Farmer Selection and Conservation of Crop Varieties

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INTRODUCTION

After domestication, plant species were often transported widely, and many genetically distinct farmers' varieties (FVs, crop varieties traditionally maintained and grown by farmers) developed in specific locations.[1] FVs continue to be grown today by many small-scale farmers in traditionally-based agricultural systems (TBAS), fulfilling both local or regional consumption needs, as well as the larger social need for the conservation of genetic diversity.[2]

Crop genetic variation (V_G) is a measure of the number of alleles and degree of difference between them, and their arrangement in plants and populations. A change in V_G over generations is evolution, though one form of this change, microevolution, is reversible. Farmers and the biophysical environment select plants within populations. Farmers also choose between populations or varieties. This phenotypic selection and choice together determine the degree to which varieties change between generations, evolve over generations, or stay the same. Conservation in a narrow sense means the preservation of the V_G present at a given time. However, in situ conservation in farmers' fields is commonly understood to mean that the specific alleles and genetic structures contributing to that V_G may evolve in response to changing local selection pressures, while still maintaining a high level of V_G.[3] In contrast, ex situ conservation in genebanks attempts to conserve genetic diversity present at a given location and moment in time, preserving the same alleles and structures over time. Thus, different forms of conservation include different amounts and forms of change.

Sometimes farmers carry out selection or choice intentionally to change or conserve V_G. However, much of farmer practice is intended to further production and consumption goals and affects crop evolution unintentionally. Therefore, in order to understand farmer selection and conservation, it is important to understand the relationship 1) between production, consumption, selection, and conservation in TBAS, and 2) between farmer knowledge and practice and the basic genetics of crop populations and their interactions with growing environments [genetic variation, environmental variation and genotype-by-environment interaction (G×E), and response to selection] (Table 1).

FARMERS AND FVs IN TRADITIONALLY-BASED AGRICULTURAL SYSTEMS

TBAS are characterized by the integration within the household of production, consumption, selection, and conservation, whereas in industrial agriculture these functions are spatially and structurally separated. Farm households in TBAS typically rely on their own food production for a significant proportion of their consumption and this production is essential for feeding the population in TBAS now and in the future, even with production increases in industrial agriculture[4]—by 2025 three billion people will depend on agricultural production in TBAS.[5]

TBAS are also characterized by marginal growing environments (relatively high stress, high temporal and spatial variability, and low external inputs) and the continued use of FVs, even when modern crop varieties (MVs) are available.[6] 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). The V_G of farmer-managed FVs is not well documented, but is presumed to support broad resistance to multiple biotic and abiotic stresses, making them valuable not only for farmers because they decrease the production risks in marginal environments, but also for plant breeders and conservationists as the basis for future production in industrial agriculture.[7] 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 (e.g., maize varieties grown for purple husks used in tamale production).

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FARMER CHOICE: GENETIC VARIATION, CLASSIFICATION, GENOTYPE × ENVIRONMENT INTERACTION, AND RISK

The way farmers classify and value traits, which can vary between women and men, and between households in a community,[2] affects adoption and abandonment of varieties and populations, farmers' tolerance of intravarietal gene flow, and, thus, intraspecific V_G. Experimental evidence suggests that farmers can choose among large numbers of genotypes—in Syria, farmers were able to identify efficiently high yielding barley populations from among 208 entries, including 100 segregating populations.[7] Farmers' choice of varieties and populations when adopting or abandoning them from their repertoires, saving seed for planting, and procuring seed, does not change the genetic makeup of those units directly, and there is no evidence that farmers have any expectation of changing them. However, farmers' choice of crops, varieties, and populations does affect the total V_G farmers manage and the number of populations within which farmers can select plants.

The FV reproductive system, in combination with farmers' propagation methods, are important determinants of interspecific and intraspecific V_G both directly and indirectly, because resulting differences in the consistency of the V_G present over generations affects farmers' perception and management.[8] V_G in asexually propagated outcrossing crops such as cassava is exactly replicated in amount and structure between generations with discrete, fixed types (clones) or groups of types maintained as distinct varieties,[9,10] that may be either homo- or heterozygous. Intrapopulation V_G, affected by the genetics of the particular trait, becomes more dynamic and less structured with the intentional inclusion by farmers of sexually propagated individuals into clonal populations based on morphological similarity.[10] The same increase in dynamism occurs with increasing rates of outcrossing in

