

Conserving Folk Crop Varieties

Different Agricultures, Different Goals

DANIELA SOLERI

STEVEN E. SMITH

Over the last twenty-five years, a substantial investment in the conservation of crop genetic resources worldwide has been made by public and private sectors in many countries. One impetus for this conservation effort came from researchers who were alarmed at the rapid disappearance of folk crop varieties (also known as landraces) as well as the habitat of wild crop relatives (see, for example, Frankel 1970). Another motivation for crop genetic resource conservation came from observing the effect of a narrowed genetic base in the agricultural systems of industrialized countries. An example of this was the southern corn leaf blight damage in the United States in 1971, a loss of an estimated \$500 million to \$1 billion, or about 15 percent of the U.S. crop that year, attributed to the broad use of the same cytoplasmic male sterility gene (Walsh 1981). The result was increased concern for genetic resources and diversity that continues today under the broader title of biodiversity.

A new issue is emerging in the discussion of crop genetic resource conservation, or perhaps more correctly, it is just now beginning to be articulated (Soleri and Smith 1995), concerning the goals of conservation and some of their implications. This paper discusses the conservation of crop genetic resources, specifically folk varieties, in terms of the genetic goals of the people for whom those resources are being conserved, how different goals require different conservation strategies, and some ideas on how we can start to conduct research that specifically addresses those goals. We look particularly at farmer-breeder selection and the characteristics of folk crop varieties for insights into the genetic goals for traditional crop varieties and the people who cultivate them.

Goals of Folk Variety Conservation

The genetic diversity of crop genetic resources is a valuable part of all agricultural systems. How this diversity is maintained and used differs, however, among different types of agricultural systems. Crop genetic resources, including folk varieties, may be conserved *in situ* (on site and in the farming system where they were most recently developed) or *ex situ* (away from that environment, usually in seed banks or occasionally in living collections). Whether *in situ* or *ex situ*, the goals of folk variety conservation differ. While there are certainly diverse goals for the conservation of folk varieties, they all lie on a continuum between the polar perspectives we label “conventional” and “farmer-breeder.” Although extreme, these nevertheless represent actual conservation goals. To understand these perspectives and the genetic goals they imply requires placing them within the agricultural systems of which they are a part.

The Conventional Perspective

The “conventional perspective” has been followed by most plant breeders and conservationists concerned with crop genetic resources over the past twenty-five years. From this perspective, crop genetic resources conservation is undertaken to meet the needs of industrial agriculture, typically large-scale, high-external-input agriculture (Plucknett et al. 1987). Industrial agriculture has been based on the creation of improved growing environments and on uniform, energy-intensive cultural practices (soil preparation, irrigation, insect and pathogen [hereafter “pest”] control) extending over large areas. Plant breeding for these agricultural systems has focused primarily on maximizing yields. This objective has been achieved by increasing the harvest index in some species (such as rice), and by exploiting the genotype by environment interaction ($G \times E$) that, when positive, makes some populations highly responsive to the “improved” growing environments that are created with high levels of inputs (Simmonds 1991b). The assumption that these inputs would always be available has meant that local adaptation, particularly to abiotic conditions such as water stress or lack of soil nutrients, has not been an important consideration in most of these breeding programs. Such adaptation may therefore have been lost during breeding in favor of yield.

On the other hand, there has been an interest in specific, usually qualitative traits such as resistance to pests or pathogens. That is, both genetic and chemical controls have been used in response to these problems. However,

pests and pathogens may rapidly evolve resistance to either the chemical or genetic controls typically used in industrial agriculture for two reasons. First, the extensive scale of these systems (large fields and often entire regions planted to the same variety or varieties and maintained with closely similar cultural practices), exerts strong selection pressure for the development of resistance (Gould 1988). Second, the vertical (monomorphic, oligogenic) resistance used in many conventional breeding programs also creates strong selection pressure for the development of resistance, and opportunity for the success of that resistance (Simmonds 1991a).

These are some of the reasons that crop varieties produced by conventional breeding efforts (hereafter “modern varieties,” including Green Revolution varieties) often require frequent replacement with newly developed modern varieties. This is sometimes referred to as the varietal “relay race” of industrial agriculture (Plucknett et al. 1987:19ff). These varieties are characteristically more homogeneous, and in the case of cross-pollinating species, they may be more homozygous relative to folk varieties of the same species (Frankel and Soulé 1981).

