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# GENES in the FIELD

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On-Farm Conservation  
of Crop Diversity

Edited by  
Stephen B. Brush

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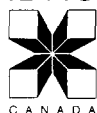
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of Crop Diversity

Edited by  
Stephen B. Brush, Ph.D.



**INTERNATIONAL PLANT GENETIC  
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# *The genetic structure of crop landraces and the challenge to conserve them in situ on farms*

*Anthony H. D. Brown*

## *Introduction*

*In situ* conservation of agricultural biodiversity is the maintenance of the diversity present in and among populations of the many species used directly in agriculture or used as sources of genes in the habitats where such diversity arose and continues to grow. Broadly, the species targets of on-farm genetic conservation include cultivated crop, forage, and agroforestry species, as well as the wild relatives of cultivated species that may be growing in adjacent disturbed sites. This chapter, however, will discuss primarily on-farm conservation of cultivated species as distinct from spontaneously growing populations. The main targets are the landraces or heterogeneous crop populations that humans deliberately cultivate: those that are not the products of modern plant breeding or subject to purifying selection. Planning for the conservation of this kind of biodiversity *in situ* is novel and contentious. The conventionally accepted role for *in situ* strategies in genetic conservation has been in the conserving of wild species. In contrast, *ex situ* collections are the predominant strategy for conserving the genetic variation of cultivated species (Frankel and Soule 1981; Marshall 1989).

For the on-farm conservation of domesticated species, the traditional cultures and cropping systems that grow and use such populations are fundamental aspects of the habitats to which they are adapted. The systems shape their present genetic structure and determine the changes within landrace populations. Hence, farmers are crucial partners in the process of



*in situ* conservation. “*In situ* conservation specifically refers to the maintenance of variable populations in their natural or farming environment, within the community of which they form a part, allowing the natural processes of evolution to take place” (Qualset et al. 1997:165).

Impetus for the plant genetic resources community to turn its attention to *in situ* conservation of cultivated populations on farms has arisen from diverse sources. Perhaps most evocative have been recent studies of crop diversity that indicate much diversity still persists on farms in regions known as centers of diversity, despite the advent of modern cultivars of crops to those areas (Brush 1995). The Rio Convention on Biodiversity (United Nations 1992) has underlined the challenge for each country to husband its genetic resources so that countries are not solely dependent on a few *ex situ* collections or on foreign public or private breeding programs.

There is now widespread recognition of the need to plan for *in situ* conservation to continue and indeed to improve its capacity to maintain genetic diversity as an adjunct to conservation in *ex situ* collections. The need for efficiency is likely to increase as the areas currently devoted to traditional varieties are subject to increasing pressures to convert to advanced cultivars. Equally, there is recognition that the scientific basis and the optimal procedures for on-farm conservation are lacking. As a basis for guiding the supporting research in population biology for on-farm conservation, this chapter reviews recent studies of the genetic structure of landraces of crops in relation to the special advantages attributed to *in situ* conservation of these genetic resources.

### *Postulated advantages of in situ conservation of landraces*

The *in situ* approach to conserving landraces is reputed in the literature to hold several important advantages over *ex situ* strategies. These advantages form a convenient framework for developing a research agenda, and for optimizing methods. In seeking to strengthen the scientific basis of *in situ* conservation, we should critically assess the nature and extent of evidence that currently support these advantages. They form the hypotheses to which research should be directed. The advantages are:

1. **Conservation of indigenous knowledge** — Farmers are central participants in the *in situ* effort. The conservation of crop genetic diversity on farms retains the diversity within its proper ethnobotanical context. At the same time, on-farm conservation maintains indigenous knowledge about the farming systems and agricultural practices that retain diversity and knowledge about direct uses of that diversity. Unfortunately, there is relatively little information about the dynamics of this kind of indigenous knowledge.
2. **Conservation linked with use** — On-farm conservation is closely connected with use directly by the farmer for food or sale. Other uses of such populations, either as the source of elite sub-lines or as donors

of characters in advanced breeding programs, require development and monitoring. The use of genetic resources conserved in collections *ex situ* has been a matter of concern, particularly if collections are underutilized and vulnerable to loss of support (Brown et al. 1989).

