

# Plant breeding and farmer participation



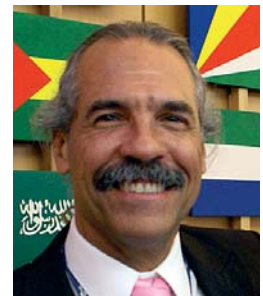
# Plant breeding and farmer participation

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## CHAPTER 14

# Breeding for quantitative variables. Part 1: Farmers' and scientists' knowledge and practice in variety choice and plant selection

Daniela Soleri and David A. Cleveland



## 14.1 INTRODUCTION

This chapter focuses on the knowledge and goals for selection of Third World farmers in comparison with those of formal plant breeders. By Third World farmers (hereafter simply ‘farmers’) we mean those in the relatively marginal (high stress, high spatial and temporal variability) growing environments of small-scale, traditionally-based agricultural systems (hereafter simply ‘small-scale’ or ‘Third World’ agriculture).

The assumption of conventional economic development has for decades been that these farmers would soon be absorbed into the industrial sector, and food production would shift to large-scale, industrial farms, and this scenario is still seen as desirable by many (e.g. Conway, 2003). There is, however, evidence that this small-scale Third World (SSTW) agriculture remains necessary for feeding a significant proportion of the world population, and will probably be necessary in the future, even with production increases in large-scale, industrial agriculture (Hazell *et al.*, 2007). More than 2 billion people live on almost 500 million small-scale farms (<2 ha) in the Third World, including half of the world’s undernourished people and the majority of people living in absolute poverty (Nagayets, 2005). Economic re-structuring beginning in the 1980s removed government support for SSTW agriculture and led to migration from rural to urban areas, creating a crisis there (Hazell *et al.*, 2007; Narayanan and Gulati, 2002; Wise, 2007). In addition to irreplaceable food production, SSTW agriculture has other benefits: it operates in many of the world’s centres of crop genetic diversity, where farmers conserve diversity in the form of crop genetic resources *in situ*, along with rich cultural and linguistic traditions (FAO, 1996; Harlan, 1992). Plant or crop genetic resources comprise wild and weedy relatives of crops in addition

to farmers’ varieties (FVs), which include landraces, traditional (folk) varieties selected by farmers, modern varieties (MVs) adapted to farmers’ environments by farmer and natural selection, and progeny from crosses between landraces and MVs (sometimes referred to as creolized or degenerated MVs) (Berg, 2009; Cleveland, Soleri and Smith, 1994; FAO, 1996; Zeven, 1998). Sustaining and increasing crop production is essential for the survival of SSTW agriculture, and, in this, seed saving and plant breeding have critical roles to play

In this chapter we review theory and data on selection by farmers, and compare it with selection by formal, scientific plant breeders (hereafter simply ‘plant breeders’ or ‘breeders’). Because selection by farmers and formal plant breeders is based on the same basic biological principles, their understanding and practice of selection may be similar. However, there are differences between farmers and breeders in the genotypes and environments they work with, including the types of agricultural systems for which they are selecting, as well as differences in their experiences, technologies and goals for selection. Similarities and differences in selection among farmers and among formal plant breeders also exist, for the same reasons. Our goal in this chapter is to review what we know about these similarities and differences, and why understanding them is important for collaboration between farmers and breeders to improve selection for varieties that could help SSTW farmers survive and prosper in the future.

We believe that respect for farmers and their knowledge is essential for achieving the maximum benefits from collaborative plant breeding. The greatest single mistake plant breeders and other outside scientists can make is to assume they understand local agricultural systems. Even if their hypothe-

ses are accepted through local research, new details and perspectives are sure to arise, and it is only by having an open minded, respectful attitude that outsiders can hope to learn and reap the benefits of collaboration with local farmers. Such an attitude facilitates new insights and understandings that can improve the accuracy and relevancy of the scientific work. If plant breeders think of their interactions with farmers as tests of how complete or accurate farmers' knowledge is, breeders will lose a critical opportunity for supporting collaboration, respect and collegiality, and for improving the quality of their own work. Thus, at least initially, experiments and discussions with farmers should be seen as opportunities to learn, not to teach.

#### 14.1.1 Choice as distinct from selection

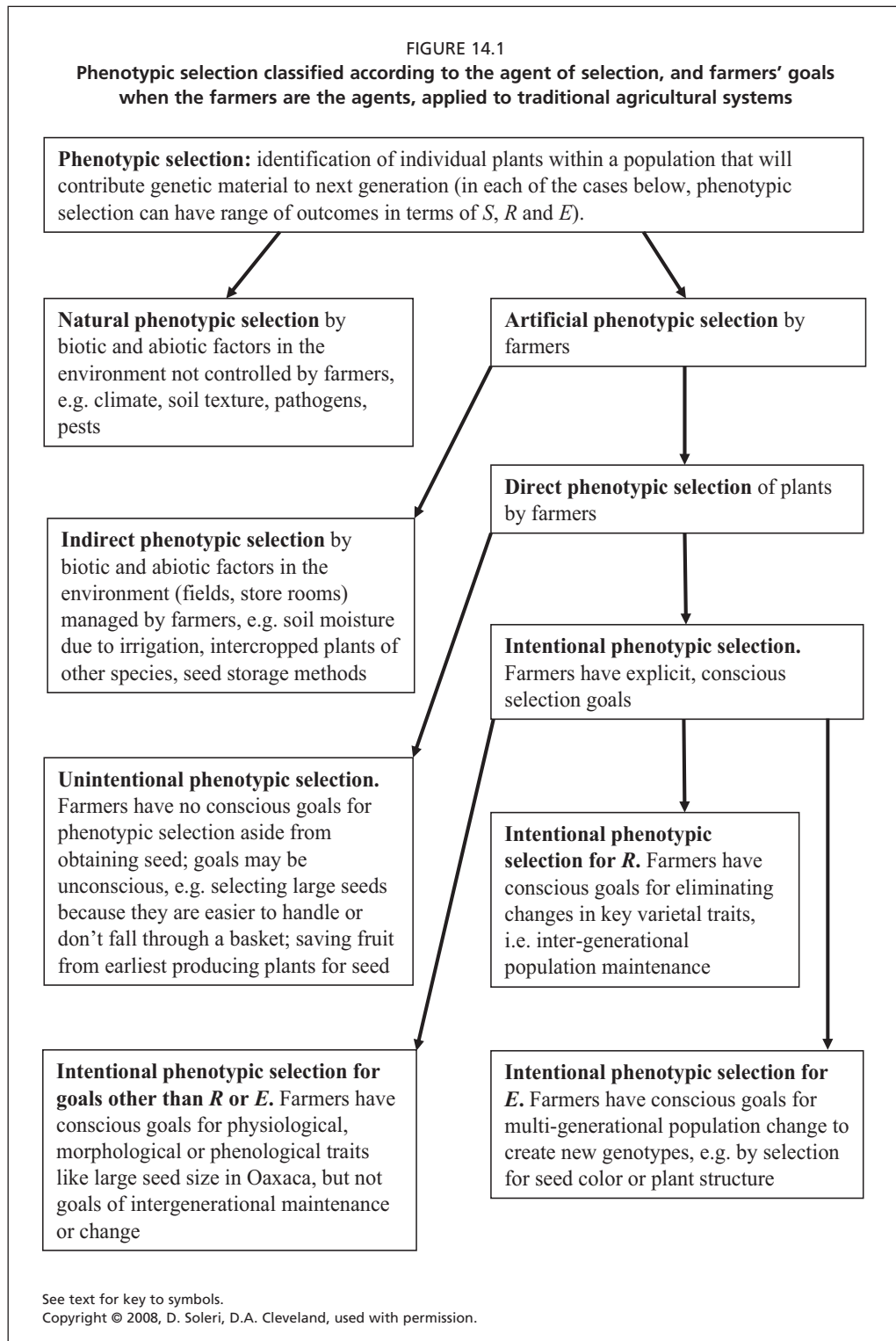
It is important to differentiate between *choice* of populations or varieties that does not change the genetic make-up of these units, and the *selection* of plants from within populations or varieties, with the potential to change the genetic make-up of these units, which may eventually result in new varieties (Cleveland, Soleri and Smith, 2000). Farmer criteria for both choice and selection include agronomic, economic, culinary and aesthetic characteristics, as well as minimizing perceived risk. While the distinction is commonly made in some participatory plant breeding literature (e.g. Witcombe *et al.*, 1996), the terms 'choice' and 'selection' are often not explicitly defined, and in some writing may be used interchangeably. Obviously, distinguishing between these is partly a function of scale, as is most clearly seen in the case of vegetatively propagated crops, in which a single clone may be chosen to establish a new variety (e.g. with cassava; Pujol, David and McKey, 2005). It also depends

on definitions: a farmer's variety of a self-pollinated crop (e.g. of barley or rice) may be composed of diverse genotypes that, from a plant breeder's perspective, may be different varieties. Therefore discriminating among these genotypes would be selection from the perspective of farmers as it can change the genetic make up of their variety, but would be choice from the perspective of plant breeders as it would not change the genetic make-up of varieties as they define them. At a more fundamental level, farmers' choice of populations and varieties determines the diversity available for hybridization and subsequent selection of plants. For all of these reasons, we can say that selection and choice together determine the degree to which varieties stay the same, change between generations, or evolve over generations.

Farmers and plant breeders make choices between varieties and populations, especially in the initial stages of the selection process when choosing germplasm for making crosses (for plant breeders), and in the final stages when choosing among populations or varieties generated from those crosses for further testing (Hallauer and Miranda, 1988: 159), or for planting (farmers) or release (plant breeders). Farmers' choices of varieties or populations when saving seed for planting, in seed procurement and in allocating different varieties to different growing environments also affects the genetic diversity of their crop repertoires, and establishes the diversity on which future selection will be based. (For simplicity, in the discussion of choice we will use the term 'variety' to refer to both populations and varieties.)

#### 14.1.2 A taxonomy of farmer selection

A taxonomy of selection and its biological effects can help to clarify the differences



and similarities between plant breeders and farmers. Selection can be categorized according to the agent carrying out phenotypic selection, and the intention of the agent when it is a human (Figure 14.1). While all types of selection function in both farmer and professional breeding, professional plant breeders see intentional phenotypic selection for micro-evolution over generations ( $E$ ) as the primary goal, with other types of selection either eliminated (e.g. applying irrigation to eliminate drought selection), controlled for (e.g. in experimental plot design to reduce  $\sigma_E^2$ ), or used to optimize selection for  $E$  (e.g. roguing off-types) (Cleveland and Soleri, 2007).

Figure 14.1 focuses on selection under farmer conditions. *Natural selection* is not influenced by farmers, in contrast with human or *artificial selection*. Artificial selection is both *indirect*, a result of the environments created by farmers and plant breeders, e.g. in their fields and store rooms, and *direct*, a result of human selection of planting material. Direct artificial selection can be both unconscious or *unintentional* (based on implicit or correlated criteria), when no conscious decision is made about the trait selected for, and conscious or *intentional* (based on explicit criteria), the result of decisions to select for certain traits.