According to the conventional perspective, crop genetic resources are recognized as one of the raw materials essential to the continuing development and replacement of modern varieties. In these agricultural systems at least some genetic diversity is maintained apart from the currently cultivated populations in collections established for conservation. Collections are screened for specific traits and, when possible, the alleles for those traits are then introduced into the elite breeding lines developed by Western-trained, formal plant breeders. This approach is reflected in the responses to a 1986 survey of seventeen U.S. wheat breeders (Cox 1991). Those breeders estimated that approximately 24 percent of the germplasm in advanced breeding lines of *Triticum aestivum* was estimated to come from “exotic” sources (folk varieties and crop relatives). Half of those surveyed intended to increase their use of exotic germplasm, and none planned on decreasing such use; they concluded that within *T. aestivum* breeding programs, folk varieties will be used only for specific problems such as apparent lack of disease or pest resistance.

The genetic goals of folk variety conservation from this perspective concern the genetic content of folk variety populations—that is, the extent of polymorphisms and allelic diversity of those populations. Sampling methods (Marshall and Brown 1975) have been based on maximizing allelic diversity, and storage and regeneration have sought to preserve this diversity. From this perspective, germplasm collections as sources of oligogenic, qualitative traits

can never be large enough and should be constantly supplemented to include the products of ongoing coevolution in nature.

The Farmer-Breeder Perspective

Another perspective on folk variety conservation, internal in its orientation, is that the role of these genetic resources within their original, local farming system is an equally valid reason for their conservation (Cleveland et al. 1994). In this paper it is referred to as the farmer-breeder perspective because it attempts to look at the genetic resources in folk varieties from the standpoint of the farmer-breeders (hereafter "farmers") of traditionally based, low-external-input agricultural communities. However, the discussion that follows is a genetic interpretation of our understanding of how these agricultural systems work and does not presume to speak for those farmers. Working with them to support their efforts to identify and communicate their own crop genetic goals is a research priority.

Interest among researchers in the farmers' perspective is based on the purported relationship between traditionally based, low-external-input agricultural systems and particular aspects of natural resource management, agricultural production, and contributions to sociocultural integrity. In plant breeding there is increasing recognition that selection in the local growing environment is the most effective approach to the development of crop varieties that are adapted to those conditions and therefore require a minimum of external inputs to grow and produce a harvest (Ceccarelli et al. 1992a; Simmonds 1991b). Locally developed crop varieties that are genetically diverse (relative to modern varieties), such as many folk varieties, often have greater yield stability (measured as variation in harvest produced from year to year) under low-input conditions than do modern varieties (Cleveland n.d.; Finlay and Wilkinson 1963). To some extent, genetic variation appears to contribute to this stability, for example in the broad or horizontal resistance to local pests or pathogens that may be present in folk variety populations (Simmonds 1991a). But the organization of that genetic variation is also important for locally adapted crop varieties.

Local adaptation in crops is a response to all of the selective forces occurring in the population's environment. Selection, the discrimination between individual genetic contributions to the next generation based on those individuals' fitness (Falconer 1989:26), can be a powerful force in changing allelic diversity and shaping population structure. The changes caused by either natural or artificial selection are the product of the intensity of selection, the pheno-

typic variability of the population for that trait, and the extent to which the trait is genetically determined (heritability; Falconer 1989:192). Folk varieties are similar to modern varieties in that both are primarily the product of many generations of natural selection plus some limited, recent, artificial (human) selection (Frankel and Soulé 1981; Harlan 1992). However, as a result of the way in which they are developed, many modern varieties have been exposed to far less natural selection in their recent history than is the case for most folk varieties.

The effect of over sixty years of natural selection on a highly variable barley population (Allard 1988) provides some valuable insights into the role natural selection might play in the amount and structure of genetic variation in folk varieties. Three findings are of particular importance. First, over time there was a trend toward increased population fitness measured as reproductive output. This phenotypic trend was corroborated by isozyme data showing an increase in frequencies of alleles at highly polymorphic loci that confer local adaptation and frequencies approaching fixation for less polymorphic or nearly monomorphic loci. In this case the increase in environmental adaptation represents a drop in genetic variation at the population level. Second, locally specific, adaptive gene complexes of increasing size were formed that behaved, in terms of selection, as single major gene complexes. It is likely that when artificial selection is combined with natural selection further linkages may be created, potentially resulting in even larger gene complexes for local adaptation. Third, the local adaptation described in the two findings above led to "ecogeographic" differentiation between populations grown at different sites. These same results were observed among cross-pollinating populations, although to a much lesser extent for the second and third findings.