3. **Allelic richness and genotypic diversity** — On-farm populations have the capacity to support a much greater number of rare alleles and of different (multilocus) genotypes than accessions in gene banks (Marshall 1989). For this feature to apply, large numbers of individual plants with autonomous ancestry must be grown over significant areas. This suggests the need for and importance of measures of the area devoted to landraces, the numbers of populations and their sizes, and the genetic diversity for marker loci, disease resistance, and morphological traits.
4. **Special adaptations** — The *in situ* strategy conserves a unique constellation of germplasm, particularly for marginal or stress environments. This provokes the question of how populations on the farm relate to material already in *ex situ* collections generally, and stored accessions from that specific region. An important indicator of the distinct value of *in situ* populations is the relative ease with which new cultivars are extracted simply and directly as controlled selections out of the variable unimproved populations.
5. **Localized divergence** — The *in situ* strategy conserves genetic variation on a relatively fine spatial scale, in theory down to the individual field. This capacity, however, raises the question of what scale of divergence is reached in practice. Further, the long-term and broad significance of fine-scale differentiation is open to question. Is it important to maintain separate populations aimed at conserving fine-scale differences separately? It is unlikely that such subtle differences will have any use in breeding programs.
6. **Diversity to meet temporal environmental variation** — Diversity itself confers long-term population fitness because it helps populations to cope with variable environments. Landrace populations of crops have survived centuries of selection for reliable production in subsistence agriculture, yielding a definite, known but probably limited benefit to the farmers that grow them (Frankel et al. 1995). Presumably they are selected for resilience and stability though modest productivity, rather than outstanding productivity in the more favorable years.
7. **Continuing crop evolutionary processes** — The *in situ* strategy conserves the crop evolutionary processes (mutation, migration, recombination, and selection). It provides scope for ongoing evolution, particularly in response to environmental changes and pathogen and pest pressures fluctuating in numbers and genetic composition. The key variables are (i) genetic diversity within populations, which is the essential raw material for evolution; (ii) breeding system variation (such as changes in outcrossing rate); (iii) variation in resistance in

- space and time, related to pest pressure and diversity; and (iv) the dynamics of seed systems, persistence, and migration.
8. **Avoidance of regeneration** — Regeneration of *ex situ* collections is currently considered a serious and enormous challenge (Brown et al. 1997). Viability is inevitably lost at rates depending on the resources for and the management regimes of such collections. The task is to regenerate accessions without incurring genetic drift (from small samples) or genetic shift (from inadvertent selection in an environment remote from the origin of the accession) (Breese 1989).
  9. **Human involvement** — In on-farm conservation, the effort is shared among many players and is thus less dependent on the commitment of one institution or country. However, steady if not rapid rural and social change can occur over wide areas with attendant loss of genetic diversity. Zeven (1996) recounts how prewar recommendations to conserve European landraces *in situ* were entirely disregarded and these populations disappeared. This experience led him to be skeptical of maintenance *in situ* in the longer term, without continuing support and a direct benefit to farmers.
  10. **Control and benefit sharing** — Local control of landraces and access to them can ensure that benefits, if any, accrue to the farmers and communities that developed them. This requires workable and not unduly restrictive policies of access.

In summary, Numbers 1 and 2 are comparative advantages that refer to farmers, Numbers 3 to 7 refer to the genetic structure of landraces themselves, and Numbers 8 to 10 refer to management issues and the policy environment. We now turn to evidence and research explicitly aimed at understanding the genetics of landrace populations.

### *Scientific research issues that underpin on-farm conservation*

Worede (1997) among others has pointed out that *in situ* conservation of landraces is already happening. Considerable evidence attests that farmers in various regions of crop diversity [e.g., cereals in Ethiopia; maize and potatoes in Peru; rice in Thailand (Brush 1995)] are growing local diverse varieties, often in small patches amid modern cultivars. This suggests the first important research question is to discover why farmers continue to do so.

### *Why are traditional varieties being grown without external financial inducements?*

Several reasons are likely to apply: advanced varieties may not be available or affordable; advanced varieties may not represent an advance for a particular farmer or meet the farmer's needs reliably; and traditional varieties have

cultural or aesthetic appeal or occupy a market niche. More survey evidence, however, is needed to answer this question fully, particularly to gauge how often landraces are grown because of the lack of other varietal options as opposed to more positive reasons such as the filling of special needs.

Qualset et al. (1997) noted that landraces continue to be grown but in shrinking-sized, minority patches. The temporal dynamics of such landrace patches (the extinction-recolonization cycle of fragmentation theory) is as yet little known. Fragmentation arises from the conversion of the land to exotic cultivars, to other cultivated species, to other land uses, or altered agricultural systems. The authors note the likely dynamic factors to include in a study of the retention of landraces at the landscape level are the division of land holdings within families, marginal agricultural conditions associated with hill lands, heterogeneous soils, economic isolation, niche market premiums, cultural values, and specific uses and preference for diversity. The parameters of this area of research suggest the need to draw on both anthropological and genetic expertise and the interaction between them.