### 14.1.3 A biological model to compare farmer and plant breeder knowledge and practice

Many plant breeders and other outsiders who work with farmers make the mistake of assuming that western scientific knowledge and practice is always more accurate and 'better' than that of farmers. To have a way of comparing plant breeder knowledge (PBK) and farmer knowledge (FK), a neutral comparator that can function as

a bridge between these is useful (Soleri and Cleveland, 2005). For plant breeding, the most fundamental model of the relationship among phenotype, genotype and environment is assumed to be a good model of reality that is the basis for PBK; we will assume it is also the basis for FK. This model is universally accepted by biologists, including plant breeders, but they disagree among themselves about its interpretation at higher levels of generalization, for example whether selection in optimal or marginal environments leads to genotypes that are better adapted to marginal environments (Ceccarelli and Grando, 2002) (see Chapter 2). This variation in scientists' interpretations suggests that, if farmers do in fact think in terms of this basic biological model, it would be a valuable comparator, facilitating understanding of variations (differences in higher levels of its interpretation) within and between FK and PBK on equal grounds.

We use the two parts of the model on which plant breeding is based (Cleveland, Soleri, and Smith, 2000), as presented in standard texts (e.g. Falconer and Mackay, 1996: 189; Simmonds and Smartt, 1999: 193).

1. Variation in population phenotype (observable characteristics) ( $\sigma_P^2$ ) on which choice (discrimination between different groups of plants) and selection (discrimination among individual plants within a group) are based is determined by genetic variation ( $\sigma_G^2$ ), environmental variation ( $\sigma_E^2$ ), and variation in genotype (genetic constitution)-by-environment ( $G \times E$ ) interaction ( $\sigma_{GE}^2$ ), thus  $\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$ .
2. Response to selection ( $R$ ) for a trait is the difference between the mean of the whole population from which the parents were selected and the mean in the next



generation produced by planting those selected seeds under the same conditions.  $R$  is the product of two factors,  $b^2$  and  $S$  ( $R = b^2S$ ), where  $S$  is the selection differential, the difference between the mean of the selected parental group and the mean of the entire original population (Allard, 1999: 101–102; Falconer and Mackay, 1996: 189; Simmonds and Smartt, 1999: 193). Narrow sense heritability ( $b^2$ ) (that part of  $\sigma_p^2$  that can be passed directly from parent to progeny, the additive variance,  $\sigma_a^2$ ) =  $\sigma_a^2 / \sigma_p^2$ . Thus, artificial phenotypic selection *per se* is a process of identifying the individuals with specific phenotypic traits within a population that will contribute genetic material to the next generation, and is distinct from the heritability of those phenotypic traits (see Section 14.5).

In our use of the basic biological model, we make several assumptions. (1) It models empirically observable patterns in the real world. (2) Among both farmers and plant breeders and other scientists, there are some who are particularly good observers of their environments, crops and interactions between these if they occur, while others are poor observers, resulting in variation within groups. (3) Variation in knowledge within and between groups can also be caused by experiences with different genotypes and environments, and by different values and pre-existing knowledge. (4) Differences between FK or PBK and the model do not mean that either form of knowledge is wrong, and differences between FK and PBK do not mean that either is inferior to the other.

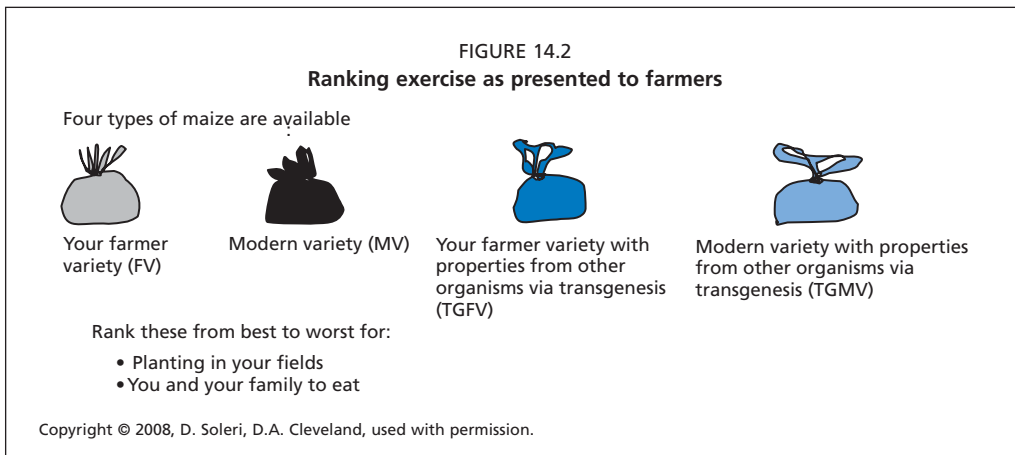
Thus, experiences under diverse circumstances can result in local interpretations of the model, by either farmers or scientists, which can be sources of learning for both scientists and farmers (Cleveland and

Soleri, 2002b). When FK differs from that presumed by plant breeders' interpretation of the model, we should try to understand the difference in terms of the specific genotypes and environments each works with, as well as other factors in their experience.

#### 14.1.4 Methods for understanding farmers' knowledge and practice

The best starting place for collaboration may be simple interviews with a representative random sample of households. Such interviews can provide insights critical for collaboration. There are many resources available describing how to conduct such interviews (e.g. Cleveland and Soleri, 1991) and analyse them (e.g. Stern *et al.*, 2004). The key requirements are that: (i) the sample is representative of the human population with which you are working, possibly requiring a stratified sampling approach, based for example on gender of farmers, household socio-economic status, or dominant soil type on farms; (ii) people conducting the interviews are consistent, respectful, open and primarily listen to and document farmers' answers and comments; and (iii) questions are relevant for understanding and collaboration.

In addition to simple questions to elicit basic descriptive data (household size, number working in farming, area sown to each crop, sources of planting seed, yields, etc.), methods such as scenarios and ranking exercises may use hypothetical varieties to better understand farmers' theoretical knowledge, or actual varieties they are familiar with for insights into specific experiences and observations (Cossa, Bellon and Franco, 2002; Soleri and Cleveland, 2005). For example, a scenario using hypothetical maize varieties was created to better understand the G×E interaction most valued by maize farmers in a study in Mexico, Cuba and



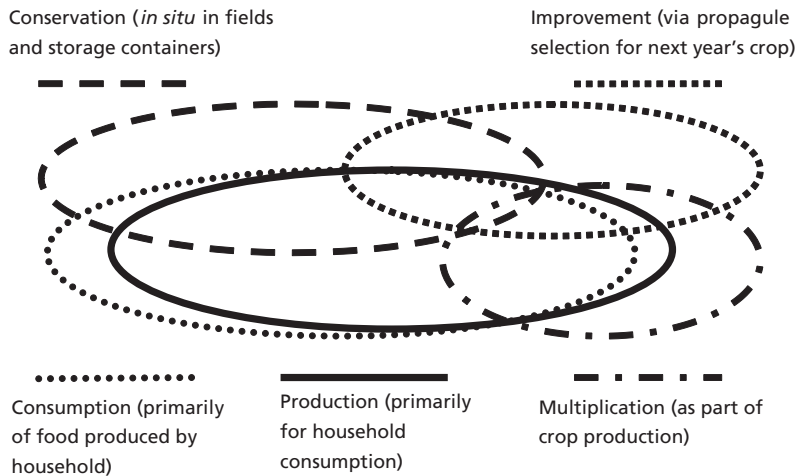
Guatemala (Soleri *et al.*, 2005). When asked to choose between two maize varieties with qualitative G×E response to annual precipitation, 61 percent of farmers preferred a variety with lower yield potential, mean and yield variation ('stable') to a variety with higher yield potential, mean and yield variation ('responsive'). The answer varied, with farmers from more difficult growing environments preferring the stable variety at a significantly greater frequency than those in more favourable growing environments. A similar scenario was created to investigate farmers' attitudes towards some of the possible consequences of pesticidal transgenes in their maize varieties and the evolution of resistance in the pests that it controlled. Some of these consequences were reliance on the formal seed system, a higher seed price and initially high but declining yields over time as pest populations evolved resistance. The hypothetical transgenic variety was not identified as being transgenic when the scenario was presented to farmers. Of those interviewed (n = 334), 70 percent chose a lower yielding but more stable and locally available variety (Soleri *et al.*, 2005). Similarly, an exercise asked those farmers to rank four types of maize: their own FV, a conventional MV they were familiar with,

and those same varieties as backgrounds for a transgene: a transgenic farmers' variety and a transgenic modern variety (Figure 14.2). We asked farmers to rank these first as maize seed for sowing in their own fields, and then again as maize grain for their family to eat. The FV and MV represented two seed systems (informal vs formal, respectively) and had different agronomic, storage and culinary characteristics with which farmers were already familiar. Farmers had no previous experience with transgenic crop varieties (TGVs). Providing these four choices allowed us to distinguish farmers' preferences for varieties or genetic backgrounds (FV vs MV) from their preference for a genetic technology (TGV vs non-TGV), an important distinction that is either overlooked or confounded in most research with farmers. TGVs were described neutrally to farmers and they were given a positive example of TGVs with the potential to decrease pest damage.

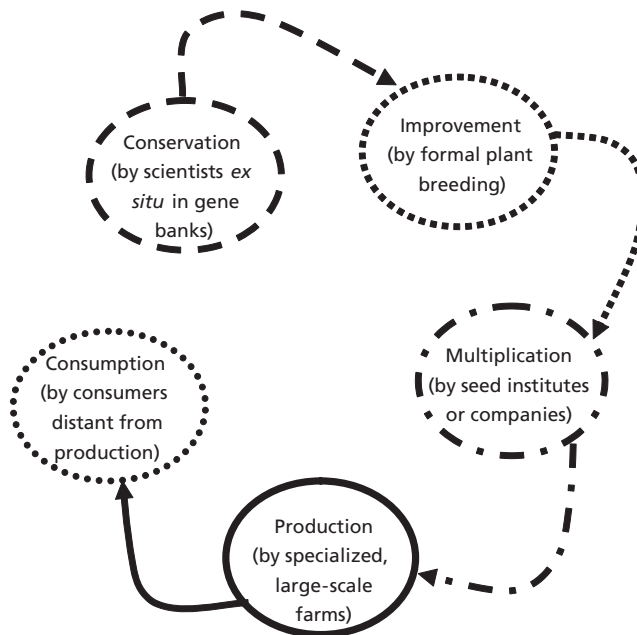
#### 14.2 THE CONTEXT: INDUSTRIAL AND THIRD WORLD AGRICULTURE

Industrial and Third World agriculture are different in important ways in terms of seed and food systems, growing environments and crop genotypes. They are also similar in

FIGURE 14.3  
**Components of agricultural systems in traditionally-based small-scale and industrial large-scale agriculture**



**a. Traditionally-based agricultural system: functions integrated in households and communities**



**b. Industrial agricultural systems: functions separated, specialized, many institutionalized**

terms of the basic principles and processes governing these variables and the interactions among them, including the outcome of choice and selection. Better understanding of these differences and similarities, and their relationship to differences and similarities between farmers' and breeders' goals, knowledge and practices, can help to further collaboration between farmers and plant breeders.

#### 14.2.1 Seed and food systems

In industrial agriculture, food production, food consumption, crop improvement, seed multiplication and crop genetic resources conservation are specialized, physically and structurally separated, and farming is often considered to be primarily a business (Lyson, 2002) (Figure 14.3a). In SSTW agriculture these functions are combined within the farm household and community (Figure 14.3b) (Soleri and Cleveland, 2004), as described below. The differences due to separation vs integration of these critical functions in seed and food systems have important implications for decisions about the best ways for farmers and breeders to improve yields and quality traits, and to minimize farmers' risk.