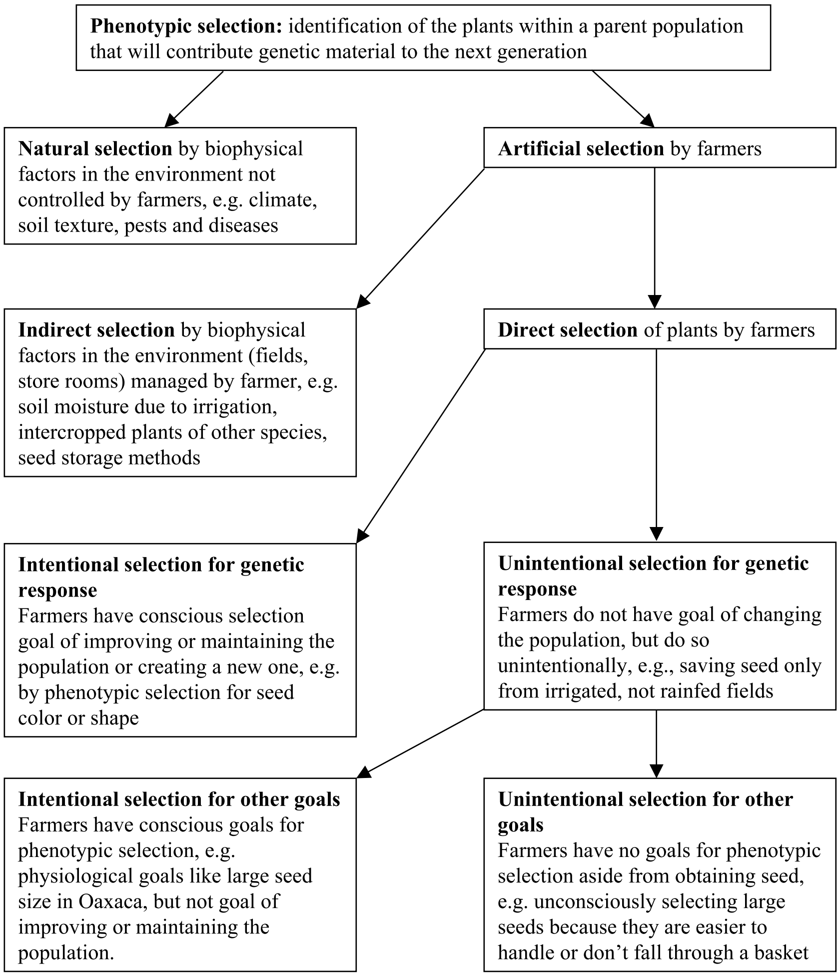

Fig. 1 Classification of farmer selection leading to genetic response, according to the agent of phenotypic selection and intent of farmer as agent.

sexually propagated crops, because variation can be continuous within a population. Moreover, segregation, crossing-over, recombination, and other events during meiosis and fertilization result in strong variability of V_G between generations. In predominantly allogamous crops such as maize, heterozygosity can be high, making it difficult to discern discrete segregation classes particularly in the presence of environmental variation, and retention of distinguishing varietal characteristics requires maintenance selection.[11] Highly autogamous crops such as rice are predominantly homozygous, making exploitation of V_G and retention of varietal distinctions easier, even if varieties are composed of multiple, distinct lines.

Farmers' choices depend in part on the range of spatial, temporal, and management environments present, the V_G available to them, and the extent to which genotypes are widely versus narrowly adapted. In turn, environmental variation in these growing environments interacts with V_G (G×E) to produce variation in yield of grain, straw, roots, tubers, leaves, and other characteristics over space and time. As a result, farmers may have different criteria for different environments, as in Rajasthan, India, where pearl millet farmers realize there is a trade-off between panicle size and tillering ability: Farmers in a less stressful environment prefer varieties producing larger panicles, while those in a more stressful environment prefer varieties with high tillering under their conditions.[12]

Farmers' seed management and choice of growing environments determine the possible extent of pollen flow between populations or varieties. In Jalisco, Mexico, farmers regularly mix maize populations together by classifying seed obtained from diverse sources as the same variety, which, together with planting patterns, leads to a 1–2% level of gene flow between maize plots during one crop cycle as detected by isozyme analysis, affecting genetic composition over several crop cycles.[13] The morphological and genetic continuum across the four major local varieties suggests that traits from a variety introduced 40 years ago have introgressed into the other varieties.

