

Extending Darwin's Analogy: Bridging Differences in Concepts of Selection between Farmers, Biologists, and Plant Breeders¹

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Extending Darwin's Analogy: Bridging Differences in Concepts of Selection between Farmers, Biologists, and Plant Breeders. Darwin developed his theory of evolution based on an analogy between artificial selection by breeders of his day and "natural selection." For Darwin, selection included what biologists came to see as being composed of (1) phenotypic selection of individuals based on phenotypic differences, and, when these are based on heritable genotypic differences, (2) genetic response between generations, which can result in (3) evolution (cumulative directional genetic response over generations). The use of the term "selection" in biology and plant breeding today reflects Darwin's assumption—phenotypic selection is only biologically significant when it results in evolution. In contrast, research shows that small-scale, traditionally-based farmers select seed as part of an integrated production and consumption system in which selection is often not part of an evolutionary process, but is still useful to farmers. Extending Darwin's analogy to farmers can facilitate communication between farmers, biologists, and plant breeders to improve selection and crop genetic resource conservation.

Key Words: Crop genetic resources, Darwin, evolution, farmers, phenotypic selection, plant breeding.

Darwin developed his theory of evolution based on an analogy between selection by plant and animal breeders of his day and what he termed "natural selection," or more generally "selection." "Natural selection" or "selection" for Darwin included what biologists came to see as being composed of (1) phenotypic selection of individuals based on phenotypic differences, and, when these are based on heritable genotypic differences, (2) genetic response, or a change in the genetic structure of a population between generations resulting from a greater contribution of the selected individuals, and which results over generations in (3) evolution (cumulative, directional genetic response). Biologists' and plant breeders' use of the terms "selection" and "natural selection" continues to be influenced by an em-

phasis on evolution. They use a linguistic synecdoche, where "selection" or "natural selection" represents the whole process of evolution, reflecting a prevailing assumption in the common use of the term "selection" in biology and plant breeding—that phenotypic selection is only biologically significant when it results in evolution. (Unless otherwise indicated, we use the terms "selection" and "phenotypic selection" synonymously to refer to phenotypic selection with no implication that it results in genetic response.)

Extending Darwin's analogy of natural selection with artificial selection by amateur plant and animal breeders to an analogy with traditional farmers' crop management illustrates how selection can have important ecological and agronomic functions when it does not result in any genetic response, or can lead to short-term intergenerational genetic change (genetic response), in addition to longer-term directional change or evolution. Evidence that farmers' concepts of selec-

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tion can be different than those of biologists and plant breeders, while at the same time useful to farmers and scientifically interpretable, may encourage collaboration between farmers and plant breeders that can facilitate improved selection efficiency and crop genetic resource conservation.

Darwin's Concept of Selection

Plant and animal breeding had an important influence on the development of Darwin's ideas of evolution. For example, in his copy of a pamphlet titled *The Art of Improving the Breeds of Domestic Animals* by the animal breeder John Sebright, Darwin wrote the following in pencil in 1838: "In plants man presents mixtures, varies conditions and destroys the unfavourable kind—could he do this last effectively and keep on the same exact conditions for many generations he would make species, which would be infertile with other species" (quoted in Ruse 1975:347).

The first two chapters of *The Origin of Species by Means of Natural Selection* were titled "Variation under Domestication" and "Variation under Nature," and Darwin elaborated at length on artificial selection in *The Variation of Animals and Plants under Domestication*. Darwin's concepts of selection appear to have been influenced by plant and animal breeders' primary interest in selection as a means of directional genetic change, i.e., to create new, stable, heritable phenotypes.

"If it profit a plant to have its seeds more and more widely disseminated by the wind, I can see no greater difficulty in this being effected through natural selection, than in the cotton-planter increasing and improving by selection the down in the pods of his cotton trees" (Darwin 1859:86).

In the first edition of *Origin* Darwin used the term "natural selection" as a synonym for the "principle of preservation" in the "struggle for life," a process resulting in evolution, "the small differences distinguishing varieties of these same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera" (Darwin 1859:128). The connections between selection, natural selection, and evolution remained a central theme in Darwin's thinking. In *Variation* he wrote "Selection does nothing without variability" (Darwin 1883 [1868]b:7), and the "struggle for existence will determine that those variations, however slight, which are favourable shall be preserved or selected, and those which are

unfavourable destroyed . . . This preservation . . . I have called Natural Selection . . ." (Darwin 1883 [1868]b:6).

Thus, Darwin used the terms "selection" and "natural selection" interchangeably to refer to the process that results in evolution, and implying evolution itself. Today these are known to be the distinct processes of (1) phenotypic selection of individuals based on phenotypic variation within a population, (2) genetic response, or change in the genetic structure of a population due to a greater contribution of the selected individuals to the next generation when individual differences are heritable, and (3) cumulative, directional genetic response over generations, i.e., evolution. Though Darwin came to think of natural selection acting on individual differences which were heritable (Provine 1971:1–10), or "inheritable variations" (Darwin 1883 [1868]b:6), determining which variations were heritable remained a major challenge for understanding evolution. The difference between heritable and non-heritable phenotypic traits is fundamental for understanding the relationship between variation and evolution, and was a major theme in the early decades after the rediscovery of Mendel's research, in the modern synthesis of the 1930s and 1940s, and it remains so today (Wilson et al. 2006; Wilson 2004), for example, in research on Mayan migrants from Guatemala to the US that showed proportional leg length, once thought to be genetically determined, to be a highly sensitive indicator of the quality of the health environment (Bogin et al. 2002).

Selection in Population Genetics and Evolutionary Biology

In the synthesis of Mendel's discoveries, Darwinian evolutionary principles and quantitative methods at the beginning of the 20th century, there was an integration of practical and applied work in which practical breeders and experimental and theoretical biologists were actively involved (Allard 1999; Provine 1971). For example, the biologist Bateson introduced Mendel's ideas into Britain, and was warmly received by plant breeders in the U.S. (Allen 1975:51–52), and East and Shull working with maize beginning in the 1900s combined biological experiment and practical plant breeding in transforming Mendelism into a breeding method (Fitzgerald 1990:30–41).

Though the question of the heritability of different traits is key to understanding selection, it

was not until the decade after the rediscovery of Mendel's work in 1900, in the early development of genetics, that the difference between phenotype and genotype in relation to trait heritability and selection came to be more fully understood. In a key paper published in 1903, the botanist Johannsen established this distinction for continuously varying traits based on experimental work with the common bean, and provided a Mendelian explanation for their inheritance (Allard 1999:71–76; Allen 1975). In experiments with wheat, the plant breeder Nilsson-Ehle established that qualitative traits can have effects necessary to account for inheritance of continuous variation (Allard 1999:76–77). De Vries, a botanist, differentiated “internal causes . . . of a historical nature” that he considered heritable, and “external ones . . . defined as nourishment and environment” which he considered non-heritable (de Vries 1909:74).

As the distinction between heritable and non-heritable phenotypic variation became better understood and widely accepted, heritable variation became the main interest as part of the evolutionary process, and Darwin's analogy with plant and animal breeding was no longer needed to understand natural selection and evolution. Today, the standard text book accounts of selection in biology (e.g., Falconer and Mackay 1996:184–189, Maynard Smith 1989:93–113) clearly differentiate phenotypic selection from genetic response and evolution. Endler, for example, defines natural selection as requiring three conditions: (a) phenotypic variation among individuals for a trait, (b) fitness variation for that trait, and (c) inheritance of that trait, and evolution as consisting of three processes: (i) phenotypic selection, (ii) genetic response (generational), and (iii) cumulative directional genetic change (evolution) (Endler 1992:220, 223) (see also Endler 1986:12–13).