##### *Production*

SSTW agriculture is essential for feeding a significant proportion of the world population now, and will probably remain so in the future, even with production increases in large-scale, industrial agriculture (Hazell *et al.*, 2007; Heisey and Edmeades, 1999). As mentioned earlier, over 2 billion people live on almost half a billion small-scale farms (<2 ha) in the Third World, including half of the world's undernourished people and the majority of those living in absolute poverty (Nagayets, 2005). Food production relies on household labour, and most house-

holds sell some portion of their production in the market, but they are incompletely integrated into these markets (Ellis, 1993). Farmers' production knowledge combines understanding based on theory and empirical observation with values about the social and cultural significance of farming, often focused on FVs (Soleri *et al.*, 2002).

Off-farm income is often critical for households' overall survival strategy, and may reduce the importance of on-farm production. Migration of household members, for example, may lead to labour shortage (Narayanan and Gulati, 2002) and to reduced time and other resources devoted to seed selection, conservation of crop genetic diversity or production, and eventually to loss of the knowledge on which they depend (for an example in central Mexico, see Fitting, 2006).

##### *Consumption*

Farm families rely on their own food production for a significant proportion of their food, and FVs are valued for traits that contribute to storage, food preparation, taste, colour, texture and specific uses (e.g. maize varieties grown for husks used in tamale production) (Soleri and Cleveland, 2001), or sticky rice FVs used for traditional foods in southern China (Zhu *et al.*, 2003). These specialized uses mean some FVs have high market values.

##### *Improvement*

Cultivation in new locations, farmers' changing selection criteria and growing environments were responsible for the tremendous increase in intraspecific crop diversity via mass selection following domestication (Harlan, 1992; Matsuoka *et al.*, 2002) (see Chapter 1, this volume), and all of these continue today. It has been best documented at a local level in vegetatively

propagated crops (Elias *et al.*, 2001), but also in predominantly self-pollinated crops such as rice (Dennis, 1987; Richards, 1986). For cross-pollinating crops like maize, farmers may not be interested in changing quantitative phenotypic traits of their varieties through selection, but rather in maintaining qualitative traits of interest (Pressoir and Berthaud, 2004b), and can do so successfully even in the presence of high rates of gene flow at other loci (Louette, Charrier and Berthaud, 1997; Pressoir and Berthaud, 2004a). Quantitative improvement in such species may more often be sought through choosing new varieties or populations, as discussed below.

### *Seed multiplication*

Farmers do not usually distinguish seed multiplication from food production, although sometimes they plant separate seed multiplication plots, as do some rice farmers in Sierra Leone (Richards, 1986: 138–144). Farmers often save a high proportion of their seed from their own harvests, but often also obtain seed through informal seed systems (Ndjeunga, 2002), and frequently experiment with new seed (Louette, Charrier and Berthaud, 1997), including planting seed obtained as grain (Soleri *et al.*, 2005). The result is extensive gene flow via seed and other propagules, as well as by pollen flow, creating seed systems that are predominantly local and genetically open (Berthaud *et al.*, 2001; Pressoir and Berthaud, 2004a; vom Brocke *et al.*, 2003a).

### *Conservation*

Farmers conserve crop genetic diversity of FVs *in situ* in their fields and storage containers (Qualset *et al.*, 1997). Most *in situ* conservation is done indirectly—perhaps unintentionally—as a result of

using or selecting and saving FV seed each year for planting (Louette and Smale, 2000; Soleri, Smith and Cleveland, 2000). This conservation is dynamic in that populations are exposed to changing natural and artificial selection pressures, often creating locally distinct and adapted populations through indirect selection.

Because food production and consumption and crop improvement, seed multiplication and conservation are all carried out within the same crop population, that population will not be optimized for any one function *per se* as it might be in industrialized systems. For example, the value of FV genetic diversity in its local conservation role may in some way be in conflict with the genetic composition ‘optimal’ for its role as an improved population (Soleri and Smith, 1995). In this sense, farmers’ crop populations are similar to semi-natural plant populations that

*...approach complex equilibria in which overall fitness is as high as the varied demands of differing sites and seasons, complex genetic control and the long term demands of adaptability allow.*

(Simmonds and Smartt, 1999: 91)

For this reason, and because of the value of this farming for production and dynamic conservation, both *in situ* conservation by farmers and *ex situ* conservation in formal gene banks are necessary and complementary. However, for conservation to play a useful role, interaction between farmers and scientists is required, e.g. to ensure that the selection environments in *ex situ* conservation do not result in evolution that makes the population unsuitable for farmers in the event that they require renewal of their seed from outside their communities (Soleri and Smith, 1995). In a similar way, collaboration between farmers and

plant breeders needs to balance the goals of the breeder, which will tend to focus on improving specific traits, with the other functions of the food and seed system.

#### 14.2.2 Growing environments and genotypes

Growing environments and crop genotypes of Third World farmers differ in important ways from those with which most plant breeders and agronomists in industrial countries are familiar. Farms often consist of a number of small, scattered fields with marginal growing environments, i.e. relatively high levels of stress and of temporal and spatial variability. For example, while the average size of maize grain farms in the United States of America in 2003 was 79.2 ha (USDA NASS, 2004), in the southern Mexican state of Oaxaca over 76 percent of maize farms were smaller than 5 ha in 1995 (INEGI, 2001), and in one of the communities in the Central Valleys of Oaxaca where we have worked, the average farm size is 3.7 ha and the average maize field size is 0.8 ha (Soleri, 1999; Soleri, Cleveland and Aragón Cuevas, 2003). In that same Oaxacan community, coefficients of variation of maize yields calculated using triangulation of farmer estimates were very high, averaging 44 percent (Soleri *et al.*, n.d.). Indeed it has been estimated that maize farmers in that area of Oaxaca experience production failure one year in four due to drought (Dilley, 1997). In addition to high levels of environmental variability, other factors contribute to high levels of yield variability and production risk. SSTW farmers typically use low levels of external inputs, and have limited access to government programmes and markets, and limited influence on the policies affecting them (Ellis, 1993; Hardaker, Huirne and Anderson, 1997).

For many plant breeders who work

with farmers, this environmental stress and variation mean that selection for improved performance in farmers' environments needs to take place in those environments, and requires re-thinking some of the assumptions of conventional plant breeding (Ceccarelli and Grando, 2002). However, many plant breeders, especially those with little experience with farmers' growing environments, believe that as a general principle selection should be done in optimal environments because there are 'spillover' effects to marginal environments (for discussion, see Atlin *et al.*, 2000; Rajaram and Ceccarelli, 1998). Thus, while plant breeders agree on the basic principles of selection, they can disagree vehemently about how those principles should be applied to farmers' environments (Ceccarelli and Grando, 2002; Cleveland, 2001). One source of such disagreements may be differing interpretations of empirical observations and theories thought to underlie them (see Section 14.2.3).

Farmers often continue to use locally selected FVs, even when MVs produced by the formal plant improvement and seed multiplication systems are available, because FVs may be better adapted to marginal growing environments, and because MVs may be agronomically, culinarily and economically inappropriate (Ceccarelli *et al.*, 1994; Evans, 1993; Heisey and Edmeades, 1999). Farmers value FVs for agronomic traits, such as drought resistance, pest resistance and photoperiod sensitivity, as well as for traits contributing to storage, food preparation, taste, market value and appearance (Smale, 2002). FVs include landraces, traditional varieties selected by farmers, MVs adapted to farmers' environments by farmer and natural selection, and progeny from crosses between landraces and MVs (sometimes

referred to as ‘creolized’ or ‘degenerated’ MVs) (Zeven, 1998; FAO, 1996).

FV yields are often much lower in the Third World compared with MV yields in industrialized agriculture, e.g. maize yields in United States of America (~8 t/ha) compared with Mexico (~2 t/ha) (Aquino *et al.*, 2001) and Oaxaca (~0.8–1.5 t/ha) (Aragón-Cuevas *et al.*, 2006). However, yield stability is often greater with FVs than for MVs grown in the same environments, because MVs often have steep response regression curves, i.e. are highly responsive to marginal environments, as well as optimal ones (Ceccarelli, 1997; Evans, 1993).

An important reason for the higher yield stability of FVs is their higher level of genetic diversity compared with most MVs, presumed to support broad resistance to multiple biotic and abiotic stresses (Brown, 1999). In addition, many centres of origin and centres of diversity for crop species are in the Third World and cultivated primarily by small-scale farmers, thus SSTW agriculture is an important reservoir of genetic diversity in the form of FVs (FAO, 1996). This diversity makes FVs valuable not only for farmers, because they decrease the production risks in marginal environments, but also for the *in situ* conservation of crop diversity as a source of resources for breeding MVs.

### 14.2.3 Plant breeder knowledge

As outlined above (Section 14.1.3) the basic model of plant genotype-environment interactions are well established and universally accepted by plant breeders. However, many complexities of that model are still not well understood in terms of biological theory (Duvick, 2002), and there continue to be disagreements about the interpretation of the basic model and its implications for practice among plant breeders, such as the effect of selection environment on

the range of target environments to which a genotype is adapted (Atlin *et al.*, 2000; Bänziger and de Meyer, 2002; Ceccarelli and Grando, 2002).

In specific situations, understanding this basic theory is difficult because a great number of variables affect it, and predictions are hampered by the lack of experimental data and lack of the technologies and resources necessary to gather and analyse them. Plant breeders recognize that their theoretical understanding of plants beyond the basics is limited, and that much plant breeding has been based on intuition and empiricism rather than theory (Duvick, 1996; Simmonds and Smartt, 1999; Wallace and Yan, 1998), although intuition and empiricism are likely to be underlain to a lesser or greater extent by the basic theoretical understanding of genotype x environment relations.

This fundamental biological theory is the same no matter where plant breeding is practised. However, the biophysical, economic and sociocultural variables through which this and other theories work can be quite different. For example, think of the contrast between farmers’ fields in marginal environments and plant breeders’ research stations, or between national agricultural policy priorities of large-scale efficiencies and increased inputs and production, and farmers’ priorities of reducing risk and optimizing crop production as part of a general household survival strategy. Work under a specific set of circumstances may lead to interpretation of theory that is then generalized and broadly applied, without investigating the validity of those interpretations under all circumstances. For example, the fundamental principle that—all else remaining constant—as  $\sigma_E^2$  decreases,  $b^2$  increases has been interpreted to imply that selection in low  $\sigma_E^2$  environments provides

the best response for all environments, including ones with high  $\sigma_e^2$ . However, empirical testing has shown this not to be true in many cases (e.g. Ceccarelli, 1996; Ceccarelli *et al.*, 1994, 2003; Comadran *et al.*, 2008); two reasons are that, first, the genes responsible for a quantitative trait such as yield may be different in different environments (e.g. Atlin and Frey, 1990; Atlin, McRae and Lu, 2000; Venuprasad, Lafitte and Atlin, 2007), and, second,  $b^2$  of some important traits may not be entirely obscured by  $\sigma_e^2$  (Al-Yassin *et al.*, 2005) (see Chapter 2, this volume). Working with farmers often requires that breeders test the validity of those interpretations of theory that form the basis of conventional plant breeding. This includes comparing the genotypes and environments and goals for improvement, and testing the assumptions (biological, environmental, economic, sociocultural) on which they are based, and adjusting interpretations of theory, and hence methods used (Ceccarelli and Grando, 2002).

