield stability) over all locations compared with another variety (B) can be unproblematic in some contexts because this describes a situation in which there is only quantitative GxE, i.e., no crossovers (Tripp 1996). However, in terms of farmers' understanding, this may depend on the way in which environment is defined. When a farmer is choosing between varieties to grow in a given location, his/her choice may depend on how variation in yield (and income) is perceived over time for that location (V_{GXT}), as well as mean yield. If variety A has larger mean yield and lower yield variance than variety B through time in a given location, then the choice would be A. However, if variety A has larger mean yield but also a larger variance, then the choice between the two varieties will depend on his/her attitudes toward risk and ability to manage it, and he/she may be willing to sacrifice mean yield in order have a more stable yield, or a "smoother income stream" through time. (Walker 1989).

Few data exist on farmer risk perception in terms of V_{GxT}. One study from Malawi on the dynamics of MV hybrid maize adoption, FV maize retention, and commercial fertilizer application, suggests that the ratio of coefficients of variation of MVs to those of FVs, based on farmers' subjective yield estimates, is negatively related to area planted to MVs and to fertilizer application rate on MVs (Smale, Heisey, and Leathers 1995). That is, the lower the yield stability through time of MVs compared to the FV, the less land and fertilizer are allocated to the MVs.

How do Farmers Perceive GxE in Deciding Whether to Have One or More Than One Variety for a Set of Locations?

Another situation that appears to be common for farmers is the choice of varieties for a range of locations for a given planting season (i.e., time is held constant). If farmers do not perceive qualitative GxL (crossovers) differences in performance for varieties between locations, then there may be no reason for them to grow different varieties in these locations. When farmers do perceive crossovers between varieties for two environments, then they may have to decide whether to grow one variety in both environments, or if the extra yield obtained by growing two different varieties in the two environments compared with the extra effort required, will produce a net benefit.

One sample of Rwandan farmers chose from among plant breeders' varieties of common bean for home testing. They based their choices 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, and thus of GxE, though no details of farmer knowledge were reported (Sperling, Loevinsohn, and Ntabomvura 1993). Rajasthani pearl 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 ability in the most stressful (Weltzien R. et al. 1998), suggesting that in the most variable environments, traits contributing to yield stability are more important than those contributing to more yield. There are similar results from research in Cambodia, where rice farmers' criteria for varietal choice differs according to level of 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).

Farmers' perceptions of qualitative GxE differences appear to depend on the range of environmental and/or genotypic diversity they must consider in making a decision about allocation of land to varieties. In our study in Oaxaca, farmers in one community (A) do not maintain distinct varieties of white maize identified for allocation to specific environments (e.g., soil type, elevation, water availability, planting season), and instead identify two varieties based on ear and kernel phenotypes with no consensus regarding a relationship to in-field performance (Soleri and Cleveland n.d.). In contrast, farmers in a nearby community (B) with less favorable growing conditions classify and maintain *violento* (short growth duration) and *tardón* (long growth duration) varieties of white maize. Whether or not distinct duration varieties of white maize are maintained appears to depend on the importance to farmers of duration for managing drought. In community B, farmers see V_E between location-year combinations as being greater than do farmers in community A, and they believe that *violento* performs better in years with late season drought, and *tardón* in years with early season drought. These findings suggest that farmers in community B perceive V_E between environments (characterized according to within and between year variation in precipitation) as greater than farmers in community A, and also perceive that the net benefits justifies maintaining separate varieties for those environments.

FARMER PRACTICE

What Growing Environment Variables are Correlated with Farmers' Choice of Varieties?

Some FVs appear to be managed for narrowly defined environments, for example, in East Africa varietal mixtures of common bean selected for different on-farm environments are often maintained separately (Trutmann 1996), and Mende farmers in Sierra Leone maintain a large and constantly changing collection of rice FVs, with selection primarily for traits, including duration, and adaptation to a variety of specific moisture regimes (Richards 1986). In contrast, 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 these varieties are harvested and planted by some groups of these farmers as bulk mixtures across all environments (Zimmerer 1996).

What Environments do Farmers Choose for Testing New Material, and How are They Related to Their Target Environments?

Research findings on farmer practice regarding new accessions are also contradictory. Farmers may test new varieties in optimal environments, for example, in home gardens, where they evaluate them for later planting in specific, more marginal environments, and researchers assume that they do this to reduce risk of loosing seedstock (Ashby et al. 1995; Soleri and Cleveland 1993). However, rice farmers in Nepal often plant new varieties on their worst land, which has been interpreted as a risk aversion strategy (Sthapit, Joshi, and Witcombe 1996), with the implication that farmers are looking for varieties adapted across a wide range of locations. It has been suggested that this is a common practice (Witcombe 1998).