The standard equation for genetic response is $R = h^2S$, where

R = genetic response to selection in one generation, measured as the difference in mean phenotypic value for a given trait between the offspring of the selected parents and the whole of the parental generation before selection,

h^2 = heritability in the narrow sense, $= V_A/V_P$, and $V_P = V_G + V_E + V_{GxE}$, where V_G = genetic variance, V_A = additive V_G , V_P = total phenotypic variance, V_E = environmental variance, and V_{GxE} = the interaction between genetic and environmental variances,

TABLE 1. ACRONYMS AND ABBREVIATIONS USED.

Term	Definition
E	evolution, or cumulative directional genetic change over generations
FV	farmer crop variety
h^2	heritability in the narrow sense, $= V_A/V_P$
MV	modern crop variety
PPB	participatory plant breeding
R	genetic response to selection in one generation, $= h^2S$
S	selection differential, i.e., difference between mean of parental population and mean of individuals selected from
V_A	additive genetic variance
V_G	genetic variance
V_{GxE}	the interaction between genetic and environmental variances
V_P	phenotypic variance

S = selection differential, measured as the difference in mean phenotypic value for a given trait between the selected parents and all individuals in the parental population before the parents were selected, $= i\sigma$, where i = selection intensity which depends on proportion of parent population selected, and σ = phenotypic standard deviation of parental population.

Thus, artificial phenotypic selection per se is a process of identifying the individuals with specified phenotypic traits within a population that will contribute genetic material to the next generation, and is distinct from the heritability of those phenotypic traits. Phenotypic selection can have four main outcomes ($S \approx 0$, $S > 0$ and $R \approx 0$, $R > 0$ and $E \approx 0$, and $E > 0$) depending on the heritability of the traits involved, the selection intensity, and the number of generations selection is carried out (Soleri and Cleveland 2004) (Fig. 1). The extent to which the heritability of phenotypic traits will influence their inclusion in selection criteria will depend on many things including the selector's knowledge of that heritability.

However, the influence of Darwin's analogy appears to persist—the term “selection” continues to be used by some as a synecdoche for intergenerational genetic response and for evolution. First, selection is often used to refer to the response or change in gene frequency between generations based on heritable phenotypic differences (R). For example, the “simplest form of selection is to choose individuals on the basis of their own phenotype,” and that the “basic effect

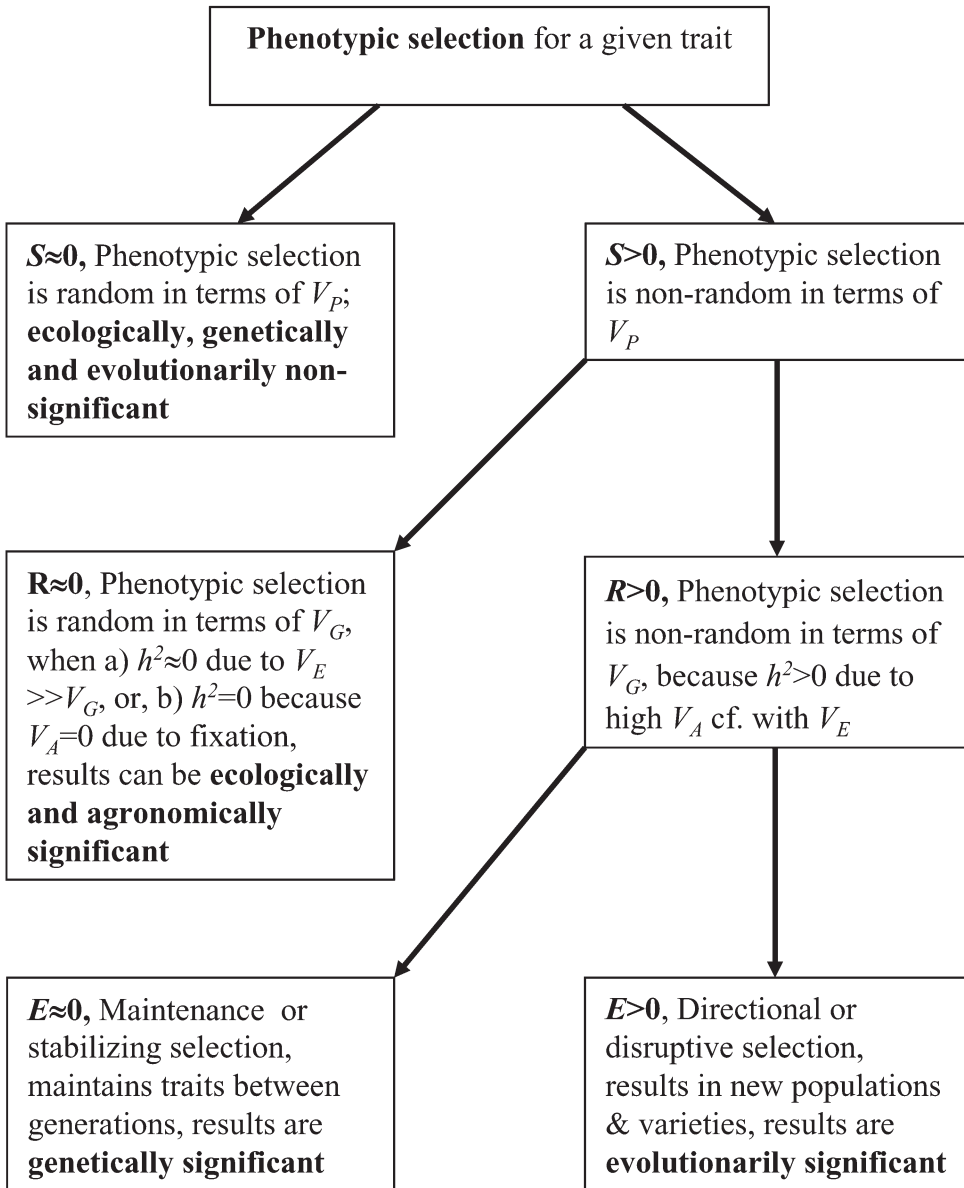


Fig. 1. Phenotypic selection classified according to outcome of selection. See Table 1 for key to symbols. (Copyright 2007, D. Soleri, D. A. Cleveland, used with permission.)

of selection is to change the array of gene frequencies" (Falconer and Mackay 1996:184), and "... for differential selection to occur in a population there must be genetic variation in fitness" (Hedrick 2005:133). In *A Dictionary of Genetics*, "selection" is defined as "the process of determining the relative share allotted individuals of

different *genotypes* in the propagation of a population" (King and Stansfield 1990:286, emphasis added), thus conflating phenotypic selection per se and selection based on genotype, since there is no entry in the dictionary for "phenotypic selection." Michod states that only in special cases is it useful to distinguish the effects of selection from

heritability (1999:181), and defines selection as change in frequencies based on a heritable properties (1999:164). His interest in selection only as a component of evolution (Michod 1999:15–16) eliminates by definition the possibility that phenotypic selection can be uncorrelated with genotypic frequencies. “Any attempt at a general formulation of natural selection that begins by partitioning phenotypic selection from heritability seems fated from the beginning to be of limited generality” (Michod 1999:181). In contrast, Endler says, “To say that natural selection is synonymous with phenotypic selection is to trivialize it—this is tantamount to saying that there are differences among phenotypes, which can easily lead to tautology” (Endler 1986:13).