It is the combination of both local adaptation to often difficult growing conditions and the presence of culturally valued traits such as seed or cob color that can make some folk varieties important cultural symbols that contribute to the maintenance of social relations within and between communities (see, for example, Dennis 1987; Richards 1986). For example, this appears to be a likely hypothesis for the persistence of many Hopi Native American maize folk varieties in Hopi agriculture today (Soleri and Cleveland 1993).

Admittedly, the outline given above is an extremely simplistic description of the forces responsible for the diversity and structure of farmer-managed folk variety populations. Some of the other factors involved will be discussed later. Yet we can make the following genetic interpretation of folk variety "conservation" based on even this limited understanding of these agricultural systems. This perspective is concerned with both the genetic content and structure of

folk variety populations, and emphasizes qualities such as overall population structure and the presence of genetic diversity affecting local adaptation. In these agricultural systems, genetic diversity is maintained within the currently cultivated populations, not separate from them. Seen from this perspective, in situ "conservation" is not really conservation at all, as it is commonly defined, but rather the ongoing crop genetic component of a larger agricultural system (Friis-Hansen 1993, Soleri and Smith 1995). This interest in "conservation" for meeting current needs and maintaining future adaptive potential is also being discussed for nondomesticated plant species (Hamilton 1994).

For meeting the needs of farmers, ex situ conservation would be far less desirable than would continued maintenance in the local farming system itself. Sampling for ex situ preservation would require a different approach than is taken for conventional goals, especially a much larger sample size than would be taken when concerned solely with allelic diversity rather than population structure (Marshall and Brown 1983). Preservation and regeneration would need to be particularly sensitive to maintaining local adaptation to the "native" growing environment.

These different perspectives reflect a central, although often unstated, division in the discussions of the "conservation" of folk varieties, between those who see the role of this process as being primarily one of conservation (Brush 1991), and those who see it as ultimately being a local development issue (Cleveland et al. 1994; Cooper et al. 1992). The existence of such differences in perspective is not unique to research concerning the conservation of folk varieties. Historians and philosophers of science have pointed out the role of subjectivity in scientific investigation at many levels, acknowledging, for example, that the researcher's perspective or the assumptions of his or her larger social paradigm can affect research design, choice of hypotheses that are to be tested, and in some cases the findings themselves (Gould 1981; Harding 1991). Recognizing the nature of one's subjectivity is a significant step toward reducing confounding issues in research design and execution. For example, delineating the different perspectives on the conservation of folk varieties as clearly as possible enhances researchers' ability to ask fundamental questions that will best improve our understanding of the conservation process, its potential, and its utility to both farmers and conservationists.

Perspectives on the Conservation Process: An Example

The genetic implications of these different perspectives in terms of conservation goals in general and for specific aspects such as the conservation process itself have not been addressed in the past. From the conventional perspective it is assumed that conservation, accomplished almost exclusively *ex situ*, generally maintains the genetic fidelity of crop genetic resource collections unaffected by genetic changes (NRC 1991:76). From the farmer perspective, a requirement for conservation to meet their needs is that populations remain locally adapted and thus able to produce an acceptable harvest, and be capable of responding to changing local conditions. To understand whether the conservation process is addressing the concerns of either perspective requires first identifying some of the problems that may occur during that process.

Two significant threats to the conservation of crop genetic resources are genetic drift and genetic shift. Genetic drift is the random change in allele frequencies resulting from the sampling process (Falconer 1989:51), and represents a reduction in effective population size and allelic diversity. Genetic drift operating in two or more subpopulations may result in differentiation between those subpopulations; similarly, genetic drift operating in one subpopulation will result in its being different from the larger population from which it was drawn. The extent of the loss of diversity and the effect on population structure will depend on the severity of the population size reduction and the number of generations that reduction persists (Ellstrand and Elam 1993).