FARMERS' GROWING ENVIRONMENTS AND VARIETIES

Are FVs Adapted to a Narrow or Wide Range of Environments?

Commonly used definitions of FVs include the statement that they are adapted to a narrow range of environments (Frankel, Brown, and Burdon 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, Myers, and Scully 1993), especially when discussing farmers' systems (Bjørnstad 1997).

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, Whitaker, and Weltzien R. 1996). One study in Ethiopia found that 13 wheat (*Triticum turgidum* L.) 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 (*Lens culinaris* Medick) appear to have specific adaptation to locations, temporal patterns, and management levels (Erskine 1997).

On the other hand, some FVs may be geographically widely adapted, and be planted across a wide range (Witcombe 1999). The widespread exchange of crop varieties by farmers suggests such wide adaptation (Wood and Lenné 1997), although the range of environmental variation and its components and the degree of genetic variation between FV populations grown by different groups are largely unknown. In southwestern North America maize varieties have been shared frequently 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). The high level of variation within farmers' fields planted to a single FV also suggests that such FVs can be widely adapted to a large range of locations within a small geographical area (Soleri, Smith, and Cleveland n.d.).

How do FVs Compare with MVs in Range of Adaptation?

MVs that are widely adapted geographically may be narrowly adapted to the high-yielding, low-stress conditions of locations and management environments used by many plant breeders in selection (Bänziger, Edmeades, and Lafitte 1999; Ceccarelli 1989; Witcombe 1999). Qualitative GxE interaction of varieties across environments when the range is wide enough are well known (Evans 1993 and Ceccarelli 1996 summarize the data) and may explain the lack of adoption of some MVs for farmers—they may be out-yielded by FVs in farmers' high-stress environments (Bänziger, Edmeades, and Lafitte 1999; Ceccarelli, Grando, and Impiglia 1998; Weltzien and Fischbeck 1990).

On the other hand, MVs may be widely adapted to a range of locations, including not only low-stress locations, but also high-stress ones where they out yield FVs. For example, the experience of the International Maize and Wheat Improvement Center (CIMMYT) 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 high-stress environments, such as Western Australia (Rajaram, Braun, and van Ginkel 1997; 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).

PLANT SELECTION

Selection of plants from a heterogeneous population to obtain planting material for the next generation can affect allelic frequencies through time, and thus genetic gain, or R. Mass selection appears to be the most common form of selection used by farmers. It involves the identification of superior individuals in the form of plants and/or propagules from a population and the bulking of seed or other planting material to form the planting stock for the next generation. This approach 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 extent to which the selected trait is heritable, GxE for the trait, the proportion of the population selected (selection intensity), and gene flow in the form of pollen or seeds into the population.

FARMER KNOWLEDGE

What are Farmers' Explicit Selection Criteria?

Farmers stated selection criteria are often complex. In our Oaxacan case study the most important criteria appear to be those related to seed viability—all maize ears with evidence of pest or disease damage to the seed or cob are usually discarded (Soleri, Smith, and Cleveland n.d.). 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. Our sample included traits like grain type (e.g., flinty vs. starchy), grain form (round vs. flat), and cob and husk color. Although criteria in the third category varied between households and communities, the first two categories were universally the most important. Explicit criteria in the Cuzalapa case study were similar (Louette and Smale 1998).

Selection criteria can vary within a community. In a panicle selection exercise in Rajasthan, India, farmers with good land or more land selected a wide range of pearl millet panicle types for seed because they said they wanted seed stocks useful for a broad range of planting conditions, including variations in soil fertility as well as in rainfall, and they frequently purchased seed. In contrast, farmers with poor land chose only one panicle type, one rejected by the former group, and were proud of saving their own seed for 100 years (Weltzien R. et al. 1998).

What are Farmers' Explicit Selection Goals?

Weltzien et al. noted that surprisingly little research has been done on selection goals considering their importance for the selection process, especially for marginal environments and for farmers (1998). The implicit assumption often has been that farmers must be attempting directional selection for quantitative, relatively low heritability traits like yield, the main goal of plant breeders. However, there appear to be relatively few data demonstrating that farmers have directional selection for quantitative traits as a conscious goal, in contrast with data on farmers' conscious choice of new varieties.

As researchers' understanding of the complexity of farmers' knowledge and traditional farming systems increases, it seems possible that disruptive, stabilizing, and random selection may either be an explicit (conscious) goal of farmers, or occur as an unintended result of selection practices. In informal interviews in Cuzalapa, 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 were similar to those in Cuzalapa. They suggest that for traits with low heritability, farmers generally did not hope to change a variety (Soleri, Smith, and Cleveland 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. These farmers typically have low expectations for change regarding traits that comprise their seed selection criteria. They 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) in traits with medium to low h^2 (<0.5), the 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). In contrast, the Oaxacan farmers we worked with clearly understood qualitative, relatively highly heritable traits like tassel color differently. They perceived of the possibility of directional selection for this trait, and showed us examples of the successful results of such selection in their fields.