For this reason, farmer–breeder collaboration may often benefit from making a clear distinction between (a) fundamental biological theory, (b) interpretations of fundamental theory, and (c) methods and practice, with ‘c’ possibly very different depending on whether it is based on ‘a’ or ‘b’, or on different versions of ‘b’. Many of the disagreements about plant breeding methods for participatory plant breeding (PPB) may grow out of disagreements about differences in the *interpretation* of fundamental biological theory, and disagreements about these interpretations may in turn be based on the belief of proponents that their interpretations of fundamental theory are *not* based on their unique experiences and assumptions, but rather are part of fundamental theory.

Therefore, especially for those biophysical aspects of genotypes and environments that are less well understood in terms of plant breeding theory, PBK may more likely be based on each person’s or institution’s specific experiences with the particular environments and crop genotypes they work with, and thus may be less generalizable, and more apt to be influenced by pre-existing knowledge (including values) specific to the plant breeder’s social environment. This means that disagreements between farmers and plant breeders, and among plant breeders, could arise even though fundamental genetic and statistical principles remain constant across a range of contexts, because the ‘art’ of plant breeding is more tied to specific individuals or environments (Ceccarelli and Grando, 2002; Soleri and Cleveland, 2001).

#### 14.2.4 Farmer knowledge

A lack of empirical research and theoretical analysis has contributed to using overly simplified definitions of FK (and often of PBK as well), and the common failure to test the many assumptions underlying these definitions (Cleveland, 2006; Sillitoe, 1998). We can very roughly divide current views of FK into two categories: there are those that see FK as fundamentally different from PBK, and those that see it as fundamentally similar. These views also form the basis of particular advocacy perspectives; generally neither considers the theoretical content of FK.

In the first category, definitions of FK emphasize that it is primarily value-based, comprising intuition and skill, socially constructed, and based on the local social and environmental contexts and culture. According to this perspective, farmer and PBK are seen as fundamentally different, and attempts to explain FK in scientific terms impede true appreciation of FK.



The second category emphasizes that FK consists primarily of rational empirical knowledge, usually focusing on either economic or ecological knowledge. Definitions of FK as economically rational tend to assume that scientists are more rational, and that farmers are risk neutral and their behaviour is based on a desire for profit maximization in the form of high average yields (e.g. Zilberman, Ameden and Qaim, 2007). According to this definition, the role of outsiders should be to facilitate the replacement or modernization of small-scale farming, including replacement of FVs with MVs (Mohapatra, Rozelle and Huang, 2006; Srivastava and Jaffee, 1993). The definition of FK as ecologically rational tends to assume that farmers have detailed, accurate and therefore sustainable ecological knowledge of their environments. The first part of that definition is supported by much empirical data, especially ethnotaxonomic studies of plants and animals, while recognizing variation in distribution of cultural knowledge as the result of factors including age, gender, social status and affiliation, kinship, personal experience and intelligence (Berlin, 1992).

Participatory research has usually been based on the second definition of FK. As a result, the focus in using farmer knowledge has been on the details it can provide in the form of a discriminatory or, most frequently, descriptive tool in PPB. For example, a major survey of 49 PPB projects found that the primary focus was soliciting farmers' descriptions and rankings of selection criteria. For about two-thirds of these projects, "identifying, verifying, and testing of specific selection criteria was the main aim of the research", and 85 percent obtained farmers' selection criteria for new varieties (Weltzien *et al.*, 2003: 17–18, 51, 75). The main impact on scientific plant breeding

appears to have been "better understanding of new ideotypes based on farmers' experiences, specific preferences and needs" that will affect priorities of formal plant breeding and the "process of formal variety development" (Weltzien *et al.*, 2003: 75).

More recently, using FK of crops as a discriminatory tool has become more common. This has been important in some PPB work, with farmers asked to choose among varieties already released in other areas (e.g. for rice and chickpea; Joshi and Witcombe, 1996), among new and experimental varieties (e.g. for pearl millet; Weltzien *et al.*, 1998), or among segregating populations (e.g. F<sub>3</sub> bulks with barley; Ceccarelli *et al.*, 2000), or to select individual plants within segregating populations (e.g. F<sub>5</sub> bulks of rice; Sthapit, Joshi and Witcombe, 1996; and F<sub>4</sub> bulks of rice; Virk *et al.*, 2003). When such choice or selection is accomplished using actual plants, plant parts or propagules, analysis of results can reveal farmers' implicit criteria that they may not be able to verbalize easily, if at all (i.e. it may be unconscious) (Louette and Smale, 2000; Soleri, Smith and Cleveland, 2000).

These approaches to understanding FK have made valuable contributions to achieving more effective crop improvement for farmers' conditions. However, the theoretical basis of FK is not usually considered, and rigorous comparisons with PBK have not been carried out, "opportunities rarely develop for interaction between breeders and farmers beyond the survey", with the discussion "driven by the breeders' concepts of the present situation, making it difficult for farmers to express their views in the context of their reality" (Weltzien *et al.*, 2003: 51). It may also be difficult for farmers to communicate to outsiders their knowledge that goes beyond description or discrimination. For this reason a

definition of knowledge—both farmer and scientist—as complex, and including values, empiricism, theory and experience is useful (Cleveland, 2006). This definition underlies an approach that starts with basic theoretical knowledge and clearly distinguishes theory from its local interpretation, in an attempt to better understand farmers' choice and selection, and to identify possible bases for substantive collaboration between farmers and scientists. In the rest of this chapter we use this definition to look at two key processes in plant breeding: choice of populations (or varieties) for direct use or for further breeding, and selection of individuals within a population. We focus on our understanding of FK and practice of choice and selection, how farmers and scientists can better collaborate in those steps, and why such collaboration is important.

### 14.3 FARMER CHOICE AND SELECTION: PAST, PRESENT AND FUTURE

While this chapter is primarily about contemporary farmer and plant breeder choice and selection, a brief look at the broad trends in the past, present and future of crop improvement in relation to farmers will help in understanding the challenges and potential for plant breeding with farmers. This section is not essential for understanding the rest of the chapter, and might be quickly skimmed and used as a reference.

As measured by the rate of desired crop genetic changes achieved by selection, three broad stages have been suggested (Gepts, 2004). Initial rapid progress with domestication was followed by long periods of much slower change as original domesticates spread to new environments and responded to a range of new natural and artificial selection pressures, and with modern plant breeding the rate of change in MVs increased substantially, while most

farmers continued as before. There have also been marked changes in crop genetic diversity over time, especially at specific and intraspecific taxonomic levels.

#### 14.3.1 Domestication and subsequent changes in diversity

While domestication resulted in a large decrease in the number of plant species exploited, it was followed by large increases in intraspecific diversity, as FVs evolved as a result of natural and artificial selection in new biophysical and sociocultural environments (Harlan, 1992) (see Chapter 1, this volume). For many of the more widely grown food crops, domestication resulted in evolutionary changes making them genetically distinct from their closest wild relatives today, and most became dependent on humans for reproduction (Harlan, 1992; Simmonds and Smartt, 1999). Exceptions exist, especially among some perennial fruit crops, more accurately described as semi-domesticates, where crops are not the result of selection resulting in *E*, but rather are choices of superior genotypes from among those extant in the wild (for olive, see Baldoni *et al.*, 2006, and Breton *et al.*, 2006).

Domestication seems likely to have been the result of indirect selection and unintentional direct selection (e.g. when farmers select for large seed size or brittle rachis as a result of their seed collection behaviour; Harlan, 1992), and perhaps some intentional selection for evolutionary change (see Section 14.1.2). However, it is very difficult or impossible to determine the type of selection that resulted in past crop evolution, and experts differ on the type they believe was most important. For example, Allard emphasizes direct, intentional selection,

*The consensus is that even the earliest farmers were competent biologists*

*who carefully selected as parents those individuals ... with the ability to live and reproduce in the local environment, as well as with superior usefulness to local consumers.*

(Allard, 1999)

In contrast, Simmonds and Smartt (1999: 13) emphasize indirect selection: “the art of cultivation is perhaps the peasant’s most potent contribution.”

Similar to studies based on archaeological data, results of molecular analyses support the hypothesis that farmers’ selection has been successful in achieving evolutionary change for traits in the ‘domestication syndrome’ that might be indirectly or unintentionally favoured because of agronomic superiority (see Chapter 1, this volume). There is also evidence that farmer selection has been a powerful force for evolutionary change based on other preferences as well. For example, three major genes involved in starch metabolism in maize were found to have unusually low genetic diversity compared with its closest wild relative (teosinte, *Zea mays* subsp. *parviglumis*), which is strong evidence of selection for specific processing and culinary qualities important for the primary manner in which maize has been consumed in its regions of origin and diversity (Whitt *et al.*, 2002). In addition, three other loci contributing to sweet maize grain phenotypes showed low diversity (resulting from strong selection) in only certain varieties in particular locations, evidence of further specialization in the non-agronomic selection pressures farmers have exerted on maize (Olsen *et al.*, 2006; Whitt *et al.*, 2002). Similarly, it appears that strong directional selection for sticky, glutinous grain quality resulted in a selective sweep affecting an area over 250 kb long that includes the locus coding for this quality (low amylase produc-

tion) and other linked loci. The presence of this sweep distinguishes the sticky rice favoured by upland northeast Asian peoples from the non-glutinous rice varieties used by other Asian groups, and presumably would be among their fundamental choice criteria, perhaps as an adaptation for eating with chopsticks (Olsen *et al.*, 2006).

Increasing evidence for a number of crops suggests that domestication could have occurred over short periods relative to the ~12 000 years that crop plants have been cultivated (Gepts, 2004). Domestication syndrome traits often appear to be determined by a small number of genes with large effects, suggesting that domestication could proceed relatively rapidly. For example, Paterson *et al.* (1995) found a small number of quantitative trait loci (QTLs) coding for the domestication syndrome traits of seed size, photoperiod sensitivity of flowering, and brittle rachis in taxonomically distinct cereals with diverse centres of origin (sorghum, rice and maize). In common bean (*Phaseolus vulgaris* L.), control of the domestication syndrome involves genes that have a large effect (>25–30 percent) and account for a substantial part of the phenotypic variation observed (>40–50 percent) (Koinange, Singh and Gepts, 1996). Simulations based on sequence variations at loci coding for biochemical or structural phenotypes in maize and its close and distant relatives have estimated that domestication could have taken from 10 (Eyre-Walker *et al.*, 1998) to between 315 and 1 023 generations (Wang *et al.*, 1999). In addition to selecting for characteristics of the ‘domestication syndrome’, especially in cereals and small pulses (Harlan, 1992), domestication in sexually propagated crops may have resulted in increased autogamy and therefore homozygosity, expressed

phenotypically in greater trueness to type in a population over generations. In contrast, some vegetative propagation may have selected for heterozygosity (via heterosis) and therefore for allogamy, as contemporary evidence suggests for cassava (Pujol, David and McKey, 2005).

The genetic changes that define crop domestication are inextricably linked with changes in selection pressure. These pressures are not only exerted by direct human selection of propagules for planting, but perhaps more often with the differences in selection pressures created by human modification of growing environments (Figure 14.1). In southeast China, for example, evidence for the earliest cultivation of both wild and domestic rice (~7 700 BPE) suggests that this occurred where farmers were intensively managing coastal wetlands with fire to control vegetation and bunds to control flooding, and increased nutrient concentration in fields (Zong *et al.*, 2007). Bringing wild plants into human modified environments, such as compost heaps near houses, as well as exchange of seeds and other propagules, also facilitated domestication via hybridization, as with *Leucaena* in southern Mexico, and probably with two other important domesticates from that region, agave (*Agave* spp.) and prickly-pear cactus (*Opuntia* spp.) (Hughes *et al.*, 2007). Domestication generally decreased the fitness of plants in natural environments, and made them more dependent on humans and human-managed environments.