Genetic shift, the natural selection that occurs during *ex situ* seed maintenance and multiplication (Breese 1989), has been a specific concern of crop genetic resource conservationists and formal plant breeders. Selection changes population structure and can reduce allelic diversity. Its specific effect will depend on the heritability of the traits affected by selection, selection intensity and duration, and the population's original diversity and structure (Falconer 1989:192). Although selection is seen as a threat to the *ex situ*, static preservation of allelic diversity from the conventional perspective of formal breeders and conservationists, folk varieties are produced and maintained by natural and artificial selection, constant features of the *in situ* environment. For *in situ* maintenance to support local farming systems, therefore, the key is to keep selection coefficients sufficiently high to maintain local adaptation while still low enough to conserve as much genetic diversity as possible. "The difficulty," as stated by Frankel, "is to find the borderline between adaptive change and genetic erosion" (Frankel 1970:476). Thus genetic drift may occur *in situ* but

Table 8.1. Contrast of first and most recent regenerations of USDA Hopi kokoma and blue maize varieties conserved ex situ.

Characteristic	ORTHOGONAL CONTRAST (F VALUE)	
	USDA Kokoma 1956 vs. USDA Kokoma 1989	USDA Blue 1954 vs. USDA Blue 1985
Plant height	6.5*	9.22*
Central spike length	0.25	19.55*
Tassel branch region	9.8*	14.76*
Primary tassel branches	39.44*	1.98
First tassel	1.1	5.46*
Second silk	18.63*	0.03
Second tassel	4.66*	0.20
Ear length	5.60*	6.21*
Ear ratio (diameter/length)	0.98	4.60*
Kernel width	2.07	108.40*
Kernel length	18.72*	1.50
Kernel ratio (width/length)	27.10*	46.98*

Source: Soleri and Smith (1995).

*Contrast is significant at 0.05 level.

genetic shift will not. Both genetic drift and shift may occur ex situ during storage as well as regeneration (see, for example, Roos 1984a, 1984b).

An example of how concerns for the conservation process and threats to genetic diversity such as genetic drift and shift may differ based on the conservation perspective is discussed in a comparison of the in and ex situ conservation of two Hopi Native American maize varieties (Soleri and Smith 1995). In that research, data on the morphological and phenological characteristics of two Hopi maize varieties conserved in situ by Hopi farming households, and the same varieties conserved for over thirty-five years ex situ in Ames, Iowa, by the USDA/ARS/NPGS (U.S. Department of Agriculture/Agricultural Research Service/National Plant Germplasm System) were used to test hypotheses regarding change during ex situ conservation of a variety and differences between in and ex situ populations of the same variety.

The first hypothesis regarding change during ex situ conservation was tested by comparing early with later USDA regenerations (seed multiplications)

Table 8.2. Example of first phenological characteristics of populations of USDA Hopi blue maize conserved *ex situ*.

Population	MEAN ± STANDARD ERROR ^a	
	First Tassel (c.v. = 17.2%)	First Silk (c.v. = 32.6%)
1954 regeneration	3.0 ± 0.2	2.5 ± 0.2
1962 regeneration	3.7 ± 0.1	3.2 ± 0.2
1973 regeneration	3.7 ± 0.1	3.4 ± 0.2
1985 regeneration	3.9 ± 0.1	3.6 ± 0.2

Source: Soleri and Smith (1995).

^aScored on a scale of 1–5 (1 = least advanced stage of development; 5 = most advanced stage of development) sixty-four days after planting.

of a variety. For both varieties used in the study, Hopi blue field maize and Hopi kokoma, a purple-kerneled field maize, significant differences between first and most recent regeneration were found for a majority of the traits documented (table 8.1; Soleri and Smith 1995).

These phenotypic differences likely represent changes in allele frequencies and allelic complexes between populations and the possibility of allele loss. An unreversed and linear change in first tassel phenology (timing of male inflorescence development) was observed in the USDA blue maize populations, suggesting that a genetic shift may have occurred (table 8.2). No significant differences were observed among the 1962, 1973, and 1985 USDA blue regenerations for days to first tassel or first silk (female inflorescence). However, the first regeneration (1954) was significantly different from all later ones for both characteristics. Overall, with the amount of data available from that study, it is difficult to determine if those differences are due to genetic shift or genetic drift. However, it is worth noting that in terms of the conventional goal for folk variety conservation, the implied decrease in allelic diversity is a concern.

Because genetic drift is random, rare (presumably nonadaptive) alleles are eliminated sooner than are common (adaptive) ones (Breese 1989:40–41). This may be of particular concern from the conventional perspective, as researchers search collections for rare alleles that confer unique phenotypes such as resistance to specific pests. If the *ex situ* environment differs from the “native” one, as is typically the case, genetic shift may reduce or eliminate alleles that are common and adaptive in a population that originated elsewhere. Therefore,

Table 8.3. Contrast of Hopi kokoma and blue maize varieties conserved in situ (Hopi) and ex situ (USDA).