To understand the dynamics of local crop diversity in farming systems, we need to relate farmers' decision making to the pool of varieties available for planting. Bellon (1996) outlines a framework to accomplish this. The framework assumes that the farmer has several concerns, including adverse climate, soils, labor or fertilizer shortage, poor yield or storage life, and lack of appeal for home use or lack of marketability. The farmer's experience enables him to rank the populations or varieties available for planting for meeting these concerns. In population genetic terms, the farmer's concerns generate a mult niche model with different populations being differentially adapted to each niche. Bellon hypothesizes that the farmer retains the variety that best meets each concern. A variety is discarded if it no longer ranks first in meeting anyone of the concerns. Overall, a suite of varieties is needed to meet all of a farmer's concerns. The concerns themselves are dynamic, changing with new market structures, technology, and government policies. Bellon's model thus suggests that the focusing or narrowing of concerns at the farm level may be the trigger for loss of diversity. A challenge for this model, however, is the relative size of each niche, and the integration of concerns across the whole farm when survival — for example, during drought — becomes overriding.

### *Indicators of the genetic composition of landraces*

The next major question is to assess the genetic diversity of populations still *in situ*. How genetically variable are the landrace populations currently growing on farm? How much do they differ in their genetic makeup from one another and from scientifically bred varieties, in terms of the particular alleles and the level of variation they contain?

Genetic diversity and divergence require assessment for two sets of attributes, analogous to the characterization and evaluation data of genetic resources. The first set is *marker diversity*, or the extent of differences between

individual copies of genes. The differences should be detected as close as possible to the DNA level, for a sample of homologous sequences representative of various classes of sequences (nuclear, organellar, structural, control, spacer). This set of attributes is informative as to the ancestry or breeding history of the populations. They are indicators of the recency of bottlenecks in population size, the prevalence of outcrossing, the ease with which genes are recombined, and the level of gene flow between populations. The second set is *variation in adaptation*. This set comprises indicators of the degree to which populations are adapted to their environment and of their potential for continued performance or donors of characters in plant breeding. Both biotic and abiotic aspects of the environment are involved.

### *Marker diversity*

Hamrick and Godt (1997) have recently summarized the published estimates of genetic diversity based upon the allozyme data for crop species. Typically in such studies, the summary measures are observed heterozygosity, expected heterozygosity (gene diversity), and number of alleles detected per locus (allelic richness). While most similar studies are based on gene bank material, breeders' collections, or cultivars, this study is particularly useful for indicating broad trends. Crop species on average have *more* genetic diversity than wild plant species at the species level, although they generally are *less* diverse than their close wild relatives. Populations of crop species are more genetically divergent among themselves than are those of wild species both in the alleles they contain and in their differences in levels of diversity between them. In broad terms, this reflects the effect of breeding system, range expansion, and diversifying selection through human agency.

Examples of studies of marker diversity (allozymes, RFLPs, RAPDs) in landraces are those in barley (Brown and Munday 1982; Bekele 1983a, b; Demissie and Bjornstad 1997); maize (Doebley et al. 1985; Geric et al. 1989); and cotton (Brubaker and Wendel 1994). Bekele (1983a) estimated allozyme diversity in 158 landrace populations of barley in Ethiopia. About 20 individuals per population from 72 areas distributed among 19 regions in Ethiopia were assayed for isozyme variation at five loci. Diversity is measured as the probability that two seeds drawn from within a population, or from two different populations, etc., will differ at a locus. The diversity had a well-developed hierarchy with average gene diversity within localities of 0.163; between localities within areas of 0.236; between areas within regions of 0.304; and, at the broadest level, between regions of 0.363. Assuming equilibrium under the island model of migration, these estimates of diversity translate to migration rates of 0.6, 0.8, and 1.3 migrants per population per generation, respectively.

Far fewer studies are available on the multilocus structure of landrace populations, that is, the extent to which genetic variants at one locus are correlated in occurrence with variants at another. Such structure arises from selection, genetic drift, or fragmentation of the population, and is retained through selection, isolation and the lack of migration, and restrictions on

outcrossing and genetic recombination. Bekele (1983b) computed Brown et al.'s (1980) standardized variance measure to assess multilocus association within the regions of Ethiopia sampled. The average of the 17 median values indicated a 70% inflation of variance due to correlation of alleles at the different loci within regions. This value is comparable to that for natural populations of *Hordeum spontaneum* (80%). Part of the association among loci in landraces would be due to differentiation among the populations sampled within each region. A major cause, however, would be the "metapopulation structure" of landraces over a whole region, in which sporadic replanting (colonization), introduction from elsewhere, and migration (gene flow) oppose local extinction and divergence in individual fields. The mating system of predominant self-pollination greatly slows the decay of the resulting disequilibrium, as well as assists in the retention of any adaptive combinations of alleles at loci governing adaptive traits.

