

Chapter 2

Indicators of Genetic Diversity, Genetic Erosion, and Genetic Vulnerability for Plant Genetic Resources

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Abstract This chapter surveys the conceptual basis of indicators of genetic diversity, genetic erosion, and genetic vulnerability. These are summary measures of genetic diversity in cultivated plants and their wild relatives that guide decisions, monitor progress, and warn of emerging issues of genetic resources for resilient agricultural production. Such indicators measure the genetic diversity currently present in agricultural populations on farm and held in germplasm collections, and aim to detect genetic erosion, or serious loss of diversity in time, and to warn of vulnerability due to adverse deployment of genetic diversity in space. While diversity itself encompasses many concepts, *richness diversity*—the number of different kinds of individuals regardless of their frequencies—is the most important theme, followed by *evenness diversity*—how similar the frequencies of the different variants are. Many variables are plausible as indicators of diversity. The more practical are based on number of individuals or area occupied in situ and on the number of accessions and the number of genebanks ex situ. Genetic erosion is measurable as the proportion of richness of genetic diversity no longer existing in current populations, when compared with the crop a decade previously or predicted to be lost in the next decade without remedial action. Genetic vulnerability

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is inversely related to richness diversity that is present locally, particularly if it is known to possess adaptation to exotic or new mutant pathotypes or insect strains or environments. Census information forms the primary data. For cultivated species, these data are based on the farmer's unit of diversity management, most often their named varieties, their number, relative frequencies and divergence over various units of spatial and temporal scale. For wild species, the analogous units of diversity are the lowest recognized (e.g. subspecies, morphological types, ecotypes). Census data should be supplemented and validated using more direct assays at the DNA level with molecular techniques in carefully constructed samples.

Keywords Richness and evenness diversity • Population sizes • Sampling • Varieties • Subspecies • Extinction probability

2.1 Introduction

Plant breeders, farmers and managers of biodiversity continue to make crucial decisions that shape the genetic diversity of crop plants and their wild-related species. Such decisions include the making of genetic resources available to farmers, the defining of broad conservation targets, and the warning of impending genetic impoverishment. These decisions are made at many levels—local, national, and international—and require reliable indicators that measure genetic diversity and how it is responding to human impacts.

Three types of measures are needed in the case of plant genetic resources for food and agriculture (PGRFA). The first type addresses the current state of PGRFA, or the standing **genetic diversity**, including that existing in fields or natural areas in situ, and that stored away from its site of origin ex situ in orchards, seed banks, or gene banks. The second type aims to measure changes in the *status quo* of diversity over time, in particular to monitor the loss of diversity or **genetic erosion**. The third type has to do with deployment of diversity in space, but with particular perspective of **genetic vulnerability**. Such vulnerability arises when genetic homogeneity, or the lack of diversity, renders the crop growing in a region liable to ruin from detrimental environmental changes, or if a new biotype of pest or pathogen were to invade it.

2.1.1 Interpretation

Brown and Brubaker (2002) discussed a number of properties that indicators for managing plant genetic resources should possess. Importantly for reliable interpretation, indicators should be scientifically valid, readily estimable, readily

understandable and aggregative. Once the decision of which indicators to use is taken, the interpretation of the actual estimates will present further challenges. One procedure is to ascribe a meaning or action to a specific ‘**benchmark**’ **value** by having absolute standards (e.g., an absolute limit to land clearing, a minimum number of varieties that should underpin crop production in a given area, or the minimum value of germination for gene bank accessions). Alternatively, the purpose may be to monitor **trends over time**, with desirable or acceptable rates of change specified. The choice of the values that will trigger action requires inputs from both scientist and users so as to assure meaningful outcomes follow from the use of indicators. Even so, there is need for a process to confirm that the indicator actually measures the quantity intended.

2.1.2 Sampling

Because of the constraints of costs, virtually all indicators involve a sampling process to estimate their current values. Sampling is a key step that determines the avoidance of bias and the validity of up-scaling. Stratified random sampling is a basic technique that allows the aggregation of values for heterogeneous strata, and of data from finer scales. In addition, stratified sampling has the advantage that the overall statistics can be disaggregated, to recover the values for contributing strata if targeted action is required.

2.1.3 Aggregation

Aggregation is a common process in obtaining the numerical values for indicators. Aggregation is combining of values for component regions, or time periods, or species. For example, Hamrick and Godt (1989) summed estimates of diversity over different plant species, categorized by breeding system, to obtain overall estimates of genetic diversity in plants. Averaging over unlike entities raises a general problem: should the contributing entities be counted equally, or weighted according to some factor? The weighting factor for each component might be some function of its relative size, frequency, quality, productive capacity, or importance, for example, in weighting the components of a sustaining diet. Alternatively, an appropriate weighting factor might be a relative measure of the economic value of the component. For example, the member crops of a suite of fruit species might be weighted according to their total market value. For studies of trends over time it will be important to retain the component diversity values, or unweighted composite value, particularly, if weighting factors themselves change over time.

2.1.4 Comparability

A second pitfall in making comparisons of averages based on heterogeneous elements is the failure to base comparisons on common elements. An extreme example of this problem would be changes in the average proportions of traditional varieties when estimates for, say, horticultural crops are included in some, but not all, averages. The numbers of traditional varieties of these crops may be an order of magnitude higher than those of major arable crops. Any changes in overall patterns could be due to differences in the composition of the averages, and not to changes in diversity level of any element.

2.2 Genetic Diversity

At the outset, the task of devising a limited set of variables to measure the amount of genetic diversity seems to be straightforward. A manager or decision maker simply wishes to be able to report, for example, that it has stayed at a constant value under the current stewardship. In this way the indicator functions to monitor any change in genetic diversity, or to reflect managerial achievement. Another major use of PGRFA indicators are comparison of variability status of different crops (e.g., is the recently domesticated crop sugar beet, more genetically diverse than pea, an ancient crop?). How do different kinds of crops fruit trees versus field crops, inbreeding versus outcrossing crops differ in diversity patterns? Comparisons within species are also of critical importance. For example, where, if any, are the 'hot spots' of diversity in *Glycine* the wild relatives of soybean (Gonzalez-Orozco et al. 2012).

2.2.1 Location in Plant Genomes of Genetic Diversity

Genetic diversity arises primarily as variants in the linear sequence of nucleotides in DNA. Mutations can happen in the coding region of genes or in the spacer regions within and between genes, in the number of copies of genes, in the patterns of DNA methylation that affect the epigenome, in the linkage relation between several genes or indeed in whole chromosomes. A small portion of these changes translates into protein variation, into marker polymorphisms, into physiological, developmental and morphological variation in agronomic characters and ultimately into varieties given different names by farmers and plant breeders. Some correlation exists between the variations for different characters, but, even so, the choice is unclear of which kind of character is the best for assessing diversity. We cannot rely solely on any one kind, and that it will be important to cross-check major trends in diversity over several kinds.