Second, the terms selection or natural selection are used as synecdoches for evolution (*E*). Fisher felt compelled to state in the first sentence in his preface to *The Genetical Theory of Natural Selection*, “Natural Selection is not Evolution,” because “natural selection” was commonly and incorrectly used as a “convenient abbreviation” for the theory of evolution (1999 [1930]:vii). Evolutionary biologists and philosophers continue to equate the term “selection” directly with evolution (Endler 1992:223), as in Hull’s definition of selection, which has “organized the professional discussion on units of selection ever since” it was first proposed (Gould 2002:615). Hull distinguished replicators (genes) and interactors (organismal phenotypes) (Hull 1980), and defined “selection” as “any process in which differential extinction and proliferation of interactors causes the differential perpetuation of the replicators that produced them” (Hull 2001:22–23), and as “repeated cycles of replication, variation, and environmental interaction so structured that environmental interaction causes replication to be differential” resulting in “evolution” (Hull 2001:53, 60).

Because evolutionary biologists’ and population geneticists’ main interest is evolution, they see phenotypic selection not based on inherited differences primarily as a problem, because it obscures the extent of evolution, and much effort has been expended on separating heritable and non-heritable phenotypic variation (e.g., Winn 2004). Wilson is one of the few evolutionary biologists who has discussed non-heritable phenotypic selection as ecologically and evolutionarily important (Wilson 1980; Wilson 2004).

Most philosophers dealing with evolution have also tended to follow biologists in viewing pheno-

typic selection as important only as a component of evolution, so when they have dealt explicitly with phenotypic selection as a distinct process, it has been primarily to understand evolution (e.g., Hull 1980, Sober 1984). At least one philosopher, however, has suggested that the lack of biologists’ interest in selection of non-heritable phenotypic variation is a result of research agendas, and not an indication of its “importance in the causal structure of nature,” and emphasized the conceptual and scientific importance of not conflating phenotypic selection and evolution, so as to encourage “the empirical investigation of evolutionarily neutral but ecologically significant processes” (Shanahan 1990:222, 224).

Selection in Plant Breeding

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 U.S. (Wallace and Brown 1988:87–90). As the importance of formal science in plant breeding increased in comparison with empirical heuristics, and later as plant breeding moved from the public to the private sector (Kloppenborg 1988), plant breeders began to eliminate farmers from their work (e.g., Schneider 2002). Plant breeders’ and farmers’ practice and concepts subsequently developed independently of each other, effectively separating the formal from the 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 varieties for their diverse, more marginal growing environments (Ceccarelli and Grando 2002; Cleveland 2001). When farmers are involved by contemporary plant breeders in their work, it has generally been limited to the stage of evaluating the plant breeders’ populations or varieties in their fields (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). Like evolutionary biologists, all breeders agree on the theory of the relationship between phenotypic selection, genetic response, and evolution (Cleveland et al. 2000), while in practice they often use the term “selection” as a synecdoche for genetic response and evolution because “only . . . directional selection . . . is of practical concern” (Simmonds and Smartt 1999:91–97). For example, two of the most respected English language plant breeding textbooks define “selection” as “differential reproduction of genotypes in a population so that gene frequencies change and, with them, genotypic and phenotypic values of the character being selected” (Simmonds and Smartt 1999:91), and “Any nonrandom process that causes individuals with different genotypes to be represented unequally in subsequent generations” (Allard 1999:239). This makes sense given the goals of scientific plant breeding. 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 which is assumed to account for crop domestication and for the ensuing proliferation of crop varieties, and 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.

COLLABORATION BETWEEN FARMERS AND SCIENTIFIC PLANT BREEDERS

However, any differences in farmers’ and plant breeders’ understanding or use of selection may have important practical effects because they could impede communication between farmers and plant breeders. Such communication may be critical for the success of collaborative or participatory plant breeding (PPB), a process that is seen by some as especially important for developing crop varieties appropriate for farmers in marginal growing environments who cannot afford external inputs (Ceccarelli and Grando 2002; Cleveland and Soleri 2002; Weltzien et al. 2003). Farmer-scientist communication and collaboration is also important for in situ conservation of crop genetic resources by farmers (Perales et al. 2003).

However, even in PPB, farmer knowledge of selection as understood by plant breeders has been strongly influenced by breeders’ assumptions. Farmer knowledge has most frequently been seen as

descriptive, as in a major survey of 49 PPB projects which 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% obtained farmers’ selection criteria for new varieties (Weltzien et al. 2003:22, 60, 89). 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. 2003:89). More recently, using farmer knowledge as a discriminatory tool has become more common, with farmers asked to choose among varieties or among segregating populations, or individual plants within segregating populations (Soleri et al. 2002).

These approaches to understanding farmer knowledge have made valuable contributions to crop improvement for farmers’ conditions. Yet, PPB projects may assume that farmers know little about selection, because those projects are unaware that farmers have different definitions and practices concerning selection, and rigorous comparisons with scientist knowledge have not been carried out. Plant breeders’ assumptions about farmer knowledge, in combination with those about selection discussed above, often lead to a further assumption that farmers’ goal for selection within a crop population or variety is cumulative, directional genetic change (E), and therefore, is only successful when this is accomplished. These untested assumptions can lead to an interpretation of farmers’ selection as inefficient (in terms of genetic change achieved for the resources invested), and PPB has focused on teaching farmers the scientific basis of selection that results in E and on methods to improve their selection efficiency. For example, some maize PPB projects in Mexico have attempted to teach farmers basic maize reproductive biology and selection techniques, because in-field plant selection can achieve more rapid progress toward evolutionary goals than the traditional method of selection of ears post-harvest (CIMMYT 2000; Rice et al. 1998).

Preliminary results from one project with Mexican maize farmers showed that with stratification within fields to increase heritability, simple mass selection by breeders without pollination control resulted in significant yield gains over three generations (Smith et al. 2001). The

researchers emphasized the importance of further research to compare the yield benefit with costs to farmers for the extra time involved, from farmers' perspectives. Using farmer estimates of maximum, normal (modal), and minimum yields in their farming experience documented in research with over 470 farmers in six countries (Soleri et al. 2005; Soleri et al. 2002), coefficients of variation for yield averaged 30%, suggesting that for farmers to be able to discern positive returns to the extra investment for in-field selection, annual gains would have to be substantial and sustained.

To the extent that farmers' goals for selection other than evolutionary change are not considered, the important and innovative steps in PPB toward reintegrating farmer and scientific breeding may not realize the full potential of farmer-scientist collaboration. The PPB review mentioned earlier has emphasized the need to understand farmers' concepts of selection (Weltzien et al. 2003:109), because "opportunities rarely develop for interaction between breeders and farmers beyond the survey . . . (thus) discussions are 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. 2003:60). However, without careful research, it may be difficult for farmers to communicate to breeders and other outsiders their conceptual or theoretical knowledge of selection that goes beyond description or discrimination (Soleri and Cleveland 2005).