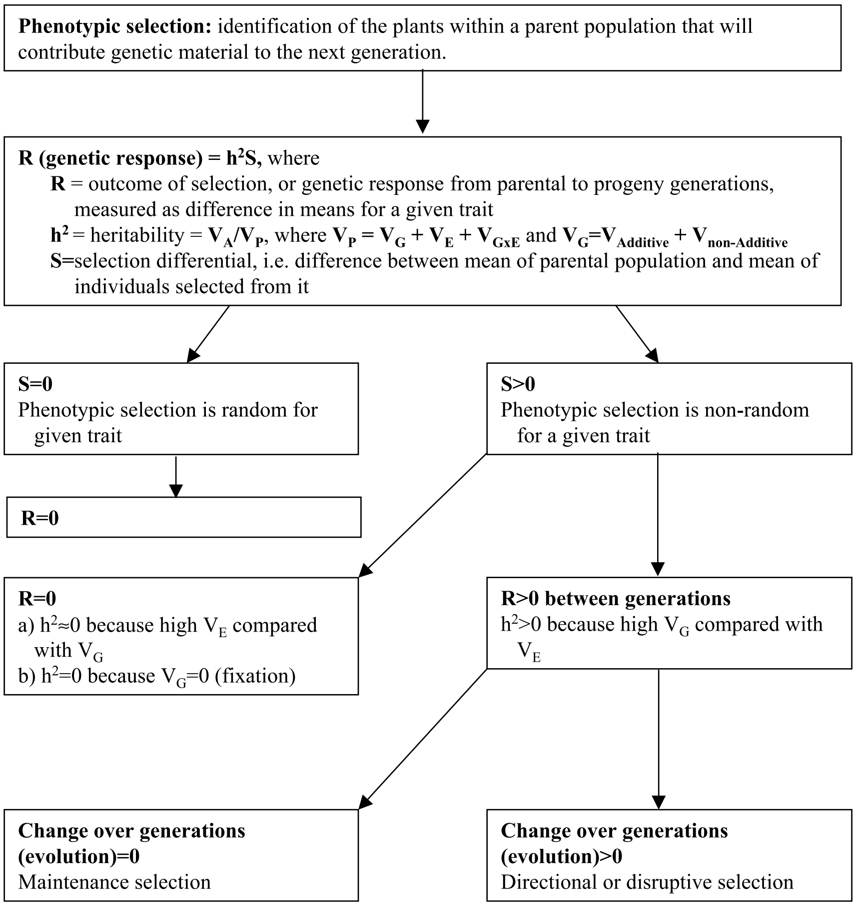

Fig. 2 Classification of farmer selection according to genetic response as an outcome of phenotypic selection. V_A = additive genetic variation, V_P = phenotype variation, V_G = genetic variation, V_E = environmental variation, V_{GXE} = variation in genotype by environmental interaction.

Patterns of variation in yield affect farmers' choice of crop variety via their attitude toward risk. In response to scenarios depicting varietal G×E and temporal variation, farmers from more marginal growing environments were more risk-averse compared to those from more favorable environments, the former preferring a crop variety with low but stable yields across temporal environments, the latter choosing a variety highly responsive to favorable conditions but with poor performance under less favorable conditions.[14]

Table 1 Farmer selection and choice and the change and conservation of crop varieties

Farmer knowledge (including values) on which practice may be based	Farmer practice	Potential effect of farmer practice on selection and conservation of populations/varieties	Example
Indirect selection/conservation by farmer-managed growing and storage environment			
Understanding of G×E	Allocation of varieties to spatial, temporal, and management environments	Selection pressures in environments result in maintenance of existing or development of new populations/varieties, including evolution of wide or narrow adaptation	*Spatial*: varieties specified for different soil or moisture types; rice, Nepal; pearl millet, India. *Temporal*: varieties with different cycle lengths, maize, Mexico
	Management of growing environments	Changing selection pressures	Changes in fertilizer application, maize, Mexico.
Risk, values, G×E	Choice of environments for testing new populations/varieties	↑ or ↓ V_G	High stress, rice, Nepal; Optimal conditions, barley, Syria
Escape from economic or political pressure; desire for different way of life	Abandonment of fields or farms, reduced field size	↓ V_G within due to reduced area for planting, ↓ effective population size, genetic drift	Pooling of subvarieties, maize, Hopi and Zuni; Reduction in area, potatoes, Peru; maize, Mexico
Direct selection/conservation, intentional re. population change			
Discount rate (values re. future), altruism (values re. community)	Conservation of varieties for the future, for other farmers	↑ intraspecific V_G	Rice, Thailand; maize, Hopi
Interest and expertise in experimentation	Deliberate crossing	↑ V_G	Maize-teosinte, Mexico; MV-FV pearl millet, India; MV-FV and FV-FV, maize, Mexico.
Understanding of h^2	Selection of individuals (plants, propagules) from within parent population	↑ or ↓ V_G via R	Among seedlings, cassava, Peru; among panicles, pearl millet, India.
Direct, selection/conservation, unintentional re. population change, but intentional re. other goals, as result of production/consumption practices			
Attitudes towards risk re. yield stability	Adoption and abandonment of FVs, MVs	↑ or ↓ intraspecific diversity	Maize, Hopi Rice, Nepal
	Adoption and abandonment of lines in multiline varieties of self pollinated crops; seedlots in cross-pollinating crops	↑ or ↓ intravarietal diversity	Common bean, East Africa Maize, Mexico
Agronomic, storage, culinary, aesthetic and ritual criteria, implicit and explicit	Selection or choice based on production/consumption criteria	↑ or ↓ intra- and intervarietal diversity	Storage and culinary criteria: maize, Mexico; and ritual criteria, rice, Nepal
Choice criteria	Acquisition of seed, seed lots	Gene flow via seed then pollen flow, hybridization, recombination within varieties	Cycle length, maize, Mexico; cuttings and seedlings, cassava, Guyana