2.2.2 Diversity Richness and Evenness

The appropriate statistical measures of diversity to use have long been a matter of discussion (Magurran 2003). Indicators of diversity should account for two basic concepts of diversity, namely richness and evenness (see the Appendix for further discussion of these two concepts and how they relate to the so-called evenness index $[h]$ of diversity, which is the complement of the Simpson index $[D = 1 - h]$).

2.3 Genetic Diversity Indicators by Resource Category

In order to devise a set of indicators to measure progress toward the sustainable management of plant genetics resources, Brown and Brubaker (2002) delineated four categories of resources, based on two kinds of gene pools and two conservation strategies (in situ or ex situ). The two kinds of gene pools are broadly distinct: cultivated species with populations that have been deliberately planted; and wild evolutionary relatives or species belonging to the same genus as cultivated species.

This construct focuses primarily on cultivated species, and does not explicitly take account of the many plant species that humans use directly from their wild populations for purposes other than being sources of genes from crop improvement. Such harvested species include forest trees, forage and medicinal plants, and ‘keystone’ species crucial for ecosystem services or survival (Frankel et al. 1995). However, the indicators of genetic diversity for the natural populations of these extra “plant species that matter” are the same as for wild crop relatives. Indeed monitoring provenance genetic diversity in forest and medicinal species could be even more important than for crop relatives. This is because direct human use of natural populations will inevitably be selective, generating intense selection pressure for desirability or efficacy. The ‘best’ populations could then become heavily depleted leading to accelerated genetic erosion and heightened genetic vulnerability.

2.3.1 Indicators by Category, Numbers, and Diversity

Table 2.1 is a list of indicators of biodiversity based on the resource categories. The lead indicators for each of the four categories in this table are in essence based on numbers. This reflects the fact the total genetic diversity within a taxon broadly tends to increase with increasing population size, increasing area occupied, or increasing total numbers. Thus, monitoring a change in numbers of populations or numbers of individuals of one species over time usually indicates a trend in the level of genetic diversity they harbor. Comparisons among species are less

Table 2.1 Indicators of genetic diversity in four categories of plant genetic resources for food and agriculture, managed in a particular region or country for conservation and use

Gene pool	In situ	Ex situ
Cultivated	Number and frequency of landraces, and proportion of the area planted that is growing them	• Number of crop species, subspecies or geographic categories adequately sampled in gene banks
	Environmental amplitude of crop area	• Number of accessions held in the genebank
	Number of farmer selection criteria, and evolution of farmer management	• Number of collections or gene banks
		• Country distribution of seed gene banks • Coverage in collections of crop diversity
Wild	• Number of species, subspecies or geographic subdivisions of taxa distributed in protected areas, that cover the species environmental range	• Number of wild species, subspecies or geographic subdivisions of taxa related to crops adequately sampled in the genebank
	• Abundance as population numbers and sizes, particularly of rare wild crop relatives, forest trees, forage and medicinal plants	• Coverage of species range
	• Gene diversity, divergence and distribution	• Evolutionary relationships and taxonomic resolution
	• Loss of habitat or land clearing in native range	• Accession viability, documentation and duplication

The **lead** or primary indicator are in **bold**; the secondary or support indicators are important measures that aid the interpretation the values of the primary variables
Source Brown (2008)

clear cut; abundant species may not always be more diverse than rarer species of the same genus. Research is needed to test the reliability and confirm of the relationship between numbers and diversity at and below species level.

2.3.2 *Logarithm Transformation*

As mentioned above, aggregation is a key feature of indicators and numbers lend themselves readily to summation. However, values for the more abundant species will clearly dominate the total of numbers of entities (accessions, individuals, populations, or subspecies) when the total includes different species. Two individuals from the same population (or species) are more likely on average to share the same gene than are two individuals that come from different populations (or species), because their most recent common ancestor is likely to be closer in time. To reduce this effect, a logarithmic transformation should be applied; the aggregation should be the sum of the log of numerical values for each entity, and the

sum converted back to the numerical scale. The theory of sampling neutral alleles supports such a logarithmic transformation in a hierarchical system (Brown and Hardner 2000). The logarithmic transformation has the virtue of being straightforward, and well known in ecology. Although theoretical distributions or empirical data are generally lacking to establish equivalences among aggregating categories, it is tempting to speculate that the log transform could be extended to each higher level in a hierarchy. Thus, for example, to aggregate values from populations of different sizes, one would use as weights the logarithm of those sizes. Then aggregating species within a genus can be based on the logarithm on the number of populations per species, and in like manner for genera within families.

2.3.3 *Wild Relatives*

2.3.3.1 Lack of Species Equivalence

While we may treat the wild species related to cultivated plants as entities distinct from crop species, they themselves do not form a single homogenous class. The main problems to note are:

1. The number of taxa involved can be very large. For example, crop wild relatives (CWR species) are said to number 20,000 in Europe alone (Flor et al. 2006).
2. The taxa may differ greatly in their likely importance for the improvement of the related crop. They also differ in their importance to farming communities or to farm management (e.g., some species are key in pastoral ecosystems, others in disease or weed management).
3. The number and conservation status of the subspecific entities, such as ecotypes, morphotypes, outliers, etc. vary widely among genera.
4. The taxa within any one genus differ greatly in their distribution, their population numbers and sizes and the likely viability of their populations.

The oat genus, *Avena*, is a typical example. Some species of this genus are among the world's worst and most abundant weeds, other species are rare and endangered taxa restricted to a few islands. In a simple sum of all wild oat populations, the rare and interesting taxa would be swamped. Autogamous or apomictic species can multiply relatively few genotypes over large areas. The population sizes of such species could mislead as indicators of their standing genetic diversity. For aggregation, we need to build on formally defined genotypic differences within species (subspecies, morphotypes, ecotypes, etc.), despite problems in their recognition. For example, to count the number of morphotypes of the species *Glycine clandestina* (Pfeil et al. 2001) as an indicator of managed diversity is more instructive than knowing the total number of populations of this species complex extant.

2.3.3.2 Management Versus Diversity

Because of the problems just listed, Brown and Brubaker's (2002) previous discussion of indicators for wild relatives focused on two aspects of the management of these resources, and not on diversity per se. Their first indicator was a crisis-based approach applied to populations in situ, and addressed only the rare or endangered elements of wild crop relatives. It borrowed the experience of natural conservation agencies in codifying their 'red lists.' The management indicator for in situ resources was simply the proportion of such elements that were comparatively safe in that they occurred in protected areas such as natural reserves. For examples, Gonzalez-Orozco et al. (2012) measured the degree to which 'hot spots' of perennial *Glycine* species diversity were found in reserves in Australia. The second aspect was applied to samples held ex situ, and emphasized the actual use (use in its broadest sense), or the number of requests to gene banks for wild resources. This too is a resource managerial indicator that aims to display the importance of collections and the need for their continued support. Like the proportion of endangered species or subspecies that is conserved in situ, statistics summarizing use are not measures of genetic diversity.