When farmers' knowledge and practice fail to conform to conventional, untested assumptions about selection, it may not indicate failure to understand selection or practice it effectively. Instead, farmers' knowledge and practice have to be understood in the context of the environments and genotypes they work with (Ceccarelli and Grando 2002).

Selection in Traditionally-Based Agricultural Systems

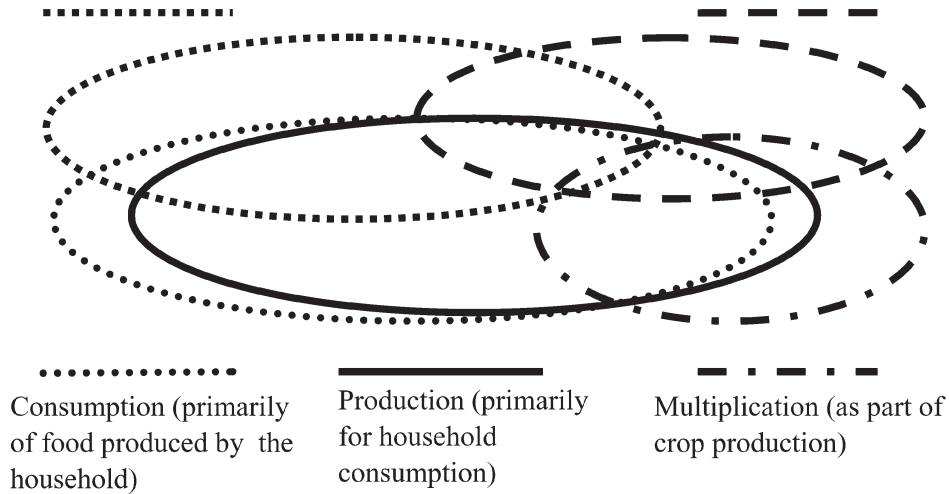
Traditionally-based agricultural systems (hereafter "traditional agriculture") are different than industrial systems in several important ways that affect the goals and results of selection. *First*, they are often dominated by farmers' varieties (FVs), which include landraces, traditional varieties selected by farmers, MVs (modern varieties) which have been adapted to farmers' environments by farmer and natural selection (sometimes referred to as "creolized" or "degenerated" MVs), and

progeny from crosses between landraces and MVs. Overall, the genetic variation within and among FVs in traditional agriculture is much greater than in industrial agriculture (Frankel et al. 1995:57 ff.). *Second*, growing environments are often more variable in space and time, which contributes to increased phenotypic variation for many crop traits, including most yield-related traits, reducing proportion of phenotypic variance that is additive genetic variance and thereby reducing heritability (Ceccarelli et al. 1992). *Third*, traditional agriculture is characterized by the integration within the household or community of production, consumption, crop improvement, seed multiplication, and conservation of genetic diversity, whereas in industrial agriculture each of these functions are spatially and structurally separated and specialized (Fig. 2).

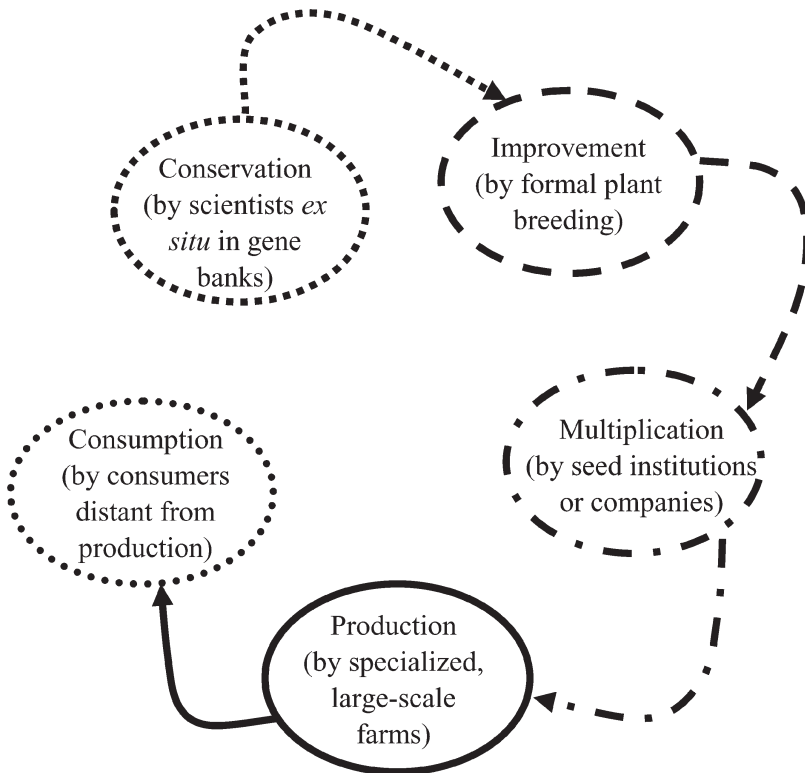
Therefore, farmers may value FVs not only for agronomic traits, such as drought or pest resistance or photoperiod sensitivity, but also for traits contributing to storage qualities, food preparation, taste, appearance, the potential for developing new varieties, and longer-term conservation of crop genetic diversity (Berthaud et al. 2001). This combination of high levels of genetic and environmental variance, low heritability, and integrated multiple functions affecting selection goals means that farmers' selection is likely to be different in many ways than that of plant breeders. However, this does not necessarily mean that their understanding of the basic relationships underlying selection are different than those of biologists and plant breeders; in fact, they can be quite similar. For example, farmers appear to understand $G \times E$ as the basis for some phenotypic differences (e.g., Sperling et al. 1993), and heritability as the basis for selection for R or E . Farmers can also distinguish between high and low-heritability traits and, especially in cross pollinating crops, consciously select for the former to create populations which express these new traits across a range of environments, while considering it not worthwhile, or even possible, to create similar populations when selecting for low-heritability traits (Soleri and Cleveland 2001; Soleri et al. 2002).

The agents of phenotypic crop selection in traditional agriculture are environmental factors not controlled by farmers (natural selection), farmer-managed growing environments (artificial indirect selection), or farmers themselves (artificial direct selection) (Fig. 3). Most often, these three types of selection occur simultaneously. Artificial direct selec-

Conservation (*in situ* in fields and storage containers) Improvement (via seed selection for next year's crop)



a.



b.

Fig. 2. Components of agricultural systems in traditionally-based small-scale and industrial large-scale agriculture. (Copyright 2007, D. Soleri, D. A. Cleveland, used with permission.) a. Traditionally-based agricultural system: Functions integrated in households and communities. b. Industrial agricultural systems: Functions separated, specialized, many institutionalized.

tion can be further classified in terms of whether the farmer has conscious goals (intentional selection) or does not have conscious goals (unintentional selection) (a distinction made by Darwin, 1883 [1868]a:4), and intentional selection can be further classified according to farmers' goals.

In the following sections we describe phenotypic selection by farmers organized in terms of these possible goals—longer-term genetic change or evolution (E), intergenerational genetic change or response (R), and within generation phenotypic differentiation (S , selection differential) (Fig. 3). We emphasize farmer goals, but also describe examples where farmer intentions are not documented, since many studies of farmer selection that document genetic or agronomic effects do not document farmers' knowledge (and vice versa). Note that regardless of goals, the results of farmer selection can be varied, as depicted in Fig. 1.