The geographical spread of domesticated crops led to great varietal diversification as a result of the increase in diversity of natural and artificial selection pressures encountered, followed by choice among preferred populations. It is generally assumed that simple mass selection by

farmers working in combination with local natural selection contributed to the large amount of intraspecific diversity that evolved following domestication:

*Probably, the total genetic change achieved by farmers over the millennia was far greater than that achieved by the last hundred or two years of more systematic science-based effort.*

(Simmonds and Smartt, 1999: 12).

### 14.3.2 Modern, scientific plant breeding

Farmer and plant breeder crop improvement began to be separated about 200 years ago in “technically advanced temperate countries” (Simmonds and Smartt, 1999: 12) with the beginning of specialized, amateur breeding. The widespread acceptance of evolution and the rediscovery of Mendel’s research after 1900 eventually led to modern scientific plant breeding, based on a combination of Darwinian evolution, Mendelian genetics and biometry (Fitzgerald, 1990; Provine, 1971), with modern plant breeders considering themselves ‘applied evolutionists’, whose goal is to develop plant varieties better adapted to growing environments, measured primarily as increased yield (Allard, 1999).

Farmers and formal plant breeders continued to collaborate at this time, for example in making crosses and selections in maize breeding in the United States of America (Fitzgerald, 1990; Schneider, 2002). But as the importance of evolutionary theory in plant breeding increased in comparison with empirical heuristics, the economic importance of plant breeding increased and came to dominate formal plant breeding by professional plant breeders. Simultaneously, the farmer’s role in crop improvement in industrial countries decreased, for example in the United States of America (Fitzgerald,

1990; Kloppenburg, 1988) and Switzerland (Schneider, 2002). Plant breeders' concepts subsequently developed independently of farmers' concepts, effectively separating the formal from the informal systems of crop improvement and seed multiplication. When farmers are involved by contemporary plant breeders in their work it has generally been limited to the stage of evaluating and choosing among plant breeders' populations or varieties in their fields (Duvick, 2002).

### 14.3.3 Biotechnology

Advances in genetics and molecular biology have led to developments in biotechnology that have dramatically enhanced the ability to understand and manipulate plant genomes. Functional genomics has elucidated the relationship among genetic components and to phenotypes; marker assisted selection (MAS) has increased the efficiency of breeding for specific traits; and genetic engineering has made it possible to transfer genes from almost any organism into a crop species. When these genes come from a different species the process of transformation is called transgenesis, and the resulting crop variety a genetically engineered (GE) variety, genetically modified organism (GMO) or, most accurately, a transgenic crop variety (TGV).

TGVs are a rapidly growing agricultural technology, with the area planted increasing by 9.4 percent from 2007 to 2008, to over 125 million hectares (James, 2006, 2008), or over 9 percent of cultivated land globally (calculated from FAO, 2007, 2009). Currently grown TGVs are primarily targeted to industrial agriculture and designed to enhance yield and net profit for farmers by directly reducing pest damage or facilitating herbicide use. Globally, most of the area planted to TGVs is in large-scale

industrial agriculture, and is expanding in the Third World. Of the 23 countries growing TGVs in 2007, 12 were 'developing' countries, and estimated to account for 43 percent of the area planted and 90 percent (11 million) of the farmers growing TGVs. Of these, 99 percent (10.9 million) were in China and India, growing mostly Bt cotton (James, 2006, 2007). Currently, TGVs of food crops for Third World farmers are either planned, being developed, in field trials, or approved and in production.

TGVs are currently being promoted by development organizations, governments and corporations as the key to increasing production and income and reducing hunger and malnutrition in SSTW agriculture (FAO, 2004; Rockefeller Foundation, 2007; World Bank, 2007). However, the focus on TGVs to improve Third World agriculture is very controversial (Abate *et al.*, 2008; Stokstad, 2008). A number of studies, mostly by economists and of Bt cotton, maize and rice, have concluded that farmers readily adopt TGVs because they increase yield and income, reduce pesticide applications or improve farmer health (Gouse *et al.*, 2006; Huang *et al.*, 2003, 2005; Morse, Bennett and Ismael, 2006; Qaim and Zilberman, 2003). Other studies have found that adoption may be the result of fads (Stone, 2007) or a lack of freedom to choose (Witt, Patel and Schnurr, 2006), and that higher yields and reduced pesticides may be reversed after several years due to the emergence of secondary pests (Wang, Just and Pinstrup-Andersen, 2006). Others have suggested that the net benefits of TGVs may not be as great as those of alternative improvements in agriculture (e.g. Uphoff, 2007). The potential ecological and genetic effects of TGVs and transgene flow into non-TGV crop or wild or weedy populations, especially in Third

World agriculture, are not well understood (Ellstrand, 2003b; Heinemann, 2007; NRC, 2002; Snow *et al.*, 2005).

The spread of biotechnology has also resulted in unintentional transgene flow, including into centres of diversity, e.g. maize transgenes documented in Mexican FVs (Alvarez-Morales, 2002; Pineyro-Nelson *et al.*, 2009; Serratos-Hernández *et al.*, 2007). Such transgene flow can be difficult to prevent (NRC, 2004), the early stages of transgene flow to FVs are extremely difficult to monitor (Cleveland *et al.*, 2005), and the effects may often be irreversible (Ellstrand, 2003a). Potential effects of transgene flow on FVs and farmers are both positive and negative, and will require risk analysis and evaluation specifically adapted to each location – crop combination within the Third World (Cleveland and Soleri, 2005; Soleri, Cleveland and Aragón Cuevas, 2006). Transgenes can introduce novel forms of diversity into the crop populations being selected upon by farmers and plant breeders, but there is no reason to expect that farmers will be able to retain, discard or manipulate them any differently from other genes.

#### 14.3.4 Privatization

In the early 1980s, some countries and farmer support groups sought to do away with all intellectual property rights (IPRs) in crops, establishing 'farmers' rights' to all crop genetic resources, but this move was defeated by the United States of America and other industrial nations (Fowler, 1994), and private rights in plants and other living organisms now dominate, with industrial patents leading the way (Atkinson *et al.*, 2003). Farmers were left with having to defend themselves from the advances of an IPR system in plants designed by industrial nations and corporations, a system that generally does not recognize farmers'

traditions or current needs (Cleveland and Murray, 1997).

Much plant breeding has moved from the public to the private sector (Frey, 1996) and thus selection criteria are increasingly vulnerable to being dominated by private profit motives rather than public good motives (Simmonds, 1990), which is especially evident for TGVs. The major share of agricultural biotechnology processes and products are controlled by private multinational corporations with little incentive to develop TGVs most appropriate for Third World farmers who cannot afford to pay the premium for TGV seed (CGIAR, 2006; World Bank, 2007: 178).

Similarly, there is increasing concentration in the seed sector, which potentially reduces competition and limits the kinds of crops and crop varieties produced and made available. The largest seed companies control an ever larger proportion of the seed market; according to one estimate, between 1997 and 2004 the companies with the largest sales increased their market share from 27 percent to 33 percent, and in 2004 the top four companies owned 38 percent of biotechnology patents (World Bank, 2007: 135–136).

The drive to globalize industrial-world IPRs in plants has been intensified as a result of pressure from agricultural biotechnology corporations (Graff *et al.*, 2003; Shorett, Rabinow and Billings, 2003). This means that as patented TGV crops and their transgenes move intentionally or unintentionally around the world, so could the rights of the companies who own them. Movement of transgenes into non-transgenic crop populations, whether producing a net benefit for the farmer or not, makes farmers vulnerable to IPR claims from the technology developer. In the United States of America and many other industrialized countries, patent

holders have rights to seek damages from farmers who end up with patented genes in their crops, even though farmers do not want them, and do not know they are there (Janis and Kesan, 2002). The World Trade Organization (WTO) seeks worldwide uniformity of laws for IPRs in plants and plant DNA to facilitate global enforcement, and many Third World countries have adopted the industrial world model (UPOV – International Union for the Protection of New Varieties of Plants) while others have adapted their national laws to protect small-scale farmers (World Bank, 2007: 167). The spread of IPRs and coupled economic control of agricultural biotechnology means that Third World farmers and the nation states they live in will have a difficult time gaining meaningful control of the means to intentionally create TGVs more suited to their own needs, if this is the path they choose. As a result, most organizations promoting TGVs more suited to Third World farmers are advocating public-private partnerships (CGIAR, 2006; FAO, 2004; World Bank, 2007), yet it is not clear how farmers' rights will fare in this collaboration, and they are not being rigorously addressed.

While most corporations deny they would enforce their IPRs against Third World farmers, there are no guarantees. In addition to transgenes, control of local farmers' crop genetic resources, and the traditional names and other cultural property that go with them through industrial IPRs, can legally and economically prevent local people themselves from reaping potential benefits in a global marketplace increasingly interested in traditional crops and foods (Soleri *et al.*, 1994). There are already cases of this, some of which are being challenged (Pallotini *et al.*, 2004).

#### 14.3.5 Sustainability and farmer-scientist collaboration

The search for sustainability provoked by negative environmental impacts of agriculture (Matson *et al.*, 1997; NRC, 2002; Tilman *et al.*, 2002), and its genetic vulnerability (NRC, 1991) has led to the incorporation of more genetic variation within and among varieties by the formal crop improvement system (Cooper, Spillane and Hodgkin, 2001; Ortiz *et al.*, 2007). It has also encouraged a re-evaluation of G×E in crops and how best to exploit this for farmers' conditions (Ceccarelli *et al.*, 1994, 2001). The impact on farmer selection will be in the greater intraspecific and intravarietal diversity deployed in formally developed varieties, and greater interest in that system for breeding goals more similar to those of farmers. Part of the interest in sustainability (environmental, economic and social) has led to collaboration between farmers and scientists.

Participatory or collaborative plant breeding is attempting to reverse the separation of farmers and scientists and improve the outcomes of choice and selection in farmers' terms (Cleveland and Soleri, 2002a; PRGA, 2004; McGuire, Manicad and Sperling, 2003; Weltzien *et al.*, 2003). To that end, the next sections focus on understanding farmers' choice and selection, and thereby enabling farmers and scientists to work more closely and productively in improving the crops they grow and depend upon.

#### 14.4 CHOICE OF GERMLASM

It is important for plant breeders to understand how and why farmers choose varieties of their crops, because farmer choice will ultimately determine whether a new or improved variety will be useful. In this section we consider choice based on perceived

risk and yield stability, and on other factors, including quality traits.

Just as there are factors favouring the inclusion of more than one variety in a farmer's crop repertoire, there also are factors limiting the number of varieties chosen. These include farmers' resources, growing environments and crop reproductive biology, among other possible factors. Additionally, if crop varietal diversity is maintained at a community instead of household level, then farmers may not feel the need to maintain some varieties themselves each year, even though they consider those varieties to be part of their varietal repertoire and intend to grow them in the near future (for the case of rice, see Dennis, 1987).