G×E: genotype by environment interaction
V_G: genetic variation
↑ or ↓: increase or decrease
h^2: heritability in the narrow sense
R: response selection
MV: modern crop variety, product of formal breeding system
FV: farmer developed crop variety

SELECTION: HERITABILITY, PHENOTYPIC SELECTION DIFFERENTIAL, AND RESPONSE

Phenotypic selection is the identification of individual plants within a population that will contribute genetic material to the next generation. Phenotypic selection of FVs in TBAS can be classified according to the agent of selection (natural environment, farmer-managed environment, or farmer) and according to farmers' goals for selection (Fig. 1). Farmer selection can also be classified according to the outcome (Fig. 2). Geneticists and plant breeders tend to think of phenotypic selection as seeking to produce genetic change, but farmers often do not. Whether or not farmer selection changes the genetic makeup of the population (i.e., effects genetic response or R) depends on heritability (h^2), or the proportion of phenotypic variation that is genetic and can be inherited; and the selection differential (S), or the difference between the means of the parental population and sample selected from it: $R = h^2S$. The extent to which selection maintains potentially useful V_G is a measure of its contribution to in situ conservation.

Heritability is often understood by farmers who distinguish between high and low heritability traits and consciously select for the former, while often considering it not worth while or even possible to select for the latter, especially in cross-pollinating crops.[14] When farmers' selection criteria centers on low heritability traits such as large ear size in maize, they may achieve high S, and little or no R. However, they persist in selection because they have other goals, such as improving the quality of planting seed, not high R.[11,15]

In terms of seeking genetic response, farmers may practice intentional selection either to create new varieties, best documented in vegetatively propagated and self-pollinating crops,[9] or for varietal maintenance or improvement, although much evidence for the latter is anecdotal. Unintentional selection—that is, not seeking genetic response—, as documented with maize farmers in Mexico, may be undertaken for varietal maintenance and/or to ensure planting seed quality, although this can also result in genetic response.

Quantitative research on the goals and outcomes of farmers' selection is relatively new. Selection exercises in two independent investigations of maize in Mexico found farmers' selections to be significantly different from the original population for a number of ear traits, resulting in high S values.[11,15] However, R values calculated in the Oaxaca study were zero for these as well as other morpho-phenological traits.[15] Similarly, the Jalisco study found that selection served to diminish the impact of gene flow, but not to change the population being selected on.[11] Indeed, a recent study across four sites each with different crops found that often a majority of farmers in a site did not see their seed selection as a process of cumulative, directional change.[14]

However, intentional phenotypic selection for goals other than genetic response is practiced by nearly all farmers in that study and probably in TBAS, the reasons documented to date being seed quality (germination and early vigor) and purity and because this is ‘‘the way we know,’’ that is, because farmers may not want to change (viz. ‘improve’) a variety, although genetic response may result unintentionally. To understand this from the farmers' perspective, it is necessary to take into account the multiple functions of crop populations in TBAS: production of food and seed, consumption, conservation, and improvement.

CONCLUSIONS

Selection and conservation in TBAS contrast substantially with industrial agricultural systems, and understanding farmers' practices, and the knowledge and goals underlying them, is critical for supporting food production, food consumption, crop improvement, and crop genetic resources conservation for farm communities in TBAS and for long-term global food security. The urgency of understanding farmer selection and conservation will increase in the future with the on-going loss of genetic resources, the rapid spread of transgenic crop varieties with limited genetic diversity, the development of a global system of intellectual property rights in crop genetic resources, and the movement to make formal plant breeding more relevant to farmers in TBAS through plant breeding and conservation based on direct farmer and scientist collaboration.

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ARTICLES OF FURTHER INTEREST

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Crops and Environmental Change, p. 370

Gene Flow Between Crops and Their Wild Progenitors, p. 488
Pre-Agricultural Plant Gathering and Management, p. 1055

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