2.3.3.3 Numbers

A better approach to measuring diversity builds on the basic positive relationship between number (the size of a population or sample) and genetic diversity. Such an approach uses as an indicator, the number of recognizable subspecific taxa or, conceivably, the number of organisms comprising the sample. The subspecific taxa could go beyond the formally described subspecies and include ecotypes, morphotypes, ecogeographic fragments of the full species range, or any reasonably distinct group within the whole species sample. For ex situ collections this would amount to a species or subspecies list together with the total number of accessions for each taxon. Again, the logarithmic transform is available for aggregation of broader categories.

2.3.4 Cultivated Species Germplasm Collections

2.3.4.1 Numbers

The obvious indicator for the management of crop genetic resources ex situ is some function of the number and size of germplasm collections and their spread among countries. The spread of collections among countries is included because it is desirable to have backup, and to have a diversity of agencies and cultures involved. One attractive feature of this measure is that considerable historic data are available both nationally and globally. Working with collection numbers as an

indicator thus affords the chance to exemplify the benefits and pitfalls of indicators. Interpretation can focus on the reliability of the data and the role that subsidiary variables might play to improve interpretation. Considerable thought has been given to the assessment of collections. The International Plant Genetic Resources Institute (IPGRI, now Bioversity International) and FAO have published standards for gene bank management that provide variables and benchmark values for indicators (FAO and IPGRI 1994).

2.3.4.2 Problems in Using Number as a Measure of Diversity

Broadly, two problems are of concern in using the simple number of accessions as an indicator of diversity in ex situ collections. The first is redundancy—the amount of repetition including the level of planned backup duplication within and between collections, and of inadvertent redundancy between very similar or identical samples of an accession. The second is viability and security of accessions. This includes the quality of accessions, especially, the viability of propagating material, the regeneration frequency and strategy, and the housing, staffing, security, and long-term sustainability of the whole collection and the institution that houses it.

2.3.4.3 Supporting Indicators

In principle, each of the collection variables can be handled as a weighting or adjusting factor and combined to yield a ‘score’ to attach to each accession and to the collection as a whole (Holden et al. 1993). Using fractional weights at the level of the accession, the effective size of a collection can be adjusted for variation in viability, estimated from subsamples of accessions, and taking account of the age of seed from the date of accessioning and known shape of viability curves as a function of seed age. Redundancy can be estimated as a probability of ‘identity’ for name or origin when two random accessions are compared. This could be refined using such techniques as molecular fingerprinting with an arbitrary level of divergence (e.g., 10 % of fragments different).

2.3.4.4 Aggregating Subspecies or Species Taxa

This leads us to discuss to what extent collection size is a reasonable surrogate measure of genetic diversity present in that collection. Surely the size of a germplasm collection has much to do with the significance of the plant species. The very large global collections of wheat, maize, and rice are not a measure of the inherent diversity of these crops. Hence in Table 2.2, the lead indicator is the number of recognizable taxa (e.g. varieties), which is an echo of the lead one for wild diversity ex situ as discussed above. Yet the number of accessions of a particular taxon is indicative of the intraspecific diversity collected, assuming that extreme

Table 2.2 Estimates of genetic diversity indicators in rice in the three communities in Nepal

Crop species	Rice			17 crop species
	BBara	Kaski	Jumla	25 communities in 8 countries
<i>Site or community</i>				
The sampling base—the total area of a specific crop(s) (ha)	1,034	460	88	63,610 ^a
The number of modern varieties available to the community	20	6	0	0.45 ^b
Proportion of the farm area growing landraces	27	76	100	92 ^c
Number of farms or households sampled	89	161	180	4074 ^a
Area of traditional varieties (landraces) per farm (m ²)	3,256	3500	1100	4186 ^d
<i>Varietal diversity</i>				
Farm (or household) landrace richness	1.51	3.79	1.09	1.82
Farm evenness (h)	0.15	0.46	0.03	0.26
Community richness	28	63	21	14
Community evenness	0.88	0.93	0.60	0.70
Divergence (between/total %)	83	51	95	63

^aGrand total, unweighted; ^bAntilog (i.e. exponent) of the average over farms of the log (1 + number of introduced varieties), unweighted; ^cWeighted average over crops where the weights were the log of the total area for each crop; ^dExponent unweighted average of log of farm areas

Source extracted from Jarvis et al. (2008)

biases of amplification are absent or can be corrected for. The fact that the number of wheat accessions stored globally exceeds 10^7 whereas that for rye is likely to be less than 10^6 is indicative of their comparative levels of stored diversity. This order of magnitude difference supports the suggestion that logarithm transformation should be used for combining sizes over species, regions, countries, etc. from the sizes of heterogeneous units.

2.3.4.5 Breeding System and Numbers

A question of general interest is the effect of the breeding system of a crop species on the assessment of total collection size as an indicator of diversity. In particular, it might be assumed that germplasm collections of inbreeding (self-pollinating) crops contain much less diversity than collections of outbreeding species that are of equivalent total size. However, at the level of comparing different individual accessions, the reduction in effective size of the whole collection due to close inbreeding may not be as marked as implied by the true-breeding tendencies within a line (Frankel et al. 1995). Whereas the individual seeds within an accession are likely to share the same highly homozygous parentage, the seed from different accessions may be unrelated or related through deliberate hybridization in a

breeding pedigree. Overall, self-pollination reduces effective size to some degree (theoretically a halving), and thus reduces genetic diversity, but not by an order of magnitude unless accompanied by severe bottlenecks.

2.3.5 Varietal Diversity In Situ

What are the meaningful indicators of genetic diversity for populations of crop species growing in situ on farm, particularly applicable to traditional varieties or landraces? A complete and detailed inventory of all extant populations of a crop species under study is almost invariably impossible. Instead, we must depend on estimates from a carefully chosen sample of farms, chosen so that it can be reliably up-scaled.

2.3.5.1 Varietal Data Gathering

The steps in the process are:

1. Specify the crop species, the region and the communities, as the basic source from which ideally a random or structured random sample of households is drawn for survey. The number and structure for the farms and the area cultivated are recorded.
2. Define the units of genetic diversity to be assessed, for example, so-called ‘farmer managed unit of diversity’ or named varieties (Sadiki et al. 2007). This step requires participatory techniques that ask community groups of farmers to agree on their managed units.
3. Sample communities and farms for these defined varieties and estimate the area under each variety.
4. Compute the summary statistics, for example, landrace richness, evenness, and divergence.

A recent synthesis of disparate data on diversity in traditional varieties of 17 field and horticultural crops (27 species) growing in eight countries (Jarvis et al. 2008) illustrates the compilation of simple diversity indicators. Table 2.2 is an extract of these data for rice landraces in Nepal. For comparison and as an example of aggregation, the last column contains the overall estimates for all crops and communities in the study. The data for rice in Nepal were based on three contrasting communities directly representing over 1500 ha of rice fields (line 3). The communities differed in degree of dependence on traditional cultivars (4 and 5), and rice-field size (7). For the rice fields in this study, the richness of diversity at the level of the individual farm (line 9) exceeded one landrace per household, and was very high at Kaski. The evenness index (h) (line 9) was appreciable—two random plants on one farm were almost as likely to belong to different varieties as to the same variety. Substantial differences were evident at the community level (lines 10 and 11).