Despite the expense and effort required, estimates of marker diversity are instructive as to the "coancestry" of homologous genes in individuals and populations of landraces, and the evolutionary forces that affect the whole genome. However, not all populations of all landraces conserved *in situ* can be subject to genetic analysis. The challenge is to develop a structured representative sample of such studies, from which general extrapolation to other similar populations will be reasonably sound. The key parameters in developing such a sample would be those that Hamrick and Godt (1997) have shown as useful to structure genetic data, namely breeding system, life history, taxonomy, range, isolation, and dispersal.

### *Variation in adaptation*

Much evidence and experience attests that landraces are adapted to their local environments (Frankel et al. 1995). If they come from marginal environments, they are known to match or better the performance of imported advanced cultivars in those marginal environments (Weltzien and Fischbeck 1990). Many studies have readily detected broad-scale geographic differences between landraces from different regions within a country [e.g., yield and seed-size lentils in Ethiopia (Bejiga et al. 1996); stress tolerance and stem solidity in durum wheat in Turkey (Damania et al. 1997)]. Weltzien (1989) analyzed the geographic patterns in barley landraces from Syria and Jordan for morphological and developmental traits. Nine groups of landraces were defined based on similarity of traits. Each group showed a close association to specific geographic or environmental factors. These results emphasize the importance of recording the locations of origin of samples and the reality of groups based on such data (see Ceccarelli and Grando, this volume).

Assessment of landrace populations for comparative yield and for components of yield is important for both the immediate local use of the material in participatory reselection and breeding programs, and the wider international valuation and use of the germplasm. For example, Moghaddam et al. (1997) analyzed the genetic variation for yield, its components, and other developmental traits in lines extracted from seven landraces of bread wheat

from Iran. They found most of these characters had high levels of genetic variance. They concluded the landraces could readily be improved by identifying and intercrossing the promising genotypes.

Resistance to diseases and pests are characters of widespread use, and the number of studies of resistance in landraces to exotic or to local strains of pests is growing. Here the major research issues are the scale of pattern of variation, the relative importance of major, race-specific resistance, and the relation between reaction to exotic vs. endemic pathotypes. Pronounced patterns on a macrogeographic scale are likely, with resistance common in the same areas and lacking in others. Such patterns occur because of the conjunction of genetic diversity in both the host and the pathogen species, and an environment favorable for both. A striking example is that for resistances to rust and late leaf spot in peanuts, caused by *Puccinia arachidis* and *Phaeoisariopsis personata*, respectively. Subrahmanyam et al. (1989) screened the *Arachis hypogea* germplasm accessions conserved at ICRISAT. Some 75% of the resistant accessions originated in Peru, particularly the Tarapoto region.

Ethiopian landraces of barley have been tested for resistance against two major pathogens. For *Puccinia hordei*, Alemayehu and Parlevliet (1996) found a near absence of race-specific, major resistance and a high frequency of moderate levels of partial resistance. This showed itself as pronounced variation between and within land races in latent period, a multigenic character.

The picture for this pathogen contrasts with that for *Erysiphe graminis hordei*, the causal agent of powdery mildew in barley. Negassa (1985) examined 421 landrace samples from 12 provinces of Ethiopia for their infection type response to seven stock cultures of powdery mildew. Resistance was prevalent: only 9% of samples were fully susceptible to all cultures and nearly 30% were resistant to all seven. About 70% had a single gene for resistance and a further 20% had two genes. The more surprising findings of this study were (1) the high frequency of populations with just a single resistance gene, implying that the pyramiding of many resistance genes was "of limited importance ... in subsistence agriculture" in this pathosystem; (2) that typically each accession was uniform in mildew reaction, implying that resistance polymorphism is an infrequent strategy; and (3) that almost all resistance genes confer incomplete resistance rather than immunity.

On the other hand, Jones and Davies (1985) tested the response of 39 old European barley varieties to powdery mildew. They were found to lack major genes for resistance (no hypersensitive seedling response). When tested for adult plant resistance in field nurseries over 3 years, the mean percent leaf damage ranged from 11 to 50%, which they suggested indicated a useful source of non-hypersensitive resistance. If, however, such resistance is multigenic, it would be difficult to breed into other cultivars.

### *Changes in time in population genetic structure*

One advantage to conserving *in situ* that many advocate is that it provides for dynamic conservation in relation to environmental changes, pests, and

diseases (Maxted et al. 1997). *In situ* conservation is a dynamic process. While the particular attributes, characters, or adaptations of a population may persist over generations, the underlying genotypes will change. New alleles or combinations are expected to arise and increase in frequency at the expense of other alleles that may well disappear. Strictly speaking, *in situ* strategies fail to preserve all the extant biodiversity at the gene level. As better alleles or combinations arise and enjoy selective advantage, others thereby will be less fit and decline. This is the cost of evolutionary substitution and the price paid for allowing evolution to continue. The likely flux of genetic variants in *in situ* strategies is of concern to some: Holden et al. (1993) argue that “museum farms” may not only fail to preserve the natural diversity that has evolved in the past, but the genetic changes in them may be unrelated to the needs of posterity.