SELECTION FOR EVOLUTION

The mass selection carried out over millennia which resulted in the thousands of varieties of domesticated crops is often assumed to have resulted from the full range of agents and farmer goals (Harlan 1992). Some plant breeders emphasize intentional selection for evolution—"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 1999:29) (see also Harlan 1992:127), although others emphasize "unconscious and indirect" selection (Evans 1993:94, 116).

Whether intentional or not, results of molecular analysis support the hypothesis that farmers' selection has been successful in achieving evolutionary change for traits in the domestication syndrome (e.g., in maize, Wright et al. 2005). There is also evidence that farmer selection has been a powerful evolutionary force based on other preferences as well. For example, three major genes involved in starch metabolism were found to have significantly lower genetic diversity in the allogamous crop maize as compared to its closest wild relative (teosinte, *Zea mays* ssp. *parviglumis*) than would be predicted by models of natural selection—evidence of strong selection for specific grain yield and processing qualities important for human use, including ongoing selection for starch quality best for tortilla preparation, a major form of maize consumption in its regions of origin and

diversity (Whitt et al. 2002). In addition, three other loci contributing to sweet maize phenotypes showed low diversity (resulting from strong selection) in only certain varieties in particular locations, evidence of further specialization in the nonagronomic selection pressures farmers have exerted on maize (Whitt et al. 2002). Similarly, genetic analysis of the stickiness trait in the autogamous crop Asian rice also suggests strong selection for E by farmers during domestication and early diversification, perhaps as an adaptation for eating with chopsticks (Olsen et al. 2006).

The clearest evidence for contemporary farmer selection for evolution is in species which are normally propagated clonally. For example, some Andean potato farmers search their fields for volunteer seedlings resulting from spontaneous hybridization as a way to diversify their production (Zimmerer 1996:201). Indigenous South American farmers intentionally incorporate cassava seedlings into recognized varieties, resulting in increased heterogeneity within varieties (Elias et al. 2001; Pujol et al. 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 et al. 2005).

In seed-propagated species that are predominantly autogamous, compared with allogamous 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 can 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 farmers' fields.

It is much more difficult to affect evolutionary change in predominantly allogamous, seed propagated species, especially for quantitative traits with low heritability. However, farmers can discriminate between low and high-heritability traits, and use this as a basis for decisions about selection (Soleri et

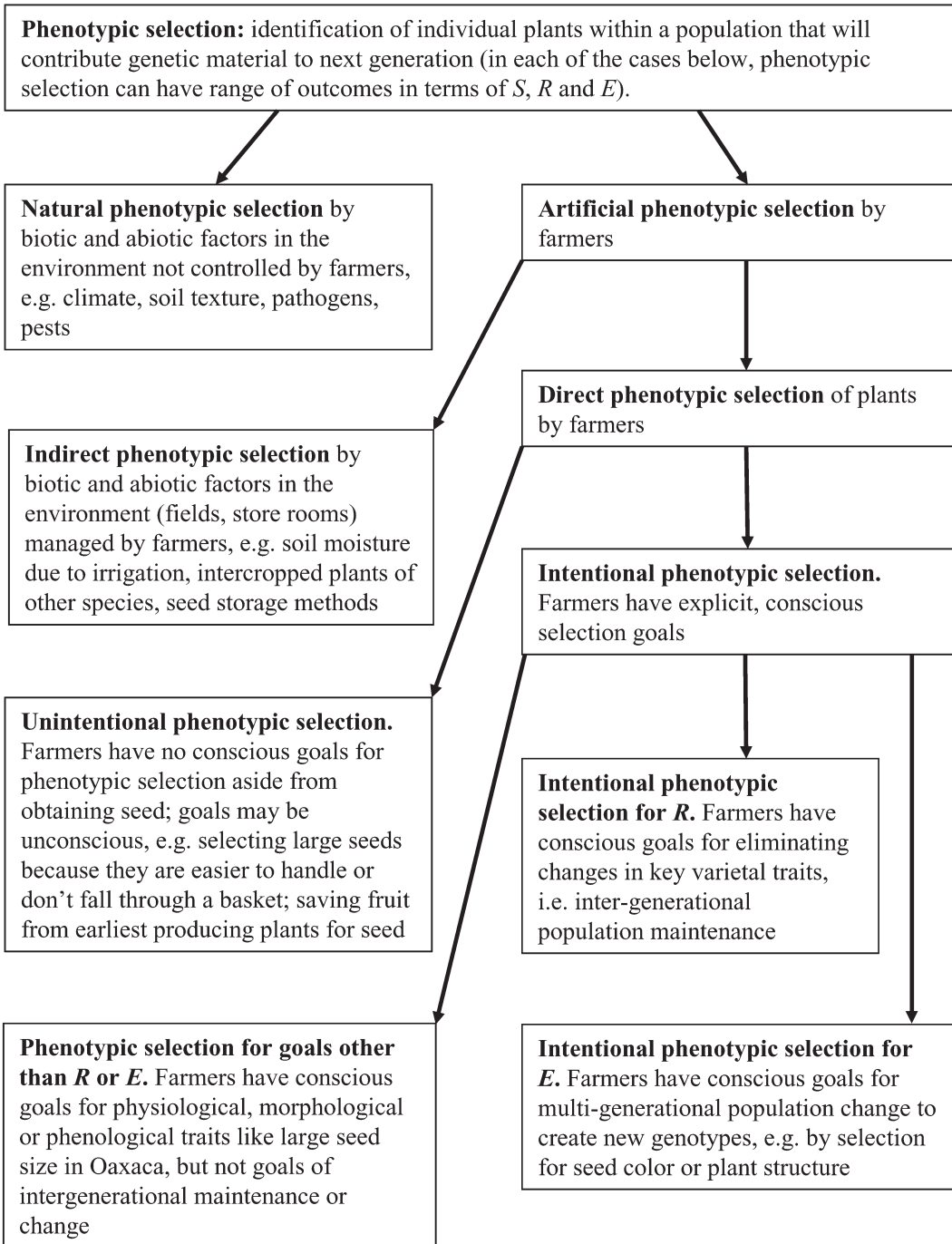


Fig. 3. Phenotypic selection classified according to the agent of selection, and farmers' goals when the farmers are the agents, applied to traditional agricultural systems. See Table 1 for key to symbols. (Copyright 2007, D. Soleri, D. A. Cleveland, used with permission.)

al. 2002). Farmers in Oaxaca often select maize seed with the goal of changing or creating populations with preferred, highly heritable traits, like kernel, tassel, and husk colors, for culinary and aesthetic reasons (e.g., maize varieties grown for purple husks used in tamale production) (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 et al. 2003). There is evidence based on research with pearl millet in Rajasthan, India, that farmers use mass selection for low-heritability traits in allogamous species with the goal of making directional change in their varieties (Christinck 2002:126; Vom Brocke et al. 2002). This research also documented intentional introgression of modern with traditional varieties of pearl millet, and subsequent selection, resulting in increased genetic variation and directional change (evolution) in selected traits, e.g., 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.

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 allogamous crops like maize, eliminating most concerns regarding gene flow.