2.3.5.2 Overall Perspectives on Crop Landrace Diversity In Situ

Most of these variables in the Jarvis et al. (2008) study were readily aggregated to more crops and to higher scales to yield very interesting overall summary measures. The remarkable features to emerge were that the majority of farmers who grew landraces were likely to grow more than one such distinct variety, and that farmers in the same community tended to adopt divergent varietal strategies. Two trends significant for developing indicators were: (1) a close empirical relationship between richness and evenness index (correlations exceeding 0.90); and (2) an appreciable positive relationship between farm field area (log scale) and diversity. These results are important for two reasons. First, farm field area (or population size) within crops, culture, and environments is a valuable, albeit surrogate, comparative indicator for on farm genetic diversity. Second, the evenness index is a good estimator of richness of diversity. The evenness index (h) is assessable in relatively small samples because it converges with the true underlying population value, whereas richness does not reach its population value until the whole of the population is counted. Furthermore, evenness may be less sensitive than richness to problems of accuracy, homonymy, or synonymy in the naming varieties and to telling rare varieties apart.

2.3.5.3 Farmer-Named Varieties and Diversity

Statistics based on farmer-named variety are questionable as valid measures of genetic diversity. For example, Nuijten and van Treuren (2007) urge caution and question their validity when lists include homonyms or synonyms or when minor discrepancies or inconsistencies at the DNA level between variety names and the genes they contain. Clearly, variety names are assessable rapidly over a wide sampling base, enabling the testing of broad hypotheses for the distribution of diversity. Many farmer managerial decisions are made at the varietal level, and many modes of selection (such as climate, soil, elevation, maturity time) operate on the whole field. By planting a reputedly tolerant variety in a stressful situation, farmers reinforce the attributes of the varieties they recognize as units of diversity. They directly benefit from correct decisions based on names, and suffer the consequences of poor ones.

Reliable, consistent recognition of identities of types (subspecies, variety names) and differences is a key assumption for indicators based on these units. Ideally, this is true not only within communities, but at broader spatial and temporal scales. Molecular techniques have a role in testing the limits of this assumption. Likewise, one issue for indicators of genetic erosion is the matter of identifying locally common alleles that are important for adaptation. Molecular techniques have a possible role in assessing the uniqueness of such alleles in test samples. In addition, molecular fingerprinting of a current and a past sample of varieties could in principle measure proportionate declines in genomic diversity. Such an approach requires the benchmarking of the significance of observed

decay rates of molecular diversity. For genetic vulnerability, it is important to add data on performance in assays of biotic and abiotic stress to measures of varietal homogeneity.

2.4 Genetic Erosion

Genetic erosion is the process of the loss of portion of the gene pool of a species in a specific region. Here, we use the term in the sense of loss of particular alleles, or the loss of genotypes, subspecies, or varieties, while acknowledging some conservationists use it to describe species extinction. The principal concept is the depletion of genetic richness. Maxted and Guarino's (2006) definition (see also Guarino 1999) specifies "the permanent reduction in richness (or evenness) of common local alleles, or the loss of (local) combinations of alleles over time in a defined area." In focusing on alleles that are highly restricted to a few populations and only there are relatively frequent, this definition underlines the aspect of local adaptation. However, it is not clear why a definition should add reductions in evenness. Changes in evenness alone without any loss of richness are unlikely because evenness and richness are correlated empirically (Jarvis et al. 2008) and theoretically (see the Appendix).

An indicator should reveal trends in time and be most sensitive to the changes of concern. If the conceptual basis of an indicator is overly inclusive, it is likely to meet the following problems:

1. It may be hard to estimate and to aggregate over different species, areas, or aspects of diversity.
2. Neutral or trivial changes could mask critical changes when summed over loci, genotypes, populations, or species. For example, the loss of a few alleles at a highly polymorphic microsatellite locus is likely to be of trivial or no importance compared with the loss of disease resistance alleles.
3. Emphasis on combinations of alleles can be confusing in sexual species where the genome multilocus genotype of an individual is unique and ephemeral. Thus, when a claim is made that some percentage of distinct clones or genotypes has been lost from a region or a species, this is not necessarily genetic erosion. The life of each genotype is finite in sexually reproduced species, although vegetative reproduction might prolong that life (such as in named cultivars of fruit trees). A reduction in population size, and not increased recombination, is the primary agent of erosion.
4. Above all, the need is for practical ways of monitoring genetic erosion so that it is clear when and where it is occurring.

As a process, genetic erosion is difficult to quantify in an index. To monitor changes in the rate of genetic erosion strictly requires directly comparable measures of the state of a system at several points in time. Alternatively, it is possible to measure the major agents of erosion (e.g., deterioration or destruction of habitat

due to urbanization, land clearing, overgrazing, salinization, drought, climate change, etc.). However, such indirect measures are very broad and have other and possibly more profound impacts than causing loss of diversity.

2.4.1 Erosion in Retrospect or in Prospect

Relevant measures of genetic erosion will often include some subjective assessment based on expertise and local knowledge on the significance of any loss. The inclusion of such evaluative information in measuring erosion is desirable. The challenge is to format it in such a way that at least a tentative quantitative treatment is possible. The FAO survey and database of reported instances of genetic erosion has the potential to provide the basic information for constructing such measures (Diulghieff 2006). Many of the records so far assembled are in descriptive, narrative style of local expert opinion. Summing these stories over crops or regions or time periods requires their conversion to quantitative estimates, which is a significant challenge.

We should adopt a procedure that can look back (retrospective) or look forward (prospective). In the former case, the researcher has before him or her a gene pool containing some variation and asks the question as to what proportion remains of the diversity that was known or assumed to have been present a decade ago. The estimate of the richness diversity that was previously extant should rely on as much evidence as possible.

Alternatively a predictive or prospective view could be appropriate. In this case, two quantities are essential for any reported instance. These are:

1. A measure of the significance of the loss of the gene pool in question. This is approached by estimating the extent of the total similar diversity that is at risk. This could in turn be based on the area cultivated or the number of varieties or populations with a factor of 0.20 as an estimate of the proportion of all diversity (in this case allelic richness) that is locally common (Brown and Hardner 2000). Suppose 20 % of the area or of the varieties are deemed to be at risk. Then this amounts to $0.2 \times 20 \% = 4 \%$ of the species genetic diversity imperilled.
2. A category of the likelihood of loss under the current situation, with no intervention (in some time period such as one decade) Classes: C = Almost certain ($P > 90 \%$); L = likely ($P > 50 \%$), U = unlikely but threat is still real ($P < 50 \%$), V = very unlikely ($P < 10 \%$). The actual area growing these varieties may affect such opinions.

