APPENDIX: MEASURING CROP GENETIC DIVERSITY

Evolutionary or ecological measures of genetic diversity focus particularly on genetic similarity or difference between different species. These kinds of comparisons might also be useful in the study of crop genetic diversity, particularly if a given crop is analyzed in the context of its wild relatives. However, most studies of crop genetic diversity are based on the similarity or difference between different crop populations within the same crop species. Most commonly, named varieties are the crop populations in question, although two distinct varieties may in fact be very similar genetically (Meng *et al.*, 1998). For the rest of this discussion, we will usually assume diversity is being measured within a particular crop species.

Spatial diversity measures

Spatial diversity—diversity within a given geographical area—may be "the most commonly recognized concept of diversity" (Meng et al., 1998). Two concepts are often used in spatial measures of genetic diversity. "Richness" refers to a simple count measure, for example of the number of varieties of a particular crop species planted in a given area. "Abundance" is a measure of the evenness of the spatial distribution of elements of the set being considered (Magurran, 1991). For example, suppose the same ten crop varieties are planted in two identical regions. In one region, each variety is planted on one-tenth the area, but in the other region one variety is planted on 91 percent of the area and the other nine varieties occupy one percent each. By a simple count measure (such as richness), the two regions are equally diverse, but introducing abundance would suggest the first region is more diverse than the second. This, along with the fact that named varieties may be very similar genetically, is why simply counting numbers of varieties is likely to be an inadequate measure of crop genetic diversity. Simple diversity indices that reflect varietal distribution (thus partially capturing the concepts of richness and abundance), include the proportion of area planted to the most popular variety or given number of varieties (equivalent to concentration measures used in the industrial organization literature.) A related index is the number of varieties covering a given percentage of total crop area (Widawsky, 1996). Another measure taken from the industrial organization literature is the Herfindahl index, which illustrates the degree of concentration among varieties (Pardey et al., 1996). The Simpson index (one minus the Herfindahl index) and the Shannon-Wiener index, taken from information theory, are often applied in ecological studies of diversity (Magurran, 1991).

Measures of relationships between varieties

Other indices of genetic diversity are built up from measures of "genetic distance," i.e., the degree to which varieties or species differ genetically (Nei, 1972; Cavalli-Sforza and Edwards, 1967; Reynolds, Weir, and Cockerham, 1983; Gregorius, 1978). To a certain extent such measures address the problem raised by simply counting named varieties that may be very similar genetically. Genetic distance indices can be calculated based on observations of different crop characteristics, including morphological indi-

¹ See Smale (1998), and particularly the chapter by Meng et al. (1998), for one of the first attempts to summarize the application of various diversity-related measures to crops and to give these measures an economic interpretation.

cators such as plant height, grain weight, and so on. As indicated, morphological indicators have the advantage that they may be closely linked to the traits on which farmers base their decisions, but the disadvantage that they are often influenced by environment and multiple genes, and therefore not reflective of genetic distance at the chemical (enzyme) or molecular (DNA) level. Genetic distance indices have perhaps most commonly been applied to this biochemical information. The use of biochemical and molecular markers requires systematic physical sampling as well as laboratory time and materials, and as a result can be quite costly (Meng et al., 1998).² An alternative approach to measuring genetic distance between varieties, at least for scientifically-bred crops with documented pedigrees, is based on comparison of the heritage of pairs of varieties.³

Building diversity indices

Genetic distance indices measure differences between different crop varieties or species, but they themselves do not measure overall genetic diversity. Weitzman (1992; 1993) describes a diversity index calculated as the total length of the branches of a taxonomic tree. Such a tree could be calculated using morphological, genealogical (i.e. pedigree), or genetic distance data. Solow, Polasky, and Broadus (1993) also incorporate the size of the set (e.g., number of crop varieties) as well as genetic distance into genetic diversity indices. Both these tree-based measures, and other measures based on matrices of similarity coefficients, permit weighting to reflect the distribution of crop varieties (Souza et al., 1994; Meng et al., 1998).

Measures of plant breeding activity using genetic resources

A number of other measures have been applied to the study of genetic resources, but they usually refer to aspects of a scientific plant breeding program, or the development of such a program from initial crosses involving landraces, rather than to direct measures of genetic diversity. These include numbers and origin of landraces in the ancestry of the varieties being studied, or the number of breeding generations since the initial cross (Gollin and Evenson, 1990); numbers of distinct parental combinations and numbers of unique landrace ancestors per pedigree (Smale and McBride, 1996; Hartell, 1996; Smale et al., 1998); or coefficient of parentage (COP) based measures (Pardey et al., 1996). Note that all of these pedigree-based measures are less useful in a crop, such as corn, that may not always follow a strict pedigree breeding system, or in crops for which pedigrees are partially or completely private for proprietary reasons.

Temporal diversity

Duvick (1984) observed that in a number of scientifically-bred crops, *temporal* diversity (or diversity through time) has replaced spatial diversity as one means of maintaining or even raising resistance or tolerance to pests and diseases. Temporal diversity depends on maintaining breeding effort by humans. Meng et al. (1998) closely identify temporal diversity with "the rate of change or turnover of [planted] varieties" as defined, for example, by Brennan (1984) and Brennan and Byerlee (1991). Other things being equal,

²Another characteristic, infrequently noted, of both morphological and genetic measures is that they obviously require informed choice of the characteristics or genes that will be analyzed. No index will be constructed, for example, based on all genes in a crop that are polymorphic, i.e., genes that have more than one variant. In the first place, such a list is unknown, and in the second, costs would become completely prohibitive. ³This approach uses the coefficient of diversity (COD), which equals 1 - the coefficient of parentage (COP). The COP is a pairwise comparison based on pedigree analysis (Wright, 1922; Malecot, 1948; Kempthorne, 1969; Cox et al., 1985). COD/COP analysis is less costly than analysis of proteins or molecular methods, but it also has some disadvantages: 1) it ignores the possibility that alleles could be identical even without common heritage; 2) it relies on the assumption that the ultimate ancestors that are recorded in a pedigree are unrelated, which may not be true; and 3) it assumes that "each parent contributes equally to offspring, despite the effects of recurrent selection and random genetic drift" (See Nightingale, 1996; Cox et al.,

1985; Meng et al., 1998)

faster varietal turnover might be expected to be associated with increased temporal genetic diversity, but like pedigree-based measures, varietal turnover is more a measure of the output of a plant breeding program than of genetic diversity *per se*. Newly released varieties might be genetically somewhat dissimilar to older varieties, or they might be very closely related genetically. Time-series of *spatial* diversity measures could provide useful information about *temporal* change in diversity, but such a series would not strictly measure "temporal diversity." More formal assessment of temporal genetic diversity could be made by statistically testing differences between genetic distance measures over temporal samples (See Souza et al., 1994 and Tessier and Bernatchez, 1999).