This type of farmer selection to eliminate changes contrasts 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 et al. 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 ones that define a variety. This type of selection is probably most important for allogamous crops, such as pearl millet and maize discussed below, since it is much more difficult to maintain populations in these compared with clonally propagated and autogamous crops. In eastern Rajasthan, 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 color, which, together with planting patterns, leads to a 1–2% level of gene flow between maize varieties during one crop cycle (Louette et al. 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 color), but did not have any effect on allelic frequencies at nine 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 were observed, but the maintenance of significantly different maize populations based on morphological traits of interest to farmers persisted (Pressoir and Berthaud 2004).

A study in Chiapas 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 mor-

phological traits (Perales et al. 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 et al. 2005), as was found in the study in the Central Valleys of Oaxaca (Pressoir and Berthaud 2004), although neither study appears to have investigated farmer goals in detail.

Selection for Intrageneration 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 farmers' primary goal in selecting seed is to obtain good planting material. Selection with this goal is also conducted as part of MV seed production (Simmonds and Smartt 1999:215). When environmental conditions change, farmers may often choose different varieties or even crop species rather than attempt to change important, low-heritability traits in existing ones (Berthaud et al. 2001; Lacy et al. 2006). While plant breeders also carry out this type of selection, for example removing small seed, they do this to decrease the contribution of V_E to V_p to increase heritability with the goal of \hat{E} .

Research on non-heritable phenotypic differences shows these can have important intragenerational 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 vigor, greater leaf area throughout life, and more rapid development from time of emergence to flowering (Pommel 1990; Revilla et al. 1999).

When the goal of selection is intragenerational phenotypic differentiation, the result may not be genetic gain or evolution, especially for low-heritability traits in allogamous crops. This hy-

pothesis was supported by results of maize seed selection exercises with farmers in two communities in Oaxaca, Mexico. Exercises were done on ears post harvest, which is the way these farmers and most others in Mexico select maize seed. Their selections resulted in high S values for a number of ear and kernel traits, including those (ear length, ear weight, 100 kernel weight) reflecting (through correlation coefficients ranging from 0.4–0.7, Soleri 1999) selection criteria explicitly identified by farmers (ear and kernel size) (Soleri et al. 2000). However, $R \approx 0$ for these as well as other morphophenological traits, measured for each generation over three generations, and did not differ from randomly selected seed from the same lot. Large seed size was a key selection criterion, and reasons given by farmers for selecting large seed included seed quality and purity, but not maintaining or changing (i.e., “improving”) a variety. Some farmers said large seed resulted in higher germination, larger seedlings, early vigor, and higher yields; however, most farmers attributed their preference for large seed to “custom.”

However, it is also possible that intentional simple mass selection for intragenerational 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 vs. intentional selection for R or E . For example, farmers in Uganda and Tanzania, like those in Mexico, were reported to select large, clean kernels from large ears for seed, apparently because they believed that these germinated well and produced high-yielding plants (Gibson et al. 2005). This practice appeared to result in decreased resistance to maize streak virus, since resistant plants had smaller ears, and plants with large ears appeared to be nonresistant escapes.

As part of a comparative five-country study of farmer and plant breeder knowledge (Soleri et al. 2004; Soleri et al. 2002), we interviewed Mexican maize farmers from two different communities in Oaxaca. Based on the previous research with Oaxacan maize farmers, we hypothesized that heritability and farmer understanding of heritability are important determinants of farmers' goals for selection, and that a goal of S only would be more likely for low-heritability traits when farmers understand the relative heritability of traits of interest. We first asked farmers to tell us their expectations of progeny phenotype for a

high-heritability trait (tassel color) and a low-heritability trait (ear length) when seed is planted in a typical, highly variable environment, and in a hypothetical uniform, optimal environment. We rejected the null hypothesis of no difference in farmer responses for low and high-heritability traits—a significant majority of farmers expected parent and progeny phenotypes for ear length, but not for tassel color, to differ in the two environments. Therefore, we concluded that these farmers understand the difference between high and low-heritability traits in terms of their interaction with environments.

Farmers were then presented a hypothetical scenario asking them to compare random with intentional selection for 10 cycles in a typical field in populations with phenotypic variation for ear length and grain yield, low-heritability traits they used as major selection criteria. 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. Only 50.9% (86/169) responded that intentional selection had greater effect on increasing yield ($p = 0.00000$). Therefore, we accepted the alternative hypothesis: a significant number of farmers differed from plant breeders and anticipated no difference between random and intentional selection for improving these traits over generations (E).

The results suggest that farmers who see an advantage of intentional over random selection see phenotypic selection as resulting either in S or R , or in E . To discriminate between these possibilities, and with the same null hypothesis as outlined above, those farmers responding to the first selection 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 were significantly different than the null hypothesis. Among these farmers, only 23.2% (20/86) saw 11 years of intentional selection as superior. These results suggest that among those favoring intentional selection, only a minority of farmers see it as providing cumulative intergenerational change (E), while the primary selection goal of the other farmers who saw an advantage to intentional selection for low-heritability yield-related traits is either eliminating changes between generations (R) or a nongenetic advantage they believe is fully

achieved within one year (S). The large number of farmers who see no advantage to intentional selection, but who, like other farmers, select for large seed from large, clean ears, probably do so because of “custom,” as did the majority of farmers in the selection experiment described above.

Conclusions

Words and their implicit cultural meanings can have important effects on our understanding of basic biological processes, emphasizing some aspects at the expense of others, as Keller argues forcefully for the term “gene” (Keller 2000). This appears to also be the case with Darwin's analogy of natural with artificial selection, which made the assumption that phenotypic selection was only important as part of the evolutionary process, an assumption which continues in evolutionary biology and plant breeding today. Although the process of phenotypic selection and its relationship to trait heritability, genetic response, and evolution became well understood, an emphasis on evolution in biology and plant breeding led to the common assumption that phenotypic selection that does not result in evolutionary change is not interesting or important. This assumption has influenced the way in which plant breeders understand farmer selection, especially important in PPB programs, where communication between farmers and plant breeders is key.

Extending Darwin's analogy of natural selection with selection by amateur plant and animal breeders to selection by traditional farmers supports a broader view of the role of phenotypic selection. Farmers in traditional agriculture carry out phenotypic selection for goals of within-generation phenotypic differentiation, between-generation maintenance of important population traits, as well as multigeneration change or evolution, though the actual results may differ from those intended. Better understanding by plant breeders of farmers' selection knowledge and practice may facilitate viewing farmers' selection as successful, even when it doesn't result in evolution. There is a need for researchers studying the genetic structure of farmer-managed crop populations to document not only farmer practices and the genetic and agronomic results, but also farmer knowledge of selection, including their goals. This could help to locate professional and farmer selection within the same scientific context, and could contribute to creating a link be-

tween plant breeders' focus on evolution and farmers' focus on production and consumption. This in turn could contribute to the success of collaboration between farmers and plant breeders to meet farmers' needs, including improvement of selection practices for both intragenerational and multigenerational goals, and crop genetic resource conservation.