Farmers' perceptions of the potential to improve their populations via selection—and thus their selection goals—will be influenced not only by their understanding of genetic variation in the population and h^2 for traits of interest, but also of alternative uses of their time and labor. If they do not believe population improvement to be possible or cost-effective, one alternative may be to choose different varieties or populations or infuse their own varieties or populations with new genetic variation as discussed above.

FARMER PRACTICE

At what Stages in the Plant Life Cycle, and by Which Farmers, is Selection Carried Out?

The stage of the plant life cycle at which selection occurs can have a strong effect on its efficiency in terms of genetic gain, and different persons may have different selection goals, conscious and unconscious. In some crops, for example, small-seeded crops like rice, farmers are more likely to carry out in-field selection on plants using a range of criteria (Richards 1986; Sthapit, Joshi, and Witcombe 1996), although major selection criteria may also include postharvest traits (Sthapit, Joshi, and Witcombe 1996). In other crops, for example, large-seeded crops like maize, selection may be almost entirely post-harvest, as in Mexico (Smale et al. 1998). 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, whereas the remaining farmers selected entirely postharvest (Janssen, Adolfo Luna, and Duque 1992).

In the Sierra Santa Marta of Veracruz, Mexico, detailed and repeated interviews with both men and women in the same farm household showed that selection occurs in four or five stages, most of which women participate in (Rice, Smale, and Blanco 1998). In Mexico, it has been a common finding of researchers, and an assumption of development workers, that men are responsible for seed selection, but new findings suggest that this conclusion may be the result of the methods employed and that women play an important role in seed selection (Smale et al. 1998).

What are Farmers' Implicit Selection Criteria?

Farmers implicit (unconscious) 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 Cuzalapa, Mexico, farmers implicit criteria reflected their explicit criteria (Louette and Smale 1998). Although all ear descriptors measured showed a significantly higher level in the selected set compared with the population selected from, the greatest differences were for the criteria farmers said were most important: ear weight, ear length, length of ear presenting kernels, total number of kernels, and kernel filling.

In Oaxaca, Mexico we carried out selection exercises with farmers on maize ears, in which they selected the best 10 ears for planting seed from a random sample of 100 ears taken from plots in their own or neighboring fields (Soleri, Smith, and Cleveland n.d.). Values for standardized S were not significant for ear traits such as kernel row number and shelling ratio, and there were only occasional but no consistent significant differences for some plant morphological and phenological traits. However, for the correlated characteristics of ear length and weight, selections were significantly different than the 100 ear sample, with standardized S values (also referred to as intensities, Falconer 1989:192) of 0.48–1.33 and 0.73–1.81 respectively (compared with an intensity of 1.8 typically sought by breeders in directional selection of a 10% sample, Hallauer and Miranda 1988). Thus their explicit selection criteria accurately reflect the traits that farmers actually seek when selecting seed for planting.

FARMERS' VARIETIES AND THE RESULTS OF FARMER SELECTION

What is the Heritability of FVs in Farmers' Selection Environments?

The success of farmer selection will depend to a great extent on the heritability of the traits included in their implicit selection criteria in the crop populations and environments they are managing. A few studies have been done on heritability of FVs in experimental plots, for example, in Ethiopia, research with wheat FVs found intermediate to high heritabilities for many traits, including grain yield (Belay et al. 1993). Assessment of heritabilities in farmers' selection environments are even more rare. One example is our study in the Central Valleys of Oaxaca, Mexico (Soleri and Smith n.d.), using a new method for estimating H in farmers' fields (Smith 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 (Rice, Smale, and Blanco 1998 describe one example), will be negligible or low. It also suggests a number of traits of interest to farmers with H values showing potential for significant response (average H = 0.65 for days to anthesis, 0.74 for ear height, and 0.63 for ear length) if mass selection was improved, for example, through in-field selection with stratification. However, this is true only if whole plant traits are relevant to farmers' selection goals, and, when only in-field selection is used, if the overall gain will be greater than for postharvest selection.

What is R for Farmers' Selection Practices?