Evidence of the nature, pace, and causation of genetic change during on-farm conservation is crucial to an understanding of on-farm conservation, and is virtually nonexistent. How rapidly do allele frequencies change, are alleles and genotypes lost, or do whole populations go extinct, locally and absolutely? What are the roles of stochastic events as opposed to systematic forces in causing such changes? (The stochastic events include bottlenecks in population size, sporadic migration, variation in mating system. The systematic forces include farmer selection, both deliberate and inadvertent, mixing, and hybridization.) What is the impact of fragmentation and decreasing area on the genetic structure of populations? What are the dynamics of seed (gene) flow between populations (see Louette, Chapter 5, this volume)?

Recognizing that fragmentation and declining area are the major trends in landrace plantings, Qualset et al. (1997) suggest that the theory of island biogeography be invoked to determine the key variables that determine the dynamics of diversity. These are patch size, frequency of migration (seed exchange between farms locally or from outside sources), and the expected positive relationships between patch (island) size or isolation and diversity.

Whereas questions of causation are perennially difficult, new technologies open up new approaches. Clegg (1997) has recently discussed the struggle to measure selection acting upon plant genetic diversity. He notes:

The fundamental research program of population genetics has been to seek a quantitative assessment of the role of the various forces of evolution in shaping patterns of genetic variation .... New insights into the relative importance of selection and random genetic drift can now be obtained from samples of DNA sequences of genes drawn from within species. The elaboration of coalescence theory together with data on gene genealogies [from DNA sequences within and between species] permits an integration over long periods of evolutionary time [ ... and thus ... ] the detection of small selection intensities” (Clegg 1997:1).



In the future, these approaches are likely to be applicable to tracing the history and relationships of landrace populations.

### *Coevolutionary changes*

Perhaps the major impetus for *in situ* conservation of the biodiversity of use to agriculture is the suggestion that such strategies provide the opportunity for continuing coevolution. It is argued that continuing pathogen evolution will render obsolete the samples of resistance genes "frozen" *ex situ* in gene banks. This led to the claim that such diversity would be better "conserved" *in situ*, where new resistance might evolve to match any change in virulence structure of the pathogen. What is usually overlooked is the reciprocal argument that the presence of resistance genes in landraces "unfrozen" on-farm will inevitably evoke changes in the pathogen population that could equally render the resistances obsolete.

Holden et al. (1993:90) have questioned whether on-farm conservation can evolve "novel" resistance genes, because of the evolutionary resilience in growing traditional varieties in traditional ways. Genetic heterogeneity for resistance genes is the rule. As Holden et al. note, however, "most disease and most pathogen strains are to be found in most years, but at a low level, and therefore applying low selection pressure to the resistance alleles." They contend, therefore, that "it is difficult to see how the preservation of landraces and old varieties in archaic but stable systems, can give rise to the evolution of novel resistance genes." Qualset et al. (1997) note a further point arising from the fragmentation of landrace planting. Crucial in the coevolutionary dynamic is whether the islands of landraces amid a sea of the same species act as an alternate host with a particular resistance structure or in rotation with bred cultivars of the same species in the same fields. In these host-pathogen interactions, the dispersal dynamics and survival structures of each pathogen species are critical variables. Dispersal, survival, and the pattern of host heterogeneity have a great effect on the anticipated coevolution because the pathogen population would be subject to an additional element of diversifying selection on the alternative populations of host. Clearly, the nature and pace of change of resistance structures in landrace populations conserved on farm are key topics about which there is much speculation and some dogma, but very little hard evidence.

### *Composite crosses*

From the above discussion it is evident there is much to learn about the temporal dynamics of genetic diversity during on-farm conservation. For such research, a paradigm would be helpful. Population genetic research on the composite crosses, notably in barley, offers such a paradigm for research into the population genetics of *in situ* conservation (Suneson 1956). These are populations synthesized from a diversity of sources and then planted over many generations at one or more specific sites. Research on

the composites at least shows the kinds of inference that attend a periodic sampling of generations and storage of samples for later comparison.

Allard (1988) summarized the results of long-term studies of changes in adaptedness in several barley composite cross populations. These studies included temporal changes in marker allele frequencies, in quantitative characters and fitness components, and fitness itself. His overarching generalization was that superior reproductive capacity (in terms of the number of seeds per plant) was the one quantitative character consistently associated with the increasingly prevailing allele at marker loci.