Both of these quantities are subjective estimates, but ideally could be based on local knowledge of the specific crop and threats to it. Any existing survey data can be used within the above framework to support the estimates. While individual estimates and predictions may be prone to error, the framework is a way to codify the best opinion and the averages will converge to give a trend. Finally, the

predicted erosion is estimable as the proportion of the resource under threat of erosion multiplied by the estimated probability of loss.

Prospective studies encounter the problem of how to foretell future climates and future responses of plant populations. On the other hand retrospective studies many lack accurate samples and information of what diversity existed in the past. They may also be subject to the bias of not knowing what has gone completely extinct and left no clear evidence of prior existence.

Examples of studies using farmers' assessment to provide data on losses include the following. Willemen et al. (2007) interviewed 285 cassava farmers in Ucayali, Peru and matched their perceived trends in diversity trends in the preceding decade, with current levels diversity for groups of varieties defined by cluster analysis of 23 morphological characters analysing socioeconomic and environmental predictors of erosion. Actual estimates of varieties and proportions lost were not reported. In a comparable study, Kombo et al. (2012) used participatory appraisal in 21 villages in the Republic of Congo. Groups of farmers assessed cassava variety diversity as for number of varieties per farm growing and those they recall as recently abandoned. The estimated rate of loss of landraces was around 30 %. While the time period is not specified, we might assume one generation of three decades.

Two studies in which landrace samples were available at both the beginning and the current time point gave results that appear to counter prevailing expectations. Teshome et al. (2007) resurveyed 260 sorghum fields in five communities in Ethiopia. They found that the overall average field size had fallen 50 %, but with little consistent change in landrace variety richness per field. Bezancon et al. (2009) revisited 79 villages in Niger that had been surveyed for sorghum and millet landrace diversity 26 years earlier. They also found no erosion of variety richness; indeed the number of varieties had apparently doubled in this time in both crops. They noted little consistency in naming varieties and "new varieties" could arise from renaming earlier ones "for ethnic reasons." Both studies paid tribute to the resilience of farmers' selection criteria in maintaining diversity.

2.4.2 From Narrative to Estimate

The basic task in estimating values for erosion measures is to convert a series of descriptive narratives of the state of a variety of gene pools into numbers that can be compared in time and among cases. Table 2.3 (from Brown (2008)) gave some examples from the FAO database of this process. In addition to the two erosion variables, several parameters specified the geographic sampling space and the three categories of aggregation: the kind of management (cultivated versus wild used versus wild unused), the taxonomic level of loss and the major kinds of threat. As date-marked reports accumulate in the database over time it should be feasible to summarize trends in estimated rates of realized erosion or predicted rates of erosion in prospect for various categories of crops within decade

Table 2.3 Measuring genetic erosion: illustrative examples of quantitative estimates of potential erosion or the rate of erosion, based on survey reports

Variable	Definition or description	Examples			
Year	Year of observation	1998	2001	2001	Unknown
Region	Sensible groupings of countries		Pacific Islands	Caucasus	Pacific Islands
Country		Ecuador	Fiji	Azerbaijan	Fiji
Area	Geographic region of observation (name/km ²)	3 provinces	Most	5	Most
Crop group and management type ^a	Cereal, pulse, fruit tree, root, vegetable, harvested wild, unused wild	H	R	F	F
Taxon	Name of taxon	<i>Vasconcella</i>	<i>Colocasia</i>	<i>Prunus avium</i>	<i>Cocos nucifera</i>
Threatened entity or taxon ^b	Genus, species, ssp., cultivars or populations (number)	2 spp.	28 cvs	2 cvs	4 cvs
Fraction threatened ^c	Proportion of the total, e.g. in first case 2 spp. threatened of a total of 7 spp.	2 of 7 = 0.29	28 of 112 = 0.26	2 of 8 = 0.25	4 of 14 = 0.29
Likelihood of loss (cf. IUCN species categories) ^d	Probability of loss under the current situation, with no intervention (in one decade)	0.95	0.50	0.95	0.05
Predicted erosion ^e	Proportion of resource × probability of loss	0.28	0.13	0.24	0.015
Kinds of threat ^f	New varieties; other species; major abiotic change; major biotic change; loss of farming area or wild habitat	A	NV	NV	NV
Data source	FAO database	*	†	‡	†

^aManagement class—*C* cereal, *R* root, *F* fruit tree, *H* wild harvested or used, *W* wild and unused by humans. Example categories for aggregation

^bLevel of potential loss or extinction and category for aggregation

^cProportion of the total number of kinds of the higher category—order of magnitude is sufficient

^dCategory of estimated likelihood of loss: Classes: Almost certain ($P > 90\%$), Likely ($P > 50\%$), Unlikely but the threat still real ($<50\%$ but $>10\%$), Very unlikely ($<10\%$). We adopted the most conservative value for each class

^ePredicted erosion = proportion of resource $\times$ probability of loss $\times$ 0.20 (locally common genes)

^fKind of threat: *NV* new varieties; *OS* other species; *C* major abiotic change; *D* major biotic change; *A* loss of farming area

*<http://www.pgrfa.org/gpa/ecu/quesreport.jsp?quesno=1&rowno=4&instid=S-58-2&tablename=xmanswers&iterationno=1> and R. Morales (personal communication)

†<http://www.pgrfa.org/gpa/fji/quesreport.jsp?quesno=1&rowno=3&instid=S-66-8&tablename=xmanswers&iterationno=1> and T. Kete (personal communication)

‡<http://www.pgrfa.org/gpa/aze/quesreport.jsp?quesno=1&rowno=4&instid=S-52-6&tablename=xmanswers&iterationno=1> and Z. Akparov (personal communication)

intervals or due to various agents. The erosion indicator is the proportion of variants (alleles, genotypes, or populations) lost or likely to be lost in a given time period (for example, a decade). Such estimates can be combined as weighted or unweighted averages.

The four essential elements of the procedure are

1. Specifying the sample basis that is the subject of the inferences. The specifications will guide the aggregation of estimates.
2. Estimating the diversity previously present.
3. Estimating the extent or fraction of the diversity that is at risk.
4. Estimating the likelihood of the loss occurring.

The key assumptions and problems of this model are that:

- diversity is uniformly spread (but overall, at risk ‘hot spots’ probably balance very safe ones);
- the likelihood of loss cannot be estimated retrospectively as the taxon is known to be present today. Past erosion rates will require guesses about what has disappeared; and
- the fraction of diversity that is ‘localized’ will increase as the proportion of threatened resource increases.

2.4.3 Role of Molecular Markers

The few “quasi quantitative” estimates of genetic erosion as outlined support generally the concern for crop genetic resources at risk. They help to address the lack of evidence that van de Wouw et al. (2009) discussed recently. However, they leave open many questions of the dynamics of diversity underlying these changes

in farmers' use of landraces, and to landrace displacement by the varieties of modern plant breeding.