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Literature Cited

- Allard, R.W. 1999. Principles of plant breeding. Second edition. John Wiley and Sons, New York.
- Allen, G. E. 1975. Life science in the twentieth century. John Wiley and Sons, New York.
- Baskin, C. C., and J. M. Baskin. 2001. Seeds: Ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California.
- Berthaud, J., J. C. Clément, L. Emperaire, D. Louette, F. Pinton, J. Sanou, and S. Second. 2001. The role of local-level gene flow in enhancing and maintaining genetic diversity. Pages 1–23 in H. D. Cooper, C. Spillane, and T. Hodgkin, eds. Broadening the genetic base of crop production. CABI, Wallingford, Oxon, U.K.
- Bockstaller, C., and P. Girardin. 1994. Effects of seed size on maize growth from emergence to silking. *Maydica* 39:213–218.
- Bogin B, P. Smith, A. B. Orden, M. I. Varela Silva, and J. Louky. 2002. Rapid change in height and body proportions of Maya American children. *American Journal of Human Biology* 14 (6):753–761.
- Ceccarelli, S., and S. Grando. 2002. Plant breeding with farmers requires testing the assumptions of conventional plant breeding: Lessons from the ICARDA barley program. Pages 297–332 in D. A. Cleveland and D. Soleri, eds. Farmers, scientists and plant breeding: Integrating knowledge and practice. CAB International, Wallingford, Oxon, U.K.
- , S. Grando, and J. Hamblin. 1992. Relationship between barley grain yield measured in low- and high-yielding environments. *Euphytica* 64:49–58.
- , S. Grando, R. Tutwiler, J. Bahar, A. M. Martini, H. Salahieh, A. Goodchild, and M. Michael. 2000. A methodological study on participatory barley breeding. I. Selection phase. *Euphytica* 111:91–104.
- Christinck, A. 2002. "This seed is like ourselves." A case study from Rajasthan, India, on the social aspects of biodiversity and farmers' management of pearl millet seed. Margraf Verlag, Weikersheim, Germany.
- CIMMYT. 2000. The Oaxaca project: Farmers conserving maize diversity in the farmers' fields. (verified 9/26/06, Project home page: http://www.cimmyt.org/Research/economics/oaxaca/overview/ov_p_a.htm).
- Cleveland, D. A. 2001. Is plant breeding science objective truth or social construction? The case of yield stability. *Agriculture and Human Values* 18(3):251–270.
- , D. Soleri, and S. E. Smith. 2000. A biological framework for understanding farmers' plant breeding. *Economic Botany* 54:377–394.
- , and D. Soleri. 2002. Introduction. Farmers, scientists and plant breeding: Knowledge, practice, and the possibilities for collaboration. Pages 1–18 in D. A. Cleveland and D. Soleri, eds. Farmers, scientists and plant breeding: Integrating knowledge and practice. CAB International, Oxon, U.K.
- Cooper, H. D., C. Spillane, and T. Hodgkin. 2001. Broadening the genetic base of crops: An overview. Pages 1–23 in H. D. Cooper, C. Spillane, and T. Hodgkin, eds. Broadening the genetic base of crop production. CABI, Wallingford, Oxon, U.K.
- Darwin, C. 1859. On the origin of species by means of natural selection. First, facsimile edition, 1967. Athenum, New York. John Murray, London, U.K..
- . 1883 [1868]a. The variation of animals and plants under domestication. Volume 2. Second, revised edition. Johns Hopkins University Press, Baltimore, Maryland.
- . 1883 [1868]b. The variation of animals and plants under domestication. Volume 1. Second, revised edition. Johns Hopkins University Press, Baltimore, Maryland.
- de Vries, H. 1909. Variation. Pages 66–84 in A. C. Seward, ed. Darwin and modern science. Cambridge University Press, Cambridge, Massachusetts.

- Duvick, D. N. 2002. Theory, empiricism and intuition in professional plant breeding. Pages 239–267 in D. A. Cleveland and D. Soleri, D., eds. *Farmers, scientists and plant breeding: Integrating knowledge and practice*. CAB International, Oxon, U.K.
- Elias, M., L. Penet, P. Vindry, D. McKey, O. Panaud, and T. Robert. 2001. Unmanaged sexual reproduction and the dynamics of genetic diversity of a vegetatively propagated crop plant, cassava (*Manihot esculenta* Crantz), in a traditional farming system. *Molecular Ecology* 10:1895–1907.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, New Jersey.
- . 1992. Natural selection: Current usages. Pages 220–224 in E. F. Keller and E. A. Lloyd, eds. *Key words in evolutionary biology*. Harvard University Press, Cambridge, Massachusetts.
- Evans, L. T. 1993. *Crop evolution, adaptation and yield*. Cambridge University Press, Cambridge, Massachusetts.
- Falconer, D. S., and T. F. Mackay. 1996. *Introduction to quantitative genetics*. Fourth edition. Prentice Hall/Pearson Education, Edinburgh, U.K.
- Fisher, R. A. 1999 [1930]. *The genetical theory of natural selection: A complete variorum edition*. Oxford University Press, Oxford, U.K.
- Fitzgerald, D. 1990. *The business of breeding: Hybrid corn in Illinois, 1890–1940*. Cornell University Press, Ithaca, New York.
- Frankel, O. H., A. H. D. Brown, and J. J. Burdon. 1995. *The conservation of plant biodiversity*. Cambridge University Press, Cambridge, U.K.
- Gibson, R. W., N. G. Lyimo, A. E. M. Temu, T. E. Stathers, W. W. Page, L. T. H. Nsemwa, G. Acola, and R. I. Lamboll. 2005. Maize seed selection by East African smallholder farmers and resistance to maize streak virus. *Annals of Applied Biology* 147(2):153–159.
- Gould, S. J. 2002. *The structure of evolutionary theory*. Harvard University Press, Cambridge, Massachusetts.
- Harlan, J. R. 1992. *Crops and man*. Second edition. American Society of Agronomy, Inc., and Crop Science Society of America, Inc., Madison, Wisconsin.
- Hedrick, P. W. 2005. *Genetics of populations*. Third edition. Jones and Bartlett, Boston, Massachusetts.
- Hull, D. L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.
- . 2001. *Science and selection: Essays on biological evolution and the philosophy of science*. Cambridge University Press, Cambridge, U.K.
- Keller, E. F. 2000. *The century of the gene*. Harvard University Press, Cambridge, Massachusetts.
- King, R. C., and W. D. Stansfield. 1990. *A dictionary of genetics*. Fourth edition. Oxford University Press, Oxford, U.K.
- Kloppenborg, J. 1988. *First the seed: The political economy of plant biotechnology, 1492–2000*. Cambridge University Press, New York.
- Lacy, S., D. A. Cleveland, and D. Soleri. 2006. Farmer choice of sorghum varieties in southern Mali. *Human Ecology* 34:331–353.
- Louette, D., A. Charrier, and J. Berthaud. 1997. In situ conservation of maize in Mexico: Genetic diversity and maize seed management in a traditional community. *Economic Botany* 51:20–38.
- , and M. Smale. 2000. Farmers' seed selection practices and maize variety characteristics in a traditional Mexican community. *Euphytica* 113:2541.
- Maynard Smith, J. 1989. *Evolutionary genetics*. Oxford University Press, Oxford, U.K.
- Michod, R. E. 1999. *Darwinian dynamics: Evolutionary transitions in fitness and individuality*. Princeton University Press, Princeton, New Jersey.
- Olsen, K. M., A. L. Caicedo, N. Polato, A. McClung, S. McCouch, and M. D. Purugganan. 2006. Selection under domestication: Evidence for a sweep in the rice Waxy genomic region. *Genetics* 173(2):975–983.
- Perales, H., S. B. Brush, and C. O. Qualset. 2003. Dynamic management of maize landraces in Central Mexico. *Economic Botany* 57(1):21–34.
- , B. F. Benz, and S. B. Brush. 2005. Maize diversity and ethnolinguistic diversity in Chiapas, Mexico. *Proceedings of the National Academy of Sciences of the United States of America* 102(3):949–954.
- Pommel, B. 1990. Influence du poids de la semence et de la profondeur de semis sur la croissance et le développement de la plantule de maïs. *Agronomie* 10:699–708.
- Pressoir, G., and J. Berthaud. 2004. Population structure and strong divergent selection shape phenotypic diversification in maize landraces. *Heredity* 92(2):95–101.
- Provine, W. B. 1971. *The origins of theoretical population genetics*. University of Chicago Press, Chicago, Illinois.
- Pujol, B., P. David, and D. McKey. 2005. Microevolution in agricultural environments: How a traditional Amerindian farming practice favours heterozygosity in cassava (*Manihot esculenta* Crantz, Euphorbiaceae). *Ecology Letters* 8(2):138–147.
- Revilla, P., R. Butrón, R. A. Malvar, and A. Ordás. 1999. Relationships among kernel weight, early vigor, and growth in maize. *Crop Science* 39:654–658.
- Rice, E., M. Smale, and J-L Blanco. 1998. Farmers' use of improved seed selection practices in Mexican maize: Evidence and issues from the Sierra de Santa Marta. *World Development* 26:1625–1640.
- Ruse, M. 1975. Darwin and artificial selection. *Journal of the History of Ideas* 36(2):339–350.
- Schneider, J. 2002. Selecting with farmers: The formative years of cereal breeding and public seed in Switzerland (1889–1936). Pages 161–187 in D. A. Cleveland and D. Soleri, eds. *Farmers, scientists and*