Characteristic	ORTHOGONAL CONTRAST (F VALUE)	
	Hopi Kokoma vs. USDA Kokoma 1989	Hopi Blue vs. USDA Blue 1985
Plant height	15.48*	0.18
Central spike length	10.87*	0.69
Total tillers	5.16*	5.60*
First tassel	8.95*	14.93*
Ear diameter	3.87*	2.37
Ear length	6.39*	1.30
Ear ratio	0.60	3.77*
Kernel width	89.81*	0.58
Kernel length	55.45*	6.13*
Kernel ratio	0.15	6.11*

Source: Soleri and Smith (1995).

*Contrast is significant at 0.05 level.

when folk varieties are conserved ex situ, the greatest concern for farmer conservation goals may be the changes resulting from genetic shift as compared with genetic drift. For example, the timing of reproductive development associated with local adaptation, and often expressed as photoperiodicity, can be extremely important for low-input farmers in marginal areas (Cromwell et al. 1993:44-45).

The second hypothesis, that in and ex situ populations of the same variety are significantly different, was supported by the research findings (table 8.3; Soleri and Smith 1995). This was tested by comparing in situ populations of a variety with the most recent ex situ regeneration of that same variety. There are several possible reasons for the differences observed, and the actual cause could not be determined from this study. However, their difference may be due to the difference between in and ex situ environments and raises questions about the relevance of conventionally defined ex situ conservation for meeting farmers' needs.

Discussion of different genetic goals for conservation is just beginning, and ideas need to be developed and tested. However, this issue warrants attention both because the differences between industrial and traditionally based,

low-external-input agricultural systems are substantial, and because of the growing interest in low-input agriculture and support for traditional agricultural communities (Ceccarelli et al. 1992b, 1994; NRC 1989). A growing number of organizations are conducting research and development efforts that will have to address this issue (see, for example, CLADES et al. 1994; Hodgkin et al. 1993; Lamola and Bertram 1994). Ideas for developing research questions useful for a farmer-breeder perspective on folk variety maintenance by farmers are the subject of the next section of this paper.

Research Questions for a Farmer-Breeder Perspective

To date, the research conducted on farmer maintenance of their own folk varieties has not addressed the farmer-breeder perspective. Early work centered on this question: Why do folk varieties persist; that is, why are they retained by agricultural households and communities after the introduction of modern varieties? More recently, a number of descriptive studies of in situ conservation, especially on the number of farmer-named varieties of a species, have been conducted, including those on potato in Peru (Brush 1986; Zimmerer and Douches 1991), maize in southern Mexico (Bellon 1991), rice in Sierra Leone (Richards 1986) and northern Thailand (Dennis 1987), and Hopi Native American crops in the southwestern United States (Soleri and Cleveland 1993). All of these studies report the retention of folk varieties by the agricultural communities studied. The extent of this retention appears to vary with a combination of environmental and sociocultural factors that differ with each situation.

These studies have provided useful insights into farmer maintenance and dispelled the assumption (see, for example, Frankel 1970) that folk varieties would be completely abandoned when modern varieties became available. Yet these studies have also raised many questions, and none of them have investigated the topic from a farmer-breeder perspective. For those interested in supporting farmer management of folk varieties for use in their own agricultural systems, and local crop improvement, it will be valuable to understand farmers' selection practices and to characterize the folk variety populations that are the product of that selection.

Discussion in the following sections focuses primarily on cross-pollinating species, although minor revisions would make it relevant for self-pollinating species as well.

Describing Farmer Selection

Just as the effectiveness of local selection is increasingly acknowledged by plant breeders (Ceccarelli et al. 1992a, 1994; Simmonds 1991b), collaborating with existing artificial selection by the farmer-breeders of the local agricultural community is also being recognized as important for developing crop varieties appropriate for local needs (Maurya et al. 1988; Sperling et al. 1993; Women of Sangams Pastapur and Pimbert 1991). Describing farmer selection practices is important for supporting the farmer perspective for two reasons. First, it is these practices that combine with natural selection to create folk variety populations (Harlan 1992). Second, these practices are the starting place for farmer and researcher collaboration to enhance local crop improvement efforts. Collaboration that builds on those practices is critical to ensure that farmers not only participate but also guide research and development.