Clearly, the newer technologies offer increased precision of estimates of genetic diversity and understanding of its structure in populations. Molecular techniques have the power to monitor genetic variation at the elemental level of DNA sequences. They offer a fundamental gain in genetic knowledge; not only is it possible to prove that two individuals or two gene copies differ, but they can be placed in a phylogenetic hierarchy of relationships based on their recency of a shared ancestor. Once this is done, the phylogenetic diversity of the collection can be estimated (Crozier 1997). They have an obvious role in the field of genetic indicators (Brown and Brubaker 2002; Brown 2008). Molecular techniques therefore have a secondary, but nonetheless important, role in indicator development. They enable a deeper appreciation of the recognition of taxa and hence provide a ground-truthing of the diversity units monitored at the phenotype level. Sequence changes introduce a temporal perspective (coalescent theory) of evolving relationships and the measurement of evolutionary processes such as migration and breeding systems.

There are a growing number of research reports that have used genetic markers (allozymes, AFLP, microsatellites, SNPs) and morphological characters along with variety statistics to assess genetic erosion. Table 2.4 is a list of such recent studies that have used data on marker genes to assess the extent of genetic erosion in the crop systems. From these studies, a disparity has emerged between hypotheses of erosion expected from varietal or morphological statistics on the one hand and the levels or patterns of molecular marker diversity on the other. The studies have employed measures of total diversity and comparison within more or less advanced varieties. These may not capture the loss of particular alleles or characters, especially those likely to feature in the displacement of landraces. Obtaining valid historical samples is itself a major challenge.

Suppose that gene marker data are available for diversity within and between populations as valid samples in historical time. Can we combine varietal or morphological class statistics with estimates of molecular identity? Bonneuil et al. (2012) have constructed an indicator of crop genetic diversity that aims to integrate varietal richness, evenness, between variety genetic divergence and within-variety genetic diversity. Their approach employs Nei's gene diversity statistics both within and between populations. It includes richness because as we have already noted, richness is related to the gene identity measures. Thus, it may offer a good summary measure for following erosion, because it also gives greater weight to loci that are showing population divergence (i.e., loci with locally common alleles). The authors applied their measure to microsatellite data in wheat varieties planted in Eure-et Loir, France since 1878, and compared trends with those for five varietal diversity statistics. The results give conflicting evidence of erosion. The number of varieties (richness) appeared to be constant around 10 for a century then suddenly achieved new levels of around 60 in the last two decades. Varietal evenness measures showed no strong temporal trend. Bonneuil's composite indicator which incorporates marker gene identity measures, declined from a

Table 2.4 Recent examples of monitoring of genetic erosion

Species/region breeding system	Circumstance, issue or concern	Genes	Diversity indicators	Conclusions regarding change with time	Authors
Maize/France outbreeder	Variety catalog 1990 inbred lines grouped in up to 5 decades	- 34 morph traits - 17 allozyme loci	Nei diversity index for gene loci and morph class	No temporal change in gene or morphological diversity	Le Clerc et al. (2006)
Peas/France inbreeder	Variety catalog 578 lines grouped in up to 5 decades	- 61 traits - 8 allozyme loci	Nei diversity index for gene loci and morph class	No temporal change in gene or morphological diversity	Le Clerc et al. (2006)
Rice/The Gambia inbreeder	- Name diversity versus morph - Whether PPB maintains diversity	- 15 morphological traits - 92 variable AFLP fragments	Shannon Index of diversity in Farmer varieties versus modern varieties	Synonymy of farmer names (i.e. name divergence without gene divergence) masks little genetic change in space	Nuijten and van Treuren (2007)
Millet/The Gambia outbreeder	- Whether breeders versus farmer better retain diversity	- 13 morphological traits - 70 variable amplicons	Shannon Index of diversity in Farmer varieties versus modern varieties	Breeding system crucial. Introduction of modern varieties likely has increased diversity within varieties	Nuijten and van Treuren (2007)
Durum wheat/Italy inbreeder	158 genebank samples from 5 breeding period, from before 1915 until after 1970	- Gliadins - 10 SSR loci	Allelic richness and Nei gene diversity	Slight decline in richness and evenness diversity detected	Figliuolo et al. (2007)
Rice/South East Asia inbreeder	5641 landrace accessions collected over 33 years, grouped to 22 populations	- 12 allozyme loci	Allelic richness and Nei diversity index	No apparent loss over time in the year total marker diversity	Ford-Lloyd et al. (2008)
Rice/Guinea inbreeder	Landrace collected in 6 villages around 1980 compared 2003	- Named varieties - 10 SSR loci	Variety and allelic richness, Nei gene diversity	Changed sampling affected results. No erosion: 46 % more varieties, changes in allelic composition and increase in 50 % richness	Barry et al. (2008)

(continued)

Table 2.4 (continued)

Species/region breeding system	Circumstance, issue or concern	Genes	Diversity indicators	Conclusions regarding change with time	Authors
Sorghum/Niger	Changes in diversity in 28 years, 71 villages	- Racial characters - 28 SSR loci	Allelic richness, Nei gene diversity	Low divergence between 1976 and 2003, allelic richness and evenness diversity were stable or increased	Deu et al. (2010)
Pearl millet/Niger	Variety and genetic changes in 79 villages in the arid Sahel	- 136 paired samples of 192 - 25 SSR loci	Allelic richness, Nei diversity, landscape richness	No change in the major varieties. No erosion in allelic richness or gene diversity. Early flowering allele at PHYC locus increased	Vigouroux et al. (2011)
Wheat/France inbreeder	305 cultivars grown since 1878 in Eure-et-Loir region. Temporal trends	- Named varieties - 35 variable AFLP amplicons	5 genetic statistics and new composite H* measure	Apparent fivefold increase in cv richness since 1980; yet H* halved since 1878 and stable	Bonneuil et al. (2012)
Lettuce/France and Holland inbreeder	878 cultivars listed in 225 French and Dutch seed catalogs since mid 19th C	- Named cultivars - 100 variable AFLP amplicons	Nei diversity index	1960 turning point—seed companies and varieties increase with UPOV rules. Cv richness increased 4 ×. AFLP declined 10 %	van de Wouw et al. (2013)

historical maximum of over 1.0 to levels of half this value that seem relatively stable since the 1960s.

2.5 Genetic Vulnerability

Whereas genetic erosion is a key aspect of the dynamics of diversity in time, the phenomenon of genetic vulnerability arises from patterns of deployment or impoverishment of genetic diversity in space. Populations of a crop species are said to be genetically vulnerable if they lack the diversity necessary to adapt to a biotic challenge or to an abiotic stress that is likely to intensify. The concept of vulnerability implies a lack or low level of genetic diversity, most graphically realized when vast areas of a region are a monoculture of a single variety. If one plant succumbs to a newly arriving disease, to a new biotype or to a new extreme of climatic stress, all the fields of the region respond similarly because of their shared genetic heritage particularly for the genes involved in the host–plant’s susceptible (or ‘compatible’) response. The concept of ‘vulnerability’ could apply to a whole range of adverse situations arising from the precariousness of living systems. It is arguable that for vulnerability to be ‘genetic’ requires that other varieties or populations exist elsewhere that contain resistance or tolerance genes that would have moderated the loss in yield if they had been present. Thus, the concept of genetic vulnerability should go beyond mere genetic uniformity per se. Ideally, genetic vulnerability should add the notion of genotype $\times$ environment interaction, i.e., not all genotypes (and in particular not all populations or varieties from other regions) succumb as readily as the home population to the new threat to yield. Indicators of genetic vulnerability should therefore include:

1. A measure of the lack of genetic diversity, particularly for resistance genes affecting host–plant response to major likely diseases; and
2. A measure of lowered diversity of host–pathogen interactions and differential responses to different biotypes, with some spatial structure.