#### 14.4.1 Varietal choice, yield stability and risk

In much of the past plant breeding for SSTW farmers, it was assumed that high yielding varieties selected in more optimal environments would outyield FVs in farmers' environments (Ceccarelli *et al.*, 1994; Ceccarelli, Grando and Booth, 1996). If farmers did not adopt these varieties it was assumed that they were ignorant of how to improve their growing environments (Aquino, 1998), or if they could not afford to do so, it was assumed that they should get out of farming. Consideration of risk provides a different understanding of farmers' varietal choices and other practices. In the conventional economic model, a risk-neutral farmer would only grow the one variety that gives the highest profits per unit area (Smale, 2002). However, many small-scale farmers in marginal environments are risk averse (Anderson and Dillon, 1992; Soleri *et al.*, n.d., 2008), and spatial environmental variation increases the likelihood of cross-overs in varietal performance (qualitative G×E; see Section 14.5.1, below) between

farmers' fields, or even within a field (Soleri *et al.*, 2002). Variation in time is also large: in the semi-arid tropics, seasonal and annual rainfall is highly variable, and even in years with adequate total rainfall, rains may arrive late, end too early, stop for a period or be too heavy during flowering or harvesting. Therefore farmers may often grow two or more varieties of many crops, each with distinct agronomic characteristics presumably "as a measure of insurance against vagaries of the weather, diseases, or pests" (Doggett, 1988).

Understanding farmers' choice can provide valuable insights for scientific plant breeders. In response to climate change in the form of the southern movement of isohyets, policy-makers in Mali argue that improved short-cycle varieties are a critical part of stabilizing the country's volatile cereal production (Dembélé and Staatz, 2000). One result is that both sorghum breeders and farmers in southern and central Mali look north for shorter cycle varieties. Interviews in four villages in the Upper Niger River valley zone of Mali found the most common reason for adoption of the three most popular sorghum varieties was early maturity (Adesina, 1992). However, since in good rainfall years long-cycle varieties generally have higher yields (Adesina, 1992) and are rated higher for quality (Ingram, Roncoli and Kirshen, 2002), farmers do not give these up entirely. Their choices thus increase the number of varieties in their repertoires, although the net impact on genetic diversity has not been investigated. Another study in Mali of farmers' choices among their traditional sorghum varieties in terms of one or more than one variety, and short-cycle or long-cycle varieties, found that farmers make these choices in an effort to optimize outputs in the face of variation in the growing environment and in



availability of human-managed inputs, such as labour and tools. For example, better rains in 2002 compared with 2001 appear to be a major factor in the general shift toward a greater number and longer cycle length of varieties, with 60 percent of farmers adding varieties between 2001 and 2002 (Lacy, Cleveland and Soleri, 2006).

The need for research on farmer choice and risk is also illustrated in the case of potato in the Andes (Zimmerer, 2002). An emphasis on potato varieties with large tubers because farmers prefer the higher yield of these varieties would ignore the fact that poorer farmers actually select small tubers for planting because they can reduce the amount of potential food used for planting material. An implication is that the varieties poor farmers would actually choose to plant may be quite different from that anticipated by breeders, indicating changes were needed to make improvement programmes more relevant for those farmers' needs.

These and other studies suggest that crop improvement programmes need to specifically target farmers' growing environments and needs, and use local germplasm as the basis for this (Ceccarelli and Grando, 2002). They indicate the importance of plant breeders supporting varietal portfolios (Ceccarelli *et al.*, 2003; vom Brocke *et al.*, 2003a; Weltzien *et al.*, 2003) available through farmer-to-farmer exchange as an alternative to the development of a small number of varieties for large-scale adoption. In addition to decreasing farmer risk, this strategy also supports conservation of crop genetic diversity *in situ* (Ceccarelli, Grando and Baum, 2007). However, there is also some evidence that MVs developed through participatory varietal selection can replace existing FVs, as with wheat in South Asia (Ortiz-Ferrara *et al.*, 2007). When environ-

mental variation is minimal, there may be little incentive for farmers to maintain FVs while adopting MVs in order to reduce risk due to qualitative G×E (Virk and Witcombe, 2007). Clearly, the diversity outcome of locally focused improvement programmes will depend on the specific situation.

#### 14.4.2 Other factors influencing choice

Farmers may also choose more than one variety because of their different quality traits. For example, interviews with 599 Nigerian farmers supported the conclusion that they grow both long-cycle and short-cycle cowpea varieties: short-cycle for food grain and long-cycle for feed during the dry season when other fodder sources are scarce (Abdullahi and CGIAR, 2003). Some maize farmers in Oaxaca, Mexico, maintain varieties specifically for their coloured husks or tassels because of their aesthetic qualities, e.g. coloured husks used to wrap tamales impart their colour to them (Soleri, field notes, 1996–1999), and families who make the traditional beverage *tejate* maintain more varieties of maize, using them in its preparation (Soleri, Cleveland and Aragón Cuevas, 2008).

The number of varieties grown by farmers may also be influenced by seed source and social variables (David, 2004). In a study of Mexican maize farmers, choice of total number of varieties grown was related to household seed source. Households planting mostly their own seed chose an average of twice as many varieties in comparison with those households that obtained all their seed from non-household sources (Louette, Charrier and Berthaud, 1997). In a review of field research on farmer crop genetic resources, wealth was a common indicator for producers who cultivated more varieties compared with resource-poor producers (Jarvis *et al.*, 2000). The choice of total number of sorghum varie-

ties may be significantly related to ethnicity, as in one area of the United Republic of Tanzania, where migrant Gogo farmers from a traditional sorghum-growing region grow more than twice the number of varieties as migrant groups from maize-growing regions (Friis-Hansen and Sthapit, 2000).

## 14.5 SELECTION

Given the historical background outlined earlier, including the emphasis on selection as practised by scientists, we now discuss the concept and process of selection, emphasizing the contexts and perspectives of farmers. We begin by reviewing research on farmer understanding of heritability and G×E, two fundamental concepts in selection.

### 14.5.1 Farmer understanding of heritability and G×E

Heritability ( $h^2$ ) is a key determinant of genetic response ( $R$ ) (see Section 14.1.3). One of the main factors that decreases  $h^2$  is environmental variability ( $\sigma_E^2$ ). Another important and related element affecting the outcome of selection is G×E. Interpretation of G×E will influence plant breeders' approaches to developing and improving crop varieties and their choices of how many and which varieties will be released across agricultural environments (Cooper and Hammer, 1996). For these two important elements that affect the results of selection, experience as well as goals will influence the knowledge of farmers and plant breeders and how each responds to variations in  $h^2$  and G×E in their crop varieties and growing environments.

In comparative research on farmers' concepts of  $h^2$ , farmers were presented with scenarios about both high and low  $h^2$  traits (Figure 14.4, Table 14.1). The goal was to determine if farmers noted the contribution

of  $\sigma_E^2$  and  $\sigma_G^2$  to  $\sigma_P^2$ , and if they distinguished between high and low  $h^2$  traits in their major crop. The first null hypothesis was that there was no difference in distribution of farmers' responses concerning consistency between parent and progeny phenotypes in a typical, variable environment and in a hypothetical, uniform environment for (i) relatively low  $h^2$  traits, and (ii) relatively high  $h^2$  traits. This hypothesis was rejected for low  $h^2$  traits, but accepted for high  $h^2$  traits (most farmers anticipated no change in phenotype regardless of environment), suggesting farmers see little or no contribution of genotype to  $\sigma_P^2$  for low  $h^2$  traits, and the opposite for high  $h^2$  traits. The second null hypothesis, that farmers' responses indicate no perception of differences in  $h^2$  for relatively low and high  $h^2$  trait expression in a variable environment, was also rejected, supporting the conclusion that farmers do perceive differences in  $h^2$  of traits. Thus, most farmers distinguish between high and low  $h^2$  traits, and consciously select for the former, while often considering it not worthwhile or even possible to seek  $R > 0$  for the latter, especially in cross-pollinated crops (Soleri *et al.*, 2002). Given farmers' experiences and the tools and methods available to them, the role of  $\sigma_G^2$  in low heritability traits is obscured by the  $\sigma_E^2$  in their growing environments. Similarly, Ceccarelli (1996) argues that plant breeders' lack of experience with growing environments as stressful and variable as those of farmers has obscured plant breeders' ability to perceive qualitative G×E in some MVs between farmers' environments and the more favourable ones they are accustomed to.

To understand farmers' perceptions of spatial G×E interactions we used a scenario with two genotypes originating in contrasting growing environments at three

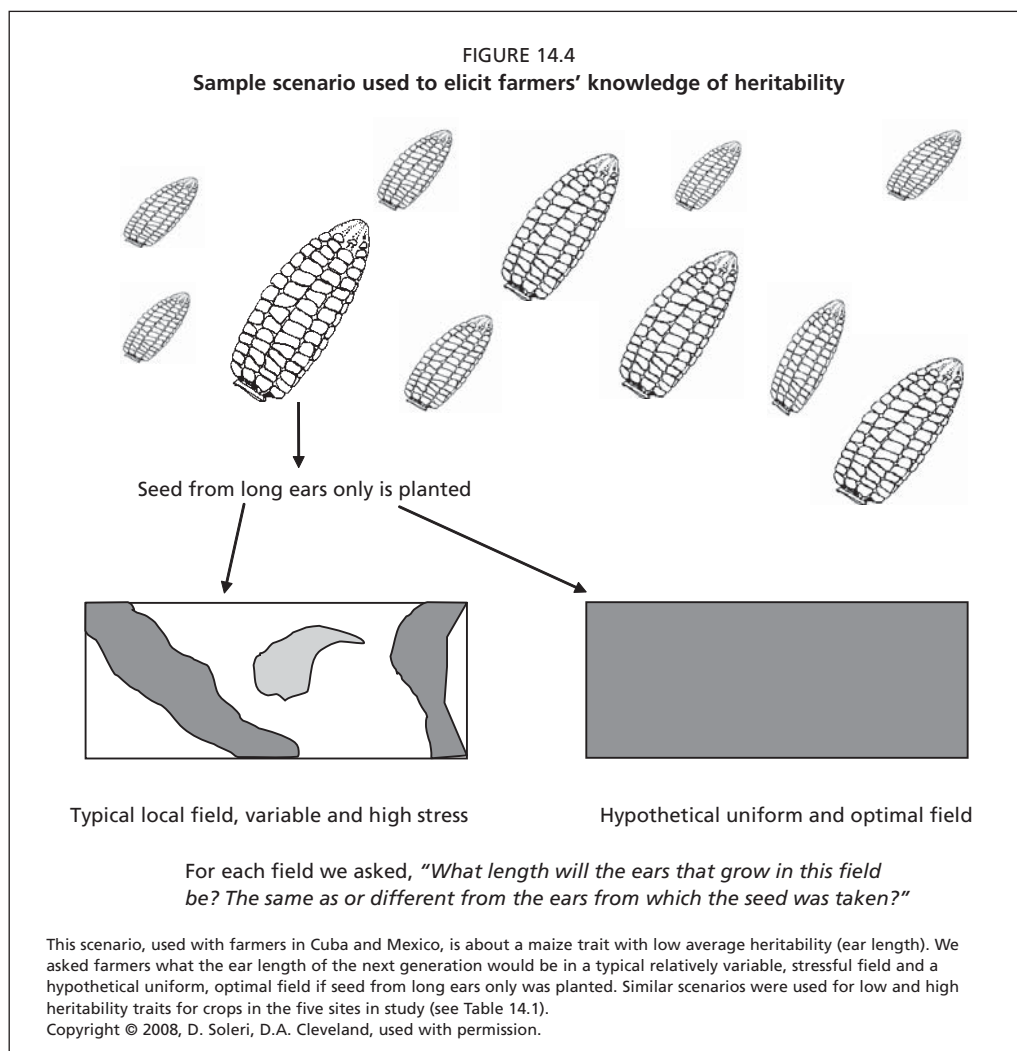


TABLE 14.1

**Understanding farmers' perceptions of heritability**

Location, crop	Null hypothesis #1: For traits with relatively low or those with relatively high $h^2$ , distribution of farmers' responses is the same whether scenarios depict typical or optimal environments, i.e. farmers do not see a contribution of environment (Env) to phenotype		Null hypothesis #2: In scenarios depicting a typical environment, distribution of farmers' responses is the same for traits with relatively low or those with relatively high $h^2$ , i.e. farmers do not see a difference in $h^2$ between traits
	(a) Low $h^2$ trait across typical and optimal Envs	(b) High $h^2$ trait across typical and optimal Envs	Low v high $h^2$ traits in typical, variable Env
Cuba, maize	Ear length*	Husk colour	Ear length v. husk colour*
Mexico, maize	Ear length*	Tassel colour	Ear length v. tassel colour*
Mali, sorghum	Panicle weight*	Glume colour*	Panicle weight v. glume colour*
Syria, barley	Plant height*	Seed colour	Plant height v. seed colour*
Nepal, rice	Plant height*	Seed colour	Plant height v. seed colour*