Farmers' crop selection practices have not been well studied. The work by Richards (1986) with the Mende rice cultivators of Sierra Leone is the best documentation of systematic farmer selection and experimentation with their folk varieties. He reports local classification systems in which farmers divide their seventy named rice varieties into three classes according to length of their growing cycle and suitability for specific soil and water conditions (Richards 1986:134). Small trial plots were used to evaluate new varieties or selections, and farmers conducted germination tests for seed viability. Artificial selection was applied both through roguing in the field and separate conservation of promising new phenotypes (p. 139).

The effect of artificial selection, resulting from farmer practices, will depend on how and when farmers do their selecting, and the genetic structure of the crop populations. Farmer selection is generally assumed to occur as mass selection. That is, based on each plant's phenotypic performance, individual plants are selected to provide seed for the next generation (Simmonds 1979: 135-42). This process may be repeated each generation.

Mass selection, especially practiced over many generations, can be effective and has been the primary basis of crop improvement since domestication. However, the rate of that improvement depends heavily on the heritability of the trait, which must be high, as selection for traits that are not the product of recombination in cross-pollinating species is based solely on maternal genotypes. For these species the heritability is half of what it would be if the paternal genotype were also selected (Simmonds 1979:139). Although heritability will vary among traits, populations, and environments, the highly heteroge-

neous environments characteristic of most low-input agricultural fields will also make heritability lower than it would be under more uniform conditions. Thus, if for example, there is little genetic variation for a trait being selected for, or the heritability is extremely low, or if the alleles for two traits being selected for are not genetically correlated in a positive way, selection will be ineffective. Farmers also select their seed sources, which can have an effect on their crop populations. Seed acquisition and distribution practices offer clues to the extent of local adaptation, size of the gene pool, and other issues important for farmer management. For all of the reasons described above, understanding the selection process is part of assessing the potential for improving local crop development.

There is little descriptive information regarding selection and seed distribution practices that will affect population structure. To understand farmer maintenance of folk varieties and its genetic consequences, descriptive information is needed about artificial selection that addresses the following questions:

What traits do farmers use to distinguish among their varieties?

What selection criteria are being used?

When does selection occur—before or after fertilization? in the field? at harvest? during processing?

What are farmers' seed/propagule sources?

What are farmers' planting patterns?

Both artificial and natural selection operating on individual genotypes change allelic frequencies and thus the amount and structure of crop genetic diversity within and between folk variety populations and human communities. Characterization of folk variety populations—specifically, understanding the distribution of the diversity that is important for local adaptation and agronomic performance—is the other information useful for contributing to a farmer-breeder perspective on local folk variety management.

Characterizing Folk Variety Populations

Characterizations of folk varieties are limited. Exceptions to this are work by population geneticists, plant systematists, and plant breeders who have evaluated the genetic diversity of field collections of folk varieties and of their nondomesticated relatives. These studies focus on gaining insights to improve collection strategies for ex situ conservation (Brush et al. 1995; Zimmerer and

Douches 1991), the evaluation of the material for use in breeding programs (Chen et al. 1994; Smith et al. 1995; Wilson et al. 1990), or on insights into the evolution and historical geography of the species (Doebley et al. 1983; Garvin and Weeden 1994; Gepts et al. 1992). All of these studies build upon the consensus that in general, folk varieties contain higher levels of both inter- and intravarietal genetic diversity than do modern variety populations of the same species (see, for example, Frankel and Soulé 1981:201).

But characterization of folk variety populations specifically for supporting the work of farmer-breeders remains to be done. The areas important for such characterizations are these varieties' genetic variation and the structure of that variation—that is, how it is organized in genotypes and distributed within and between populations of a variety. In this section we will outline why genetic variation is valuable from a farmer perspective, and briefly discuss the four other factors in addition to selection that affect folk variety population structures: history of the species in the region, population size, gene flow, and geographic distribution. Although many of these areas have rarely been studied in folk varieties, research on nondomesticated plant species provides some insights into their significance.

