Genetic Resources: Farmer Conservation and Crop Management

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Abstract
Crop genetic variation (V_G) measures the number of alleles, differences between them, and their arrangement in plants and populations. Farmers and the biophysical environment select plants within populations and farmers choose between populations. Together, phenotypic selection and choice determine the extent of population change between generations, and evolution over generations. With in situ conservation on farm there is evolution in response to local selection pressures, often maintaining a high level of V_G. In contrast, ex situ conservation in gene banks conserves the V_G present at a given time and place. Sometimes farmers carry out selection or choice intentionally to change or conserve V_G. Yet much of farmer practice is for production and consumption goals, affecting crop evolution unintentionally if at all. The need to understand farmer selection and conservation is increasing with the loss of genetic resources, spread of transgenic varieties with limited V_G, development of a global intellectual property rights in crop genetic resources, global climate change, and efforts to make formal plant breeding relevant to traditional farmers.

INTRODUCTION

Food production is essential to support human society yet agriculture is one of the largest contributors to global environmental destruction through loss of habitat and diversity, and greenhouse gas emissions that are driving climate change.[1] Identifying options for higher but more sustainable production requires consideration of diverse strategies, including understanding farmer management and conservation of crop varieties that have been the basis of our food system for nearly all of settled human history. About 2 billion people live on 500 million small-scale farms (under 2 ha) globally,[2] most of these in traditionally based agricultural systems (TBAS), and the number will grow dramatically with population growth in the coming decades. Many farmers in TBAS save their own seed to grow at least a portion, and for some most, of the food they eat, conserving valuable genetic resources in the process. Plant breeders working with TBAS farmers consider diversity at many spatial levels of the agrifood system a key to alternatives such as organic and low-input agriculture.[3]

The beginning of agriculture with the Neolithic revolution initiated a dramatic reduction in the diversity of species humans used for food. After domestication, crop species were often transported widely, and many genetically distinct farmers' varieties (FVs, crop varieties traditionally maintained and grown by farmers) developed in specific locations, greatly increasing intraspecific diversity.[4] As Simmonds stated, "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,"[5] an insight verified by a genome-wide review of maize wild relatives, FVs, and modern varieties (MVs) created by professional plant breeders.[6] FVs continue to be grown today by many small-scale farmers in TBAS, providing for both local consumption and the conservation of genetic diversity for global society.[7]

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. For our purposes, a cumulative change in crop population V_G over generations is called microevolution (E_V). Farmers and the biophysical environment select plants within populations based on their phenotypic variation (V_p). 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. With in situ conservation in farmers' fields specific alleles and genetic structures contributing to V_G may evolve in response to changing local selection pressures, while still maintaining a high level of V_G.[8] In contrast, ex situ conservation in gene banks is more narrowly defined as conserving the specific alleles and structures of V_G present at a given location

Encyclopedia of Natural Resources DOI: 10.1081/E-ENRL-120049217

and moment in 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, affecting crop evolution unintentionally if at all. Thus, in order to understand farmer selection and conservation, it is important to understand the relationship between production, consumption, selection, and conservation in TBAS.[4] This in turn involves understanding the relationship between farmer knowledge and practice in