Although mass selection has clearly been effective over time for some traits, genetic gain (R) from selection year to year may be small because heritabilities for many selection criteria such as yield are generally low (< 0.30). The results of farmer selection (R) may be different than their implicit goals (S), however, R has seldom been measured. For example, farmers may intend to perform directional 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 of their efforts may be random selection, i.e., $R = 0$. This may be the case for farmers in our Oaxaca case study because there were no significant differences between the means of random samples from the whole population and samples of farmer-selected seed derived from these as represented by their progeny generations, and significant differences were not observed among random samples of the same population over generations for the traits evaluated (Soleri, Smith, and Cleveland n.d.). However, a more accurate interpretation may be that these farmers perceive some traits as part of a group of nonheritable selection criteria related to seed quality and seedling performance. As such, their interest in and expectations for these traits may not be related to their inheritance, and S values would reflect the weighing of seed stock quality along with any other selection criteria in farmers' selection, and not the sole goal of directional selection as so frequently assumed.

It seems clear that farmers, like plant breeders, observe that the effectiveness of selection depends to a great extent on the heritability (h^2) of the traits constituting the selection criteria. Thus, and in contrast to the findings in Oaxaca, the Cuzalapa study shows that farmers can achieve discernable R in the face of high levels of gene flow from morphologically contrasting varieties into their black maize variety (Louette and Smale 1998). Specific morphological and to some extent isozyme data show farmers' selection maintains the phenotype characteristic of their varieties (ear traits and linked phenological traits that define the ideotype) in the face of gene flow, even though other characteristics not visible to farmers (isozymes) continue to evolve genetically. These farmers are apparently seeking to maintain varietal integrity, and base their selection on traits such as kernel row number, kernel width, and color, all with medium to high average h^2. In contrast, the selection documented in Oaxaca showed, for example, that kernel row number is not a criterion of interest, with selected populations not significantly different from nonselected ones for both standardized S and R. The selection in the Cuzalapa example may be most aptly described as stabilizing, though this would require further investigation.

There is overwhelming indirect evidence for directional selection by farmers achieving significant genetic gain over long periods of time for the quantitative agronomic traits that are the focus of most professional plant breeding, such as yield. However, there appears to be little evidence from research with contemporary farmers for positive R as result of conscious or unconscious directional selection for such traits. The possibility of directional selection for such traits by farmers, and the resulting R, is an area in need of more research.

CONCLUSION

In this paper we have presented a biological framework, based on scientific plant breeding theory, for evaluating farmers' plant breeding (their knowledge, practice, crop varieties, and growing environments). Building on this framework, we have posed key questions that may need to be answered if collaboration between farmers and breeders is to be successful. Our examination of the research literature (not an exhaustive review) lead to the following conclusions.

1. The data needed to answer these key questions is often scant or nonexistent, and further empirical testing of specific hypotheses based on the questions presented here is needed, especially in the context of CPB projects.
2. The explicit and implicit answers to these questions that are available in the literature are often different and even contradictory, and may be based on unexamined and even unrecognized assumptions.
3. Farmers' knowledge of their genotypes

and environments is in many ways fundamentally similar to that of plant breeders' understanding of their genotypes and environments, in terms of the biological model of plant breeding.

4. Farmers' knowledge may also be different than that of plant breeders, in part because the genotypes and environments they deal with are also different in important ways than those commonly dealt with by plant breeders.
5. Farmers' practice show a wide range of effectiveness in meeting their explicit selection goals.
6. The search for generalizations about farmer plant breeding is valid, but we need to be careful about making them at too superficial a level—generalizations based on conventional plant breeding, or on experience with specific farmers' and their varieties and growing environments, may not be a valid foundation on which to base the development of CPB.
7. Adapting professional plant breeding to CPB will require further research on farmer plant breeding, and further examination, adaptation and development of plant breeding theories and methodologies.

Ultimately, it will be necessary to greatly expand the framework we present to include more sociocultural and economic variables at both local and regional levels, and to include analysis of professional plant breeding along with farmer plant breeding. It seems that with more critical qualitative and quantitative research on farmer and scientist plant breeding, it is likely that what are frequently assumed to be either different or similar systems of plant breeding, will turn out to be two complex systems with many similarities as well as differences.

It will also be important for CPB projects to include consideration of whether alternative ways of investing scarce resources, such as managing soil organic matter, or helping farmers to gain more control over political processes, may improve farmers' well-being more effectively than CPB.

Our aim in this article is to encourage research useful for CPB work whose goal is to help farmers and plant breeders communicate more effectively with each other, so that breeders' theory, knowledge, statistical design and analysis, and access to a wide range of genetic diversity, can be used collaboratively with farmers' knowledge of their crops and environments, and techniques for management. Such research will permit testing of the idea that reuniting farmer and professional plant breeding, after 200 years of increasing separation, can increase the effectiveness of developing crop varieties that better meet farmers' needs, conserve crop genetic diversity in situ, and thus contribute to sustainable agriculture.

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