\* Hypothesis rejected, Fisher's exact test,  $P < 0.05$ Based on Soleri *et al.*, n.d.

levels: between locations, between fields in one location, and between places in one field (Soleri *et al.*, n.d., 2002). The results indicated that farmers ( $n = 208$ ) perceive inter- (57 percent) and intra- (30 percent) location  $G \times E$  for their major crop, though far fewer at the latter level.  $G \times E$  within a field (18 percent) was noted mostly, though not exclusively, by those growing self-pollinated crops, and especially those working at a small scale with intimate knowledge of within-field soil and moisture variations (e.g. rice farmers in western Nepal). Similarly, 37 percent of farmers responded that a qualitative  $G \times E$  interaction could occur in their crop due to temporal environmental variation in the form of annual precipitation. In the presence of qualitative  $G \times E$ , perceptions of the best genetic strategy may differ and be informative about the needs of particular groups or regions. As mentioned in Section 14.4.1 above, farmers tended to favour yield stability over high yield when choosing among varieties in the face of qualitative temporal  $G \times E$ . This choice was significantly more frequent among farmers in more difficult environments compared with more favourable environments.

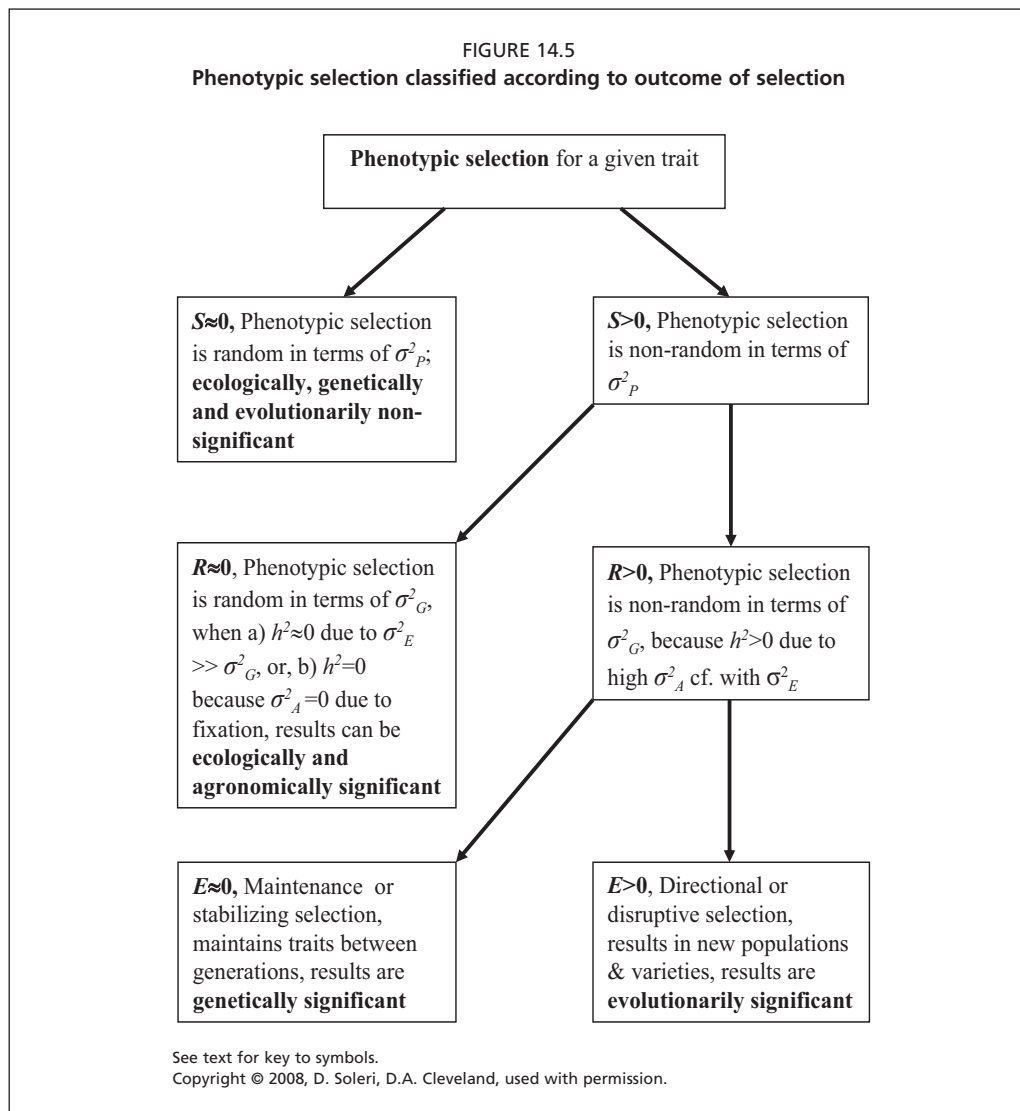
#### 14.5.2 Farmers' selection goals

If plant breeders misunderstand what farmers are and are not attempting to accomplish with their selection practices, it can limit the potential for meaningful collaboration and lead to inappropriate investments of scarce time and resources. Such misunderstandings have grown out of the historical process of separation of farmers' and plant breeders' work (Cleveland and Soleri, 2007).

Just as early evolutionary biologists looked to breeders for empirical demonstration of results of selection that illuminated

evolution, breeders looked to farmers for their applied knowledge and practice that produced practical results in the form of new varieties, as in the early commercial development of maize in the United States of America (Wallace and Brown, 1988: 87–90). With the increased importance of formal science in plant breeding compared with empirical heuristics, and later as plant breeding moved from the public to the private sector (Kloppenburger, 1988), plant breeders began to eliminate farmers from their work (e.g. Schneider, 2002). Plant breeders' and farmers' practices and concepts subsequently developed independently of each other, effectively separating the formal and informal systems of crop improvement and seed multiplication, with plant breeders coming to dominate: "a trend that has been at least locally apparent for 200 years" (Simmonds and Smartt, 1999: 13). Plant breeders focused on modern varieties widely adapted to more optimal, more intensively managed environments, while many traditionally-based farmers in relatively marginal environments continued to focus on traditional, specifically adapted varieties for their diverse, more marginal growing environments (Ceccarelli and Grando, 2002; Cleveland, 2001). When contemporary plant breeders involve farmers in their work, it has generally been limited to the stage of evaluating the plant breeders' populations or varieties in the field (Duvick, 2002), i.e. choosing among different populations or varieties, not selecting among different plants to genetically change existing populations or varieties.

Today, many modern plant breeders consider themselves to be 'applied evolutionists', whose goal is to develop plant varieties better adapted to improved growing environments, with adaptation measured primarily as increased yield



(Allard, 1999: 49). Their emphasis in selection is on achieving directional, multi-generational, micro-evolutionary change. This makes sense given the organization of industrial agricultural systems (see Section 14.2.1 above, and Figure 14.3). It also means that plant breeders often view farmers' selection of seeds or other propagules for planting as a form of mass selection for heritable traits, the process that is assumed to account for crop domestication and for

the ensuing proliferation of crop varieties. It also means formal plant breeders tend to judge the efficacy of farmer seed saving in terms of applied evolution, i.e. the same criteria they apply to their own work, and assume that farmers use these criteria as well.

In the following sections we describe phenotypic selection by farmers organized in terms of possible outcomes: longer-term (multi-generational) genetic change

or micro-evolution (E) [hereafter referred to as 'evolution', in the sense of multi-generational change in the context of agricultural crops, not in the larger biological sense of speciation]; inter-generational genetic change or response (R); and within-generation phenotypic differentiation (S, selection differential) (see Section 14.1.2 above, and Figure 14.1). Where possible, we also discuss farmer goals for selection, although many studies of farmer selection that document genetic or agronomic effects do not document farmers' goals (and vice versa). Note that, regardless of goals, the outcomes of farmer selection can be varied, as depicted in Figure 14.5.

#### 14.5.3 Selection for evolution

The clearest evidence for contemporary farmer selection for evolution is in species that are normally propagated clonally. Some Andean potato farmers search their fields for volunteer seedlings resulting from spontaneous hybridization as a way to diversify their production (Zimmerer, 1996: 201). For example, indigenous South American farmers intentionally incorporate cassava seedlings into recognized varieties, resulting in increased heterogeneity within varieties (Elias *et al.*, 2001; Pujol, David and McKey, 2005). Farmers also select the largest volunteer seedlings, which results in increased heterozygosity as a result of the most heterozygous plants also being the largest, and therefore the least likely to be eliminated during early weeding, although farmers' goals for this selection are unclear (Pujol, David and McKey, 2005).

In seed-propagated species that are predominantly self-pollinated, compared with cross-pollinated species, it is relatively easy to make and maintain evolutionary changes by selecting from among the segregating  $F_1$  plants or those

of later generations, resulting from limited spontaneous cross-pollination. Experimental evidence from Syria shows that farmers could efficiently select among over 200 barley entries (fixed lines and segregating populations), with results in terms of yield potential that equalled, and in one case exceeded, selections by plant breeders in the same environments (Ceccarelli *et al.*, 2000). These findings indicate that farmers have developed selection criteria for identifying high yielding phenotypes that are just as effective as those used by breeders, and more effective in the growing environments typical of those farmers' own fields (Ceccarelli and Grando, 2007).

It is much more difficult to effect evolutionary change in predominantly cross-pollinated, seed-propagated species, especially for quantitative traits with low heritability. However, as described earlier, farmers can discriminate between low and high heritability traits, and use this as a basis for decisions about selection (Soleri *et al.*, 2002). Farmers in Oaxaca, Mexico, often select maize seed with the goal of changing or creating populations with preferred, highly heritable traits, like kernel, tassel and husk colours for culinary and aesthetic reasons (e.g. maize varieties selected for the beauty of their purple tassels) (Soleri and Cleveland, 2001), while the majority of these same farmers see no possibility of changing the key trait of yield, which has low heritability, as discussed below (Soleri and Cleveland, 2001). There is evidence that farmers in central Mexico have selected for and maintained a new landrace, based on seed and ear morphology, among segregating populations resulting from the hybridization of two existing landraces (Perales, Brush and Qualset, 2003). In Rajasthan, India, there is evidence based on research with pearl millet that farmers use

mass selection for low heritability traits in cross-pollinating species with the goal of making directional change in their varieties (Christinck, 2002: 126; Vom Brocke *et al.*, 2002). This research also documented farmers' intentional introgression of modern with traditional varieties of pearl millet, and subsequent selection, resulting in increased genetic variation and long-term directional change (*E*) in selected traits, such as growing period (Christinck, 2002: 123; vom Brocke *et al.*, 2003a).