Genetic variation, or lack of inbreeding, is considered an important measure of viability and stability of wild plant populations (Ellstrand and Elam 1993; Huenneke 1991). Exceptions to this may be found in some self-pollinating species or species with a long history of small population size, in which frequencies of deleterious genotypes and alleles have presumably been reduced by selection. Similarly, and as mentioned earlier, genetic variation can support a crop variety's ability to survive biotic stresses such as pests and pathogens in their growing environment (Gould 1988, Simmonds 1991a), and is seen as a source of relative yield stability for folk varieties grown in low-input agricultural systems (Ceccarelli et al. 1992b; Cleveland et al. 1994). Genetic variation is important for assessing the potential for microevolutionary change in the future, determining conservation or management strategies, and in the case of folk varieties, aiding local crop improvement efforts. As mentioned, measures of heritability will also be important for determining effective selection criteria for local improvement.

The distribution and structure of intravarietal diversity within and between communities is important because it reflects the consequences of folk variety management, including the effects of natural selection. For example, comparisons of varietal population structure can be made between households or communities. The household is often seen as the primary production and

consumption unit and therefore a critical decision making body whose actions affect its environment and resources (Netting 1993). There is reason to believe that this includes the persistence of folk varieties and how they are structured genetically (Bellon and Taylor 1993; Richards 1986; Soleri and Cleveland 1993). There is evidence suggesting that in some cases varietal management and conservation may also operate at a community level (Dennis 1987).

However, investigations of genetic diversity and population structure are typically conducted at the level of the individual accession or population and are concerned with describing overall regional diversity or comparing diversity between regions. Variation at the level of the populations being grown by individual households or communities is rarely the focus of study. Exceptions are two studies of isozyme variation of Andean potato folk varieties (Brush et al. 1995; Zimmerer and Douches 1991). Both those investigations found the majority of allelic diversity to occur within populations of a variety, while genotypic diversity was greatest between populations of the same variety grown by different farmers. The high intrapopulation allelic diversity is thought to be the result of both specific growing environments and management practices that allow recombination to occur in this predominantly vegetatively propagated crop, and maintain its products in the local population of a variety. Genotypic diversity between populations may represent the natural selection forces of different growing environments that favor particular allelic complexes over others (Allard 1988).

Still, as with investigations of intervarietal diversity, these studies focused on evaluation of the populations for determining sampling strategy for *ex situ* collections. Thus their choice of how to measure genetic variation and their discussion of its significance are based on the conventional approach to folk variety conservation.

Overall, data regarding the simplest descriptions of the structure of subpopulations of a folk variety between households or between communities, or comparisons of these for two or more coexisting varieties, have simply not been available (Frankel and Soulé 1981:201). Instead this information must come from the application of theoretical models (see, for example, Marshall and Brown 1975, 1983) or from research in the population genetics and conservation biology of nondomesticated species that in some cases parallel the situation with domesticates, although that too is very limited (Millar and Libby 1991).

In addition to selection, theory and the available empirical evidence indicate that several other factors will affect the structure of folk variety popula-

tions in cross-pollinating species. The evolutionary/cultivation/utilization history of the species in the region of interest provides a theoretical baseline for the relative amount of genetic variation that might be expected (Karron 1991). For example, the center of origin of pearl millet is believed to have been Saharan or sub-Saharan Africa, especially West Africa, with the Sahelian region recognized as the major center of diversity for that species (Brunken et al. 1977). Pearl millet is thought to have reached the coast of what is today western India in 2900 B.P. Given this history, it is likely that the Indian pearl millet gene pool has a reduced level of genetic variation relative to the original African gene pool (founder effect). The extent of this reduction and its mitigation since founding depend on a number of factors.

First, the amount of seed introduced and the variability of the population or populations from which it was taken are unknown. Second, the number and size of subsequent introductions are also unknown. Third, during the nearly three millennia since introduction, the genetic variation of those original founding populations has most likely been augmented by mutation and altered through selection. Using the commonly cited mutation rate of 10^{-5} loci/generation (see, for example, Falconer 1989), assuming one generation/year indicates that almost 3 percent of loci may have experienced mutation since the introduction of pearl millet into Asia.

Reduced population size can have a significant effect on population diversity and structure (Ellstrand and Elam 1993, Menges 1991). Genetic drift results in a small effective population size (N_e) and can occur in an agricultural system when social or biological factors in that system result in the random loss of genetic resources. Genetic drift represents the loss of genetic diversity, specifically in the form of allelic polymorphisms, and over the long term, loss of heterozygosity. Where genetic drift occurs in a population divided into smaller subpopulations, genetic variation is also reorganized, as it is dispersed between those increasingly different subpopulations.