Here, we first consider indicators for genetic vulnerability to biotic challenges, and then assess the extension of this framework to indicators for vulnerability to abiotic stresses such as climate change.

2.5.1 *Kinds of Genetic Vulnerability*

Table 2.5 lists four kinds of genetic vulnerability upon which indicators can be framed. The first of these is genetic homogeneity. Losing diversity from the current cropping region increases vulnerability. Strictly, the diversity should refer to the genes determining plant response to disease. It is insufficient to have a large number of named varieties as a hedge against crop failure if they share the same

genes for resistance. This was the case in the USA, where male-sterile yet disease-susceptible cytoplasmic DNA was shared among many maize hybrid varieties in the field at that time, resulting in them all being vulnerable to the southern corn leaf blight. However, knowledge of the comparative resistance structure of the varieties available to farmers is generally lacking, so that a census of variety names may be the only readily obtainable information.

2.5.1.1 Richness and Evenness of Varieties as Indicators of Genetic Vulnerability

The indicator for the first concept of genetic vulnerability in Table 2.5 is varietal diversity measured as both richness (the number varieties per crop, reduced if any are known to be closely related) and evenness (as measured by the evenness index). Computing the latter requires estimates of the area planted to each variety. High scores of richness imply there are many future varietal options near at hand and that seed is available for increase if needed. High richness implies insurance against pathogen evolution. In some cases, richness is high but a large portion of the region is planted to a single dominant variety. When the dominant variety succumbs to a new disease biotype, losses will be incurred for a few seasons until more resistant varieties are multiplied and deployed. A further danger inherent in this pattern of varietal diversity deployment is that the dominant susceptible variety would allow the build up of large amounts of pathogen inoculum with increased likelihood of evolving virulence on the rare previously resistant varieties. On the other hand, high evenness (lack of dominance) implies resistance diversity is already deployed to meet a new stress, and could save the farmer from severe immediate loss. It is therefore arguable that a high value for evenness diversity (i.e., low dominance) is a better indicator of low genetic vulnerability than is a high richness score.

2.5.1.2 Mutational Vulnerability

The second type of vulnerability listed in Table 2.5, mutational vulnerability, specifically aims to conceptualize vulnerability to a new virulence mutation in a pest organism. Strictly speaking, the pathogenic properties of a future new virulent mutant are unknowable. One approach to a quantitative measure is to test the responses of the present cultivar(s) to a random sample of distinct isolates or defined pathotypes. From these data it is possible to compute the probability of infection or the average level of damage caused by nonlocal isolates. The scores for each pathotype are not weighted by the pathotype frequency of occurrence. The indicator is thus the probability of disease (or the measured adverse effect caused by the disease) in nonlocal environments. Clearly, this indicator requires experimental measurement, essentially the assessment of the performance of a representative sample of local material in alien stress-prone environments. Many

Table 2.5 Indicators of genetic vulnerability

Concept of genetic vulnerability	Theoretical measure	Indicator
(1) <i>Genetic homogeneity</i> —The standing crop consists of a single genotype or few varieties or genotypes	The diversity of resistances in host population. Richness diversity represents diversity near at hand that could be deployed. Evenness diversity or low dominance indicates diversity deployed to meet the current pathogen population	- The number of varieties per crop present on farm or in a region - Evenness index—more important for disease vulnerability
(2) <i>Mutational vulnerability</i> —The standing crop consists of genotypes that require a single mutation in the pathogen for virulence	The fraction of nonlocal pathotypes that can attack a random plant	Probability of disease (or quantitative adverse effect) when tested with a set of distinct experimental isolates
(3) <i>Migrational vulnerability</i> —The standing crop consists of locally resistant genotypes that are susceptible to a new migrant strain of a pathogen or pest	The probability that a random migrant pathogen propagule will succeed in causing disease on a random healthy plant in the population in question. This assumes the environment is favorable to the pathogen, and is calculated by integrating the frequency of particular compatible (diseased) interactions between alien disease strains on local crop genotypes, and could be distance-weighted. Ideally the statistic is also weighted by the relative frequency of pathotypes	Proportion of plants that become diseased when grown in other disease-prone environments
(4) <i>Environmental vulnerability</i> —The standing crop consists of genotypes that are adapted to the current abiotic environment (climate, soil) but lack adaptation to environmental stresses that are intensifying with time	The stress-induced yield depletion of current varieties relative to the performance of resistant nonlocal varieties that exhibit stress tolerance adjusted for the likelihood of degrees of stress, and for the frequency of local variety occurrence	- Relative sensitivity of local varieties when grown in clines of increasing stress - Proportional loss of cropping area for specific varieties following the increase of regions inhospitable due to climate change

Concept 1 is a crop-plant diversity concept; concepts 2 and 3 are defined on host–parasite interactions; and concept 4 deals with the physical abiotic environment

breeders routinely conduct trials for many crop-disease or pest situations, but the data are dispersed and rarely synthesized. The summing of averages of individual variety scores, weighted by the current frequency of the varieties on farm in a given region, would provide a synthetic overview of mutational vulnerability. Technical consistency of approach is obviously necessary for the comparison of estimates over time and over different locations.

2.5.1.3 Migrational Vulnerability

The idea behind recognizing migrational vulnerability as distinct from mutational vulnerability is to divide future risks into two categories. Defining the specific actual agent of risk in the mutational case is virtually impossible. The nature of a new mutant pathotype of a disease (its virulence spectrum or aggressiveness) in the future cannot be known for certain. Therefore, we cannot test specifically for genetic diversity to meet such a possible future challenge. The only strategy for unknowable risks is to retain as much diversity as possible. On the other hand, migrational vulnerability refers to pressures that are currently absent from a certain home environment, but are foreseeable as inevitably arising from an alien source at some future date if unchecked, e.g., the Ug99 pathotype of wheat stem rust (Singh et al. 2006).

2.5.1.4 Environmental Vulnerability

Abiotic environmental stresses that arise from prolonged unidirectional changes in the physical environment, such as global warming, increasing regional aridity or increasing climatic variability are another threat to crop production. Changes in the farm environment over time resemble the threats from the invasion of pest organisms of known virulent strains (e.g., Ug99). In pearl millet on farms in the Niger, a shorter cropping cycle has evolved to meet increasing aridity. This case exemplifies the importance of specific adaptive allelic diversity in crop populations to allow evolutionary change (Vigouroux et al. 2011). In this example, the comparable samples of pearl millet in 1976 versus 2003 showed adaptation by way of an increased frequency of the early flowering allele at the PHYC locus without any general change in the main varieties or their levels of genetic diversity. As with biotic stresses, the degree of vulnerability to future threats can be measured experimentally by the performance or response of a local sample of varieties to specific pressure. The values of the likely impact of several separate risks on productivity could then be integrated, weighting by an estimate of the likely probability of each threat.