The composite cross paradigm departs, however, in some key respects from landrace populations conserved on-farm. Their origins are strikingly different, with the composites founded as a hybrid swarm of many genotypes with widely dissimilar origins. Growing such a swarm at one site inevitably leads to major changes in allele frequencies and a dramatic reduction in quantitative genetic variance. For example, Jana and Khangura (1986) report that a bulk population grown at four different sites showed loss of diversity in all populations for morphological and agronomic characters in contrast to the retention of diversity at eight isozyme loci. Allard (1988) found that while most alleles are retained in the barley composites, a few alleles increased in frequency while the remainder tended to extreme rarity. Such rarity may cause problems because it will require very large samples for detection.

Fitness also differs between cereal composites and landraces, because fecundity is simpler in the composites, whereas in landraces seed selection by farmers for quality, flavor, size, appearance, market appeal, etc. comes into play. Of course natural selection in composites can be supplemented with mass screenings for traits like seed size or cullings of heavily diseased or tall plants as parents for the next generation. Le Boulc'h et al. (1994) have drawn attention to the need for countermeasures to stop the loss of dwarfing genes from their wheat composites. But such simple steps of artificial selection hardly match the complexity of culturally based farmer selection and marker appraisal. Composites, in short, aim to give scope for recombination in the context of mass selection ("evolutionary plant breeding"), while landraces aim to produce a consumable or marketable product while conserving variation ("evolutionary sustainable production"). Both are compromises, but of two sets of different functions.

The study of the evolution of disease resistance in composite crosses is of particular interest in guiding research in on-farm conservation. Allard (1990) summarized studies of the *Hordeum vulgare*-*Rhynchosporium secalis* pathosystem for barley composites, emphasizing the interactive and self-regulating adjustments that occur in genetically heterogeneous populations. The pathotype structure of this pathogen is complex, comprising a wide range of abilities to damage the host. In response, the resistance allele structure in the host is also complex, with alleles differing widely in the protection they afford. Many of the resistance alleles had net detrimental effects on yield and reproductive fitness. Yet resistance alleles that protected against the most damaging pathotypes increased sharply in frequency in Composite

Cross (CC) II. These data are evidence that composites propagated under cultivation can lead to increases in the frequency of desirable alleles.

De Smet et al. (1985) examined barley composites for resistance to another major foliar disease, powdery mildew, specifically to test whether resistance is conserved. Three populations were grown for several decades in either disease-free (Montana) or disease-prone (California) environments. Four isolates that recognized the specific resistances in the founding parents were used to test seedling resistance. Overall, resistance was conserved more consistently in the California series than in the Montana site, but without the expected increase in frequency of resistance. This result is similar to that for scald resistance in CC II (Webster et al. 1986). Selection favored alleles for resistance in seasons when scald disease was prevalent, but such alleles were associated with detrimental effects on reproductive capacity in seasons that were unfavorable to scald.

In barley CC V and CC XXI, however, the same resistances showed much less change, presumably because of genotypic associations and whole-genome effects that are common in predominantly self-fertilizing populations (Burdon 1987). This raises the crucial point in researching the temporal dynamics of genetic variation in populations conserved *in situ*. A knowledge of the mating system and its variation in time is fundamental to an understanding of the system. One example is the study of Kahler et al. (1975), who measured outcrossing rates in three generations of barley CC V. They found that the rate had doubled between generations 8 and 28, indicating an evolution toward increased recombinational potential. Landrace populations are unlikely to show a steady secular trend like that in CC V, because, as noted above, they are not in the early stages of a synthesis from diverse sources. However, such populations are likely to show temporal variation in outcrossing rates with substantial effects on their genetic structure.

Pronounced population divergence was a feature of specific resistance alleles and adult plant resistance to powdery mildew in a series of wheat composites (Le Boulc'h et al. 1994). Clear relationships between virulence frequencies and resistance structure were lacking. However, multi-resistant recombinant genotypes appeared and the overall level of resistance increased, which augurs well for the rationale of *in situ* conservation.

### *Indicators of genetic structure*

Four of the advantages of *in situ* conservation (numbered 3 to 7 in the second section above) specifically relate to the genetic structure of landraces. The following lists a series of indicators for investigating each of these advantages. The indicators range in technique from the molecular genetic to the anthropological. Many of them cannot be implemented on a broad scale in every conserved population. Yet a balanced approach to research on a representative sample of crops and farming systems is needed. If possible, the research should also consider the interaction between indicators and the various kinds of data.

## **Indicators for investigating population genetic structure of landraces**

### **Allelic richness and multilocus genotypic diversity**

- Population number and size or area of planting
- Mating system, degree of outcrossing
- Variation in human use of the produce (flavor, multipurpose varieties, etc.)
- Number of distinct morphological phenotypes (subspecies, races, varieties)
- Morphological major gene polymorphisms (color, pubescence, etc.)
- Marker diversity (isozymes, RAPD, DNA fingerprints, DNA sequences, etc.)