However, although it is clear that farmers can understand the principle of phenotypic selection and use it to achieve goals of evolutionary change with different crops, this may not always, or even usually, be their goal, or the result.

#### 14.5.4 Selection for genetic response, but not evolution

Farmers also select with the goal of eliminating changes in phenotypic traits resulting from gene flow or natural or indirect phenotypic selection, i.e. to achieve *R* but not *E*. Best documented are farmers' attempts to maintain varietal ideotypes based on quantitative or qualitative phenotypic traits over time in the face of gene flow (Berthaud *et al.*, 2001). Plant breeders can control unwanted gene flow much more effectively in their experimental plots than farmers can in their fields, and in industrial agriculture farmers often buy new seed every year, especially for cross-pollinated crops like maize, eliminating most concerns regarding gene flow.

This type of farmer selection to eliminate changes may contrast with maintenance (stabilizing) selection by plant breeders, which usually has the goal of maintaining yield in the face of changing environments by incorporating new alleles or changing allele frequencies, and may

result in new varieties (i.e. the goal is *E*) (Evans, 1993: 313–314). Like plant breeders (Cooper, Spillane and Hodgkin, 2001), farmers also encourage gene flow under some conditions, for example mixing seed from different sources, planting different populations contiguously or in same plot, and by making crosses, as a way of increasing the variation on which to select.

Farmers can be successful in maintaining varietal ideotypes through direct, intentional selection for key traits, especially for highly heritable phenotypic traits, like those that define a variety. This type of selection is probably most important for cross-pollinated crops, such as pearl millet and maize, as discussed below, since it is much more difficult to maintain populations in these compared with clonally propagated and self-pollinated crops. In eastern Rajasthan, India, amplified fragment length polymorphism (AFLP) analysis showed that farmers maintained the ideotypes of distinct introduced pearl millet FVs, even though they have the same name as local FVs, via intentional selection of panicles for their unique phenotypes (vom Brocke *et al.*, 2003b). In contrast, farmers in Jalisco, Mexico, regularly mix maize varieties together by classifying seed obtained from diverse sources as the same variety based on ear or kernel morphology and colour, which, together with planting patterns, leads to a 1–2 percent level of gene flow between maize varieties during one crop cycle (Louette, Charrier and Berthaud, 1997). A controlled experiment found that, compared with random selection, farmer selection diminished the impact of gene flow on one FV from contrasting FVs for key varietal traits (kernel rows per ear, kernel width and kernel colour), but did not have any effect on allelic frequencies at 9 polymorphic loci coding for traits invisible or unimportant to

farmers (Louette and Smale, 2000). Farmers stated that they were not interested in changing their varieties, but in maintaining varietal ideotypes, and appeared to be achieving their goal. Research in Oaxaca, Mexico, using microsatellite data supported this finding in terms of the results of farmer selection, although farmers' goals were not investigated. Extensive gene flow and little molecular genetic structure was observed, but the maintenance of significantly different maize populations based on morphophenological traits of interest to farmers persisted (Pressoir and Berthaud, 2004b).

A study in Chiapas, Mexico, found that cultural diversity, as measured by ethnolinguistic groups, was not reflected in maize diversity as measured by isozyme variation, but was reflected in some morphological traits (Perales, Benz and Brush, 2005). The differences observed may have been due to unidentified culturally-based networks or practices that structured these maize populations based on farmer selection for a few critical traits against a background of ongoing gene flow (Perales, Benz and Brush, 2005), as was found in the study in the central valleys of Oaxaca, Mexico, (Pressoir and Berthaud, 2004b), although neither study investigated farmer goals in detail.

#### 14.5.5 Selection for intra-generation phenotypic difference

Although farmers are capable of phenotypic selection that is effective in achieving goals of evolution and genetic response, perhaps the most common goal of farmer selection is not genetic, but solely phenotypic, because most of the time a farmer's primary goal in selecting seed is to obtain good planting material. This often means selection for large, clean, disease-free seeds

or other propagules for cross-pollinated (e.g. in maize; Soleri and Smith, 2002), self-pollinated (e.g. in barley; Ceccarelli *et al.*, 2000) and vegetatively propagated crops (e.g. in potato; Zimmerer, 1996). Selection with this goal is also conducted as part of MV seed multiplication (Simmonds and Smartt, 1999: 215). Plant breeders may also carry out this type of selection, for example by removing small seed, but they do this to decrease the contribution of  $\sigma_E^2$  to  $\sigma_P^2$ , and so increase heritability with the goal of  $E$ .

Research on non-heritable phenotypic differences shows these can have important intra-generational effects in terms of ecology and agronomy. Even in species with high heritability for seed polymorphisms, environment may be an important determinant of seed size and shape, and seed polymorphism can be a significant determinant of differential survival via influence on survivorship and adult plant size (Baskin and Baskin, 2001: 208–214). In maize, for example, larger seed size was found to provide significant advantages in the early stages of plant growth (from germination until stem elongation) (Bockstaller and Girardin, 1994), and was correlated with better early vigour, greater leaf area throughout the life cycle and more rapid development from time of emergence to flowering (Pommel, 1990; Revilla *et al.*, 1999).

When the goal of selection is intra-generational phenotypic differentiation, the result may not be genetic response or evolution, especially for low-heritability traits in cross-pollinated crops. This hypothesis was supported by results of maize seed selection exercises with farmers in two communities in Oaxaca, Mexico. The exercises were done with maize ears post-harvest, which is the way these farmers and most others in Mexico select maize seed. Their selections resulted in high  $S$



TABLE 14.2

**Farmers' expectations for response to selection for their primary selection criterion in the major crop they grow**

Country, crop, trait (n)	Question A. Farmers responding that response to intentional selection for 10 cycles > random selection for 10 cycles ( $IS_{10} > RS_{10}$ )				Question B. For farmers responding $IS_{10} > RS_{10}$ to Question A, those stating that response to intentional selection for 11 cycles > random selection for 10 cycles + intentional for 1 cycle ( $IS_{11} > RS_{10} + IS_1$ )			
	n	%		P	n	%		P
Mexico, maize, ear length (59)	23	39	*	0.000000	6	26	*	0.000000
Cuba, maize, ear length (29)	27	93		0.245614	12	44	*	0.000002
Syria, barley, plant height (21)	20	95		0.499999	11	55	*	0.000614
Nepal, rice, grain yield (40)	39	98		0.499999	17	44	*	0.000000
Mali, sorghum, grain yield (40)	35	88		0.057662	23	66	*	0.000078
Total (189)	144	76	*	0.000000	69	48	*	0.000000

One sided Fishers' exact test, of the null hypothesis that, similar to plant breeders, farmers would see intentional selection as achieving a greater response compared to random selection. Calculated using SISA (<http://home.clara.net/sisa/>). RS = random phenotypic selection by farmer, IS = intentional phenotypic selection by farmer.

Based on Soleri *et al.*, n.d.

Some farmers said large seed resulted in higher germination, larger seedlings, early vigour and higher yields, although most farmers attributed their preference for large seed to 'custom'.

It is still possible that simple mass selection for intra-generational phenotypic differences could result in *R* or *E* even if these are not farmer goals. As mentioned above, it is not clear what importance this had during domestication and subsequent diversification of crops, versus intentional selection for short-term change or long-term maintenance. For example, maize farmers in Uganda and the United Republic of Tanzania, like those in Mexico, were reported to select for large, clean kernels from large ears, apparently because they believed that these germinated well and produced high-yielding plants (Gibson *et al.*, 2005). Interestingly, this appeared to result in decreased resistance to maize streak virus, since resistant plants had smaller ears, and plants with large ears appeared to be non-resistant escapes.

As part of a comparative five-country study of FK and PBK (Soleri *et al.*, 2002, 2004), farmers were presented with

a hypothetical scenario asking them to compare random with intentional selection for 10 cycles in a typical field, in populations with phenotypic variation for the trait they used as major selection criterion (Figure 14.6) (Table 14.2, question A). The null hypothesis was that farmers did not differ from plant breeders, i.e. that they would all consider intentional selection to be more effective than random selection for improving or at least maintaining this trait. The majority of responses corresponded to the null hypothesis of no difference between farmer and plant breeder expectations that intentional selection was more effective for increasing yield, 76.2 percent (144/189), although those who disagreed with that idea were sufficient to reject the hypothesis statistically ( $P = 0.00000$ ). Disagreement was particularly frequent among maize farmers, probably due to recombination in that cross-pollinating crop.

These results indicate that farmers who believe there is an advantage of intentional over random selection, see their goal for phenotypic selection as either *S* or *R* or *E*. To discriminate between these possibilities, and with the same null hypothesis as

outlined above, those farmers responding to the first question that intentional selection resulted in greater yield, were asked to compare random selection for 10 cycles followed by one cycle of intentional selection, with 11 consecutive cycles of intentional selection. Results differed significantly from the null hypothesis (Table 14.2, question B). Among these farmers, only 23.2 percent (20/86) saw 11 years of intentional selection as superior. These results demonstrate that among those farmers favouring intentional selection, only a minority see it as providing cumulative multi-generational change (*E*), while the primary selection goal of the other farmers who saw an advantage to multi-generational intentional selection for low-heritability yield-related traits is either eliminating changes between generations (*R*) or a non-genetic advantage they believe is fully achieved within one year (*S*). The large number of farmers who do not consciously see an advantage to multi-generational intentional selection, but who, like other farmers, select for large seed from large, clean ears, may do so because of custom, as did the majority of farmers in the selection experiment described earlier.

#### 14.6 CONCLUSIONS

Many elements of crop variety choice and plant selection in the Third World contrast substantially with industrial agricultural systems, including the growing environments, genetic resources and organization of the agricultural system. The urgency of understanding farmer selection will increase in the future with global climate changes, the continuing loss of genetic resources, the rapid spread of transgenic crop varieties, the development of a global system of IPR in crop genetic resources, the need to make agriculture more sustainable while feeding more people,

and the movement to make formal plant breeding more relevant to farmers through PPB. Understanding farmers' choice and selection practices, their biological results, the knowledge and goals underlying them, and the similarities and differences with plant breeders provides a means for the two groups to work together more effectively. This understanding and collaboration is critical for supporting all of the important functions of SSTW agriculture, including long-term global food security.

For PPB, this means that farmers' goals for varietal choice and phenotypic selection need to be understood in the context of a system that integrates production, consumption, improvement, multiplication and conservation. The biological result of phenotypic selection needs to be evaluated in terms of its possible ecological effects (via *S*), as well as in terms of *R* and *E*. Additionally, farmers' theoretical knowledge of choice and selection, not just their criteria, need to be understood by plant breeders to fully realize the potential benefits of collaboration. The value of this research will be judged by its effectiveness in improving the efficiency and outcomes of collaborative breeding by scientists and farmers, and improvement in the well-being of those farmers and their communities.

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