Although this fourth type of vulnerability resembles migrational vulnerability in Table 2.5 it is worthwhile to recognize that it merits developing separate indicators because of the topicality of climate change, the marked difference in spatial scales, in how the stresses increase and in how agencies will respond to

such data. Plant ecologists (e.g., Gómez-Mendoza and Arriaga 2007) are developing approaches to model changes in the natural geographic distribution of species under various scenarios of future climate. These authors used current distributions to predict decreases of between approximately 1 and 50 % for different species of *Pinus* and *Quercus* in Mexico as a result of climate change. They use these estimates as measure of differential species vulnerability and recommend conservation priorities.

2.5.2 Off-Site Testing—Pursuing Measurement of $G \times E$

It may seem to be overly problematic, unduly complex, and impractical to attempt a systematic, detailed risk, and genetic remediation analysis to derive measures of vulnerability. The need to attempt such computation arises from the limitation of relying on estimates of varietal richness diversity alone. Such counts lack a test of relevance of that diversity, i.e., whether, it will help cope with future threats to productivity. As mentioned at the outset of this section, the unifying concept underlying reduced genetic vulnerability is the provision of a diversity of interactions. Whether this can be measured satisfactorily by the tools of genotype $\times$ environment ($G \times E$) analysis in plant breeding remains to be investigated. In this case ‘genotype’ represents the suite of available varieties and ‘environment’ the different pathogen populations or abiotic stress levels. Situations of low genetic vulnerability are obtained when the $G \times E$ component of variance accounts for a large fraction of the overall performance variance, particularly, when different cultivars are resistant or perform better in different stress states. Another indicator is the character of the variance–covariance matrix of performance across environments. Situations of low risk are associated with negative covariance values. This result is analogous with modern investment portfolio theory of market economics, in which risk (i.e., vulnerability) is minimized when the total investment is made over a diversity of the stocks whose performance patterns in the past feature negative covariances. A portfolio of stocks that have responded differentially provide the best hedge against risk.

2.6 Conclusions

Indicators have a clear and increasing role in the management of the genetic diversity of crop plants and its deployment within and among farmers’ fields. They are needed to guide decisions on using and conserving genetic diversity and tell us where problems exist; problems of the loss of diversity in time and problems of production increasingly vulnerable to ecological change. In this chapter, we have argued for the utility of primary measures based on population size, or the extent

of field plantings. Counts may be of individual or of the lowest of individual groups—varieties, morphological ecological types, subspecies.

Having decided on the key primary indicators of diversity, it is important to develop a set of subsidiary supporting indicators to test the reliability of the primary measures. These could range from information on population or ecological history in the target area on the one hand, to in depth genetic DNA marker data. For genetic erosion in particular, which is a process in time, explicit methods are needed to incorporate more subjective data and expert opinion into measures of erosion.

The literature attempting to amass evidence of genetic erosion in gene pool groups falls into two major kinds. The first (e.g., Bisht et al. 2007) are reports based on surveys that concentrate mainly on the extent of plantings of each of three categories: landrace varieties, improved farmers varieties derived on farm from them, and varieties that are exotic, or that are the products of modern plant breeding. The second are more detailed studies of genetic markers (Table 2.4) and changes *within* these three categories. In many studies, there seems to be a gulf between landscape versus genome evidence. Genetic erosion that was evident from studies in the statistics on varieties planted and was therefore expected, but was not seen in genomic studies.

Yet neither of these two approaches on their own is sufficient and the challenge is to choose sensible sampling and experimental procedures to give better insights into the process of genetic erosion. Crop systems, countries and trends are so varied as to defy simple overly general statements (such as a global loss of diversity from major crops since the 1960s). We need meta-analyses of data based on many cases so as to pinpoint where and when genetic erosion is a significant serious problem and the factors linked to them. For such analyses the value of indicators will be crucial.

Caution is needed when using biodiversity indices, as they are merely attempts at simplifying complex systems and may often misrepresent what they are meant to simplify. Yet major management decisions have to be made, and indeed are being made. Such decisions can either invoke diversity criteria, e.g., saving endangered gene pools, or will be made on grounds other than the biological well-being of the system. Our task is to decide on the best, simplified measures, which may be less than desirable but still ensure the most important outcomes. A clear need and golden opportunity exists for research to develop the indicators proposed, and to test them with suitable databases.

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Appendix Richness Diversity and Evenness Diversity

The measurement of diversity requires an understanding of the different concepts or meanings that belong to the statement: “Population A is more diverse than population B”. One concept is that population A harbors more recognizable, distinct types than does population B. This we call **richness diversity** and refers to the number of different kinds of individuals regardless of their frequencies. Another related concept, **evenness diversity**, refers to the similarity in frequencies of the types in population A compared with population B. Low evenness indicates the dominance by one or two types. If the frequencies of the different types in A are very similar, the variance in their frequency is lower compared with that in B.

The measure of richness is, straightforwardly, the number (k ; $k = 1, 2, 3 \dots$) of types in a sample. Its dependence on sample size can be corrected using resampling techniques. Evenness, on the other hand, is less obvious. A standard, conceptual parameter for measuring variation in biology is the coefficient of variation of the frequencies of types, where the coefficient of variation ($CV[p_i]$) is the square root of the variance divided by the mean frequency ($p = 1/k$). If all the types in the population are equally frequent, then the variance of their frequencies is very low or zero, and the evenness diversity would be high. The evenness index commonly used in genetics is Nei's ($h = 1 - \sum p_i^2$; $0 \leq h \leq 1.0$) is also called the genetic diversity index. It is the complement of the Simpson index of dominance ($D = 1/h$) in ecology. The symbol h signifies the close parallel with expected heterozygosity in population genetics. Despite these potentially confusing names, h is perhaps the most understandable measure of evenness diversity. This is because h is the average chance that two gametes drawn at random from the population will differ at a locus.

Because of close parallel with expected heterozygosity for a single gene polymorphism in a random-mating population, we use the symbol h . It is known that the evenness index (h) is a simple function of the variance evenness and richness measures:

$$h = 1 - \left\{ 1 + CV^2[p] \right\} / k$$

This formula shows that this evenness index (h) increases as the richness (k) increases, and as the coefficient of variation of the frequency of types decreases. Yet, in general, h is more a measure of evenness than it is of richness. Numerically, h is largely determined by the frequency of the most frequent, or dominant type. (Hence the Simpson Index is sometimes called the dominance index.)

There are in theory other additional concepts and measures of genetic diversity (Brown and Weir 1983; Brown and Hodgkin 2007) that could serve as indicators. However, the two measures (k and h) discussed here are the most useful and readily understandable, and these two concepts are fundamental to the present discussion.

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