### **Special adaptations to the local environment**

- Habitat diversity
- Disease and pest occurrence or damage
- Phenological variation (maturity diversity)
- Targets or purposes of farmer selection
- Stress tolerance experiments (salinity, aridity)
- Response shown by selecting outstanding sub-lines or components
- Pest and pathogen resistance genes

### **Scale of localized diversity**

- Topographic variation in the region
- Geographic cultural diversity, trading patterns, language groups, etc.
- Seed supply systems
- Transplantation experiments — field performance measurements
- Partition of marker diversity between different geographic scales
- Gene genealogies for tracing relationships between populations

### **Temporal changes in genetic composition**

- Local history of varietal use, farmer selection, and perceived changes
- Extinction-recolonization cycles in the rotation of landraces in the landscape
- Comparison of stored or historic samples with current populations
- Changes in pathogen incidence, pathotype, and resistance structure
- Allele and genotype frequency changes in time

### **Operation of crop evolutionary processes**

- Absence of factors leading to further fragmentation or loss of landraces
- Response to variation in agronomic practices

- Difference in genetic structure before and after “seed” selection by farmers
- Response to planting in disease nurseries
- Migration measured by genetic markers, or data on seed movement
- Variation in mating systems

## *Management of on-farm populations*

A major issue facing the development of on-farm conservation is formulating the rationale for management of such populations. On this rationale will depend the extent and nature of any alteration in the planting and harvesting cycles that farmers and cooperating agencies might make. The conservation of populations has any of several possible aims:

1. Conserving the maximum number of multilocus genotypes and maximum allelic richness;
2. Safeguarding the evolutionary processes that generate new multilocus genotypes; and
3. Improving the population performance and increasing the productivity in a defined range of local environments.

These objectives are not necessarily exclusive of one another; neither are they identical, yet they are potentially conflicting goals. The first aim of conserving maximum diversity is best served by growing in a benign environment with relaxed selection. The second implies discerning and maintaining the current modes and intensity of evolutionary forces (selection, population sizes, isolation, gene flow, mating system, and recombination). The third implies seeking and implementing the appropriate plant breeding methods and selection regimes for landrace improvement in participatory breeding programs.

As far as genetic management for *in situ* conservation is concerned, the question is whether to prefer options that encourage genetic change in *in situ* populations, or options that allow it to take its course, or those that slow it down (Frankel et al. 1995). The principal cause of change can be grouped under three headings or axes, namely, the selection regime, the breeding system regime, and the population structure. The selection regime requires answers to questions such as whether disease levels or weed competition should be enhanced or reduced and whether soil infertilities should be remedied or infertile sites chosen. Recombination and the breeding system are perhaps less amenable to obvious manipulation, although Worede (1997) has noted that farmers have encouraged introgression from nearby stands of wild relatives of crops. However, population structure, which is the third axis, is controllable because it varies with population size and migration rates between populations. Frankel et al. (1995:175) assert that

Each of the three axes needs to be assessed and the tempo and mode of genetic change optimized. Overall, three criteria ... should be met. These are (i) population survival; (ii) maintenance of evolutionary potential in the form of genetic diversity; and (iii) development of new genotypes.

Comparable dilemmas arise equally in the sociological aspects of on-farm conservation. Qualset et al. (1997) stress the need to conserve the agricultural system as a whole. The literal preservation of traditional agroecosystems in the face of modernization is not possible; indeed, such systems have always been dynamic. The challenge is to integrate the conservation of plant genetic resources with agricultural development, and in particular to conserve as much diversity as possible and the processes that give birth to it.

## Sampling strategies

Sampling issues enter the conduct of on-farm conservation in several ways. Assuming that species, region, and cropping system are decided, the major questions are:

1. the number and spatial arrangement of populations within the system;
2. the population size for each generation and the number of parents contributing seed to the next generation; and
3. the size and frequency of samples for research, storage, and *ex situ* conservation, as complementary to *in situ* conservation programs.

Treatments of the sampling questions include those of Brown and Marshall (1995) for samples for *ex situ* conservation, and Brown and Weir (1983) for samples to estimate population genetic parameters. Brown and Marshall's (1995) guidelines for *ex situ* samples were to start from a minimum of about 50 individuals per population and, if appropriate, 50 populations per ecogeographic area. We then discussed how to alter these guidelines to take account of biological differences among species, specific targets of a mission, prior knowledge of levels, and patterns of genetic variation or practical requirements. The basic concept behind such a strategy is that population divergence is the key to the sampling and to the conservation value of the material. Excessive effort at anyone site will seriously reduce the efficiency of the mission. A high total number of samples ensures that the variation shared throughout the region — the "rare widespread alleles" — will be captured anyway, regardless of deployment strategy (the number of sites and the number sampled at each site). If the total collection came from a single site, the diversity localized at all other sites will be lost. We

contend that the divergence between sites or between populations is *the* fundamental target determining conservation strategy, even if it appears to amount to a small fraction of the total genetic variance.