Gene flow, the movement of genetic material between populations, can have a significant effect on plant population structure (Ellstrand and Elam 1993). Gene flow in agricultural systems occurs not only through the dispersion of pollen and seeds by natural agents but also through human-managed seed distribution that can have a large effect on how genetic variation is partitioned among populations of a variety between households, communities, or regions. Ellstrand and Elam (1993:230) found gene flow of over half of rare plant species they surveyed in California to be sufficient to effectively homogenize allele frequencies between populations of a species, and cited gene flow as

an important organizer of genetic variation in those species. In the case of folk varieties of a crop species, gene flow could affect the organization of genetic variation within a variety as well as between varieties (varietal purity). Gene flow between local folk varieties and between a folk variety and a cultivar developed outside the area are possibilities for cross-pollinating crop species. The first case will affect the composition of the varieties and be affected by the number of varieties being grown, and farmers' criteria for varietal purity and methods for maintaining this.

Gene flow between local folk varieties and a relatively recent, conspecific introduction may be a valuable source of additional diversity, or it may have consequences for the adaptation of the folk variety populations that are contaminated. How then is the possibility of gene flow between local folk varieties and nonlocal introductions treated *in situ*? Although this was not addressed directly in that study, it appears that maize farmers in Chiapas, Mexico, did not prevent the mixing of local folk varieties and both open-pollinated and hybrid nonlocal introductions (Bellon 1991). On the other hand, numerous Hopi maize farmers expressed concern regarding the possibility of "contamination" of their Hopi varieties by nonlocal introductions (Soleri and Cleveland, unpublished notes). However, whether this concern is effectively addressed in crop management is not clear.

Gene flow of "inappropriate" alleles may decrease the local adaptation of a population (Ellstrand and Elam 1993:231). This reduction in fitness will occur if the immigration of nonlocal alleles exceeds selection against those alleles. In the case of folk varieties this means that the assumption that genetic diversity has been augmented by the addition of modern varieties to traditional farmers' crop repertoires (see, for example, Brush 1991; Dennis 1987:266) should be reconsidered. While such gene flow may be a "beneficial" source of genetic variation, this is not necessarily so. Indeed, Angermeier (1994) argues that biodiversity as a goal must not always be equated with absolute genetic diversity because there are inherent features of "native diversity" that make it superior to exotic diversity in terms of societal value and evolutionary potential. To the extent that those features contribute to cultural preferences, local adaptation, and evolutionary potential, the same could be postulated about gene flow from recently introduced cultivars to folk varieties.

Finally, geographic distribution can also influence genetic variation with widespread populations tending to have greater genetic variation than do those with a narrower distribution (Ellstrand and Elam 1993:219). This may also be reflected in differences between farmer-named varieties that are regionally

common on the one hand, and those confined to a specific location on the other.

Characterization of folk varieties to obtain information more relevant to the needs of farmer-breeders could include evaluation of traits and genotypes important for local adaptation and agronomic performance, especially those identified by local farmers; statistically significant comparisons of folk variety subpopulations between households and between communities; comparisons of groups of traits, or groups of genotypes (depending on the mating system) of subpopulations of the variety. Examples of questions that might be asked are:

Do populations of the same folk variety differ within a community? between communities in a region?

Do two or more folk varieties differ from one another within a community? between communities?

Is genetic variation favored by farmer selection criteria?

What is the heritability of traits favored by farmer selection criteria?

Conclusion

Being aware of the assumptions underlying our research approach will enable those working with the conservation of folk crop varieties to design and conduct research more effectively and to provide information and methods that are relevant to the people who are using those resources. To address the needs of traditionally based, low-external-input agricultural communities requires taking a different perspective on folk variety conservation than is usually assumed. This farmer-breeder perspective recognizes that the local varieties and the genetic diversity they represent are an important part of the current farming system. Folk varieties are not a genetic resource that is being “conserved” in the conventional sense for future use, but rather the actively managed genetic component of the system that is constantly being used and changed.

From this new perspective, it is possible to return to basic concepts from fields such as population genetics and conservation biology and determine their meaning for understanding and asking questions of relevance to farmer-breeders. An emphasis on locally focused research and on farmer participation and collaboration favors the development of relatively rapid, inexpensive, and accessible research methods. Perhaps by approaching local crop improvement as a collaboration between farmers and outside researchers, both of whom manage crop populations, though in different ways, farmer knowledge may be

more widely recognized, breeding efforts made more relevant and useful, and local control and continuation of the improvement process become more likely.

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