- plant breeding: Integrating knowledge and practice. CAB International, Wallingford, Oxon, U.K.
- Shanahan, T. 1990. Evolution, phenotypic selection, and the units of selection. *Philosophy of Science* 57:210–225.
- Simmonds, N. W., and J. Smartt. 1999. *Principles of crop improvement*. Second edition. Blackwell Science, Ltd., Oxford, U.K.
- Smith, M. E., F. Castillo G., and F. Gómez. 2001. Participatory plant breeding with maize in Mexico and Honduras. *Euphytica* 122(3):551–565.
- Sober, E. 1984. *The nature of selection*. University of Chicago Press, Chicago, Illinois.
- Soleri, D. 1999. Developing methodologies to understand farmer-managed maize folk varieties and farmer seed selection in the Central Valleys of Oaxaca, Mexico. Ph.D. dissertation, University of Arizona, Tucson, Arizona.
- , S. E. Smith, and D. A. Cleveland. 2000. Evaluating the potential for farmer and plant breeder collaboration: A case study of farmer maize selection in Oaxaca, Mexico. *Euphytica* 116:41–57.
- , and D. A. Cleveland. 2001. Farmers' genetic perceptions regarding their crop populations: An example with maize in the Central Valleys of Oaxaca, Mexico. *Economic Botany* 55:106–128.
- . 2004. Farmer selection and conservation of crop varieties. Pages 433–438 in R. M. Goodman, ed. *Encyclopedia of plant and crop science*. Marcel Dekker, New York.
- . 2005. Scenarios as a tool for eliciting and understanding farmers' biological knowledge. *Field Methods* 17:283–301.
- , D. A. Cleveland, S. E. Smith, S. Ceccarelli, S. Grando, R. B. Rana, D. Rijal, and H. Ríos Labrada. 2002. Understanding farmers' knowledge as the basis for collaboration with plant breeders: Methodological development and examples from ongoing research in Mexico, Syria, Cuba, and Nepal. Pages 19–60 in D. A. Cleveland and D. Soleri, eds. *Farmers, scientists and plant breeding: Integrating knowledge and practice*. CAB International, Wallingford, Oxon, U.K.
- , D. A. Cleveland, F. Aragón Cuevas, S. Ceccarelli, M. Diarra, S. Grando, S. Lacy, M. Michael, R. Ortiz, R. B. Rana, F. Rattunde, D. Rijal, H. Ríos Labrada, A. Sangar, S. Amadou, S. E. Smith, T. Issa, and E. R. Weltzien. 2004. Farmers' perceptions of crop genotype-environment interactions in five locations around the world.
- , D. A. Cleveland, F. Aragón Cuevas, H. Ríos Labrada, M. R. Fuentes Lopez, and S. H. Sweeney. 2005. Understanding the potential impact of transgenic crops in traditional agriculture: Maize farmers' perspectives in Cuba, Guatemala and Mexico. *Environmental Biosafety Research* 4:141–166.
- Sperling, L., M. E. Loevinsohn, and B. Ntabomvura. 1993. Rethinking the farmer's role in plant breeding: Local bean experts and on-station selection in Rwanda. *Experimental Agriculture* 29:509–519.
- vom Brocke, K., T. Presterl, A. Christinck, E. Weltzien, and H. H. Geiger. 2002. Farmers' seed management practices open up new base populations for pearl millet breeding in a semi-arid zone of India. *Plant Breeding* 121:36–42.
- , E. Weltzien, A. Christinck, T. Presterl, and H. H. Geiger. 2003a. Effects of farmers' seed management on performance and adaptation of pearl millet in Rajasthan, India. *Euphytica* 130:267–280.
- . 2003b. Farmers' seed systems and management practices determine pearl millet genetic diversity in semiarid regions of India. *Crop Science* 43:1680–1689.
- Wallace, H. A., and W. L. Brown. 1988. *Corn and its early fathers*. Revised edition. Iowa State University Press, Ames, Iowa.
- Weltzien, E., M. E. Smith, L. S. Meitzner, and L. Sperling. 2003. Technical and institutional issues in participatory plant breeding—From the perspective of formal plant breeding. A global analysis of issues, results, and current experience. PPB monograph. PRGA Program Coordination Office, Centro Internacional de Agricultura Tropical, Cali, Columbia.
- Whitt, S. R., L. M. Wilson, M. I. Tenaillon, B. S. Gaut, and E. S. Buckler. 2002. Genetic diversity and selection in the maize starch pathway. *Proceedings of the National Academy of Sciences of the United States of America* 99(20):12959–12962.
- Wilson, A. J., J. M. Pemberton, J. G. Pilkington, D. W. Coltman, D. V. Mifsud, T. H. Clutton-Brock, and L. E. B. Kruuk. 2006. Environmental coupling of selection and heritability limits evolution. *PLoS Biology* 4(7):1270–1275.
- Wilson, D. S. 1980. *The natural selection of populations and communities*. Benjamin/Cummings, Menlo Park, California.
- . 2004. What is wrong with absolute individual fitness? *Trends in Ecology and Evolution* 19(5): 245–248.
- Winn, A.A. 2004. Natural selection, evolvability and bias due to environmental covariance in the field in an annual plant. *Journal of Evolutionary Biology* 17(5):1073–1083.
- Wright, S. I., I. V. Bi, S. G. Schroeder, M. Yamasaki, J. F. Doebley, M. D. McMullen, and B. S. Gaut. 2005. The effects of artificial selection of the maize genome. *Science* 308(5726):1310–1314.
- Zimmerer, K. S. 1996. *Changing fortunes: Biodiversity and peasant livelihood in the Peruvian Andes*. University of California Press, Berkeley, California.