Recently, Lawrence and Marshall (1997) discussed sampling sizes (of populations and individuals) for *in situ* programs. In general their treatments play down the level and significance of genetic divergence between populations and subpopulations, which leads them to reach some rather startling and potentially misleading conclusions. Thus, they question the case for conserving more than one subpopulation, which is based on geographical structure (from local selection and drift). They argue first that most of the variation of cross-pollinating species "occurs within rather than between their constituent subpopulations" (1997:108). Furthermore, they contend that conserving the variation of one population goes a long way toward conserving the variation of the species. Second, they appeal to theory showing that migration of one or two seeds per generation between subpopulations is sufficient to prevent fixation.

These two arguments are not sustainable. First, as Hamrick and Godt (1997) have shown, the populations of crop species are on the whole more divergent among themselves than are those of plant species in general. This is divergence measured by marker-gene polymorphisms as indicators of independent ancestry. Population divergence for selected quantitative traits (which Lawrence and Marshall rank more importantly) is likely to be even greater as it would stem from combining divergent ancestry with divergent ecology. Relative divergence as a proportion is not the indicator of conservation value; rather, absolute divergence is the key. Further the measures of proportionate divergence are based on identity F-statistics, whereas measures based on allelic richness are more appropriate in conservation. The fact that there is divergence at all justifies multi population sampling. Only if there were no divergence would the restriction of sampling to a single population be justified.

The second argument appeals to population genetic theory of migration to make such a claim. However, this theory is based on selectively neutral polymorphism. Once selection comes into play, very high levels of migration will not wipe out divergence between subpopulations. Hence for the fraction of the genome that is under selection, we should expect divergence in the face of migration. This portion of the variation is the key in determining strategies. A further point about divergence is that populations may diverge not only for the kinds of alleles they contain but also for the level of genetic variance. This is particularly the case for inbreeders (Schoen and Brown 1991). The best way to avoid an unlucky outcome of conserving a population with a below-average amount of genetic diversity is to include several populations.

Therefore, the conclusion that "when resources are limited, it might be better to concentrate on the conservation of the genetical variation of one population, rather than to disperse effort in an inadequate attempt to

conserve this variation in several" (Lawrence and Marshall 1997:108) is seriously misleading. Concentrating on one population is bound to be inadequate. In contrast, dispersing effort over several judiciously chosen sites while ensuring minimum standards at each are maintained is guaranteed to sample both inter- and intrapopulation diversity.

What size should the conserved population be? Lawrence and Marshall (1997) recommend a minimum size of 5000 individuals. They deduce this figure from earlier recommendations of Frankel and Soulé (1981) for the effective population size of 500 multiplied by 10 to account for departures of actual from effective sizes. This size is required to retain quantitative genetic variation for longer term evolution and is a handy yardstick. It indicates the number of plants that ideally should contribute seed to the next generation. On the farm, the actual size will depend on many factors other than the number required to slow genetic drift to a certain level, such as field size, isolation from contaminating pollen, competing land use, other uses of the crop, seed viability, plant habit, etc. The 5000 yardstick is useful for indicating whether a given area is sufficient. From the standpoint of samples for research or gene banking, etc., it is generous, but it will ensure that very rare alleles have a chance of persisting. It is hard to understand why Lawrence and Marshall (1997:113) should conclude that "genetic diversity is more likely to be lost *in situ* than *ex situ*" with sizes of 5000 and 172, respectively. On the contrary, it is the capacity of *in situ* populations to store large number of alleles and genotypes that is its comparative advantage.

## Conclusions

J. B. S. Haldane, one of the founders of population genetics, was responsible for two concepts that seem particularly relevant to on-farm conservation, namely, what was later called "genetic load" (Haldane 1937) and the "cost of evolution" (Haldane 1957). Conserving variation on the farm will entail some sort of cost, even when, as Bellon (1996) suggests, a multiniche model of diverse uses for the several populations applies. Further, if we plan for these populations to evolve new characters, then selection that renders the current, more frequent alternatives in the population less desirable will have to operate. Thus, for example, the evolution of resistance requires the presence of pathogen in abundance and the host population will likely suffer.

Diversity conserved on-farm is subject to a range of forces and is likely to be in a dynamic state. As yet, the data are far too limited to assess the various factors — human, biological, edaphic, or climatic — to determine the requirements for optimal outcomes. The challenge is to plan for assessment of these factors in relation to changes in genetic structure over time. Population biology research for *in situ* conservation thus needs to be both descriptive and hypothesis testing in order to guide technical improvement and management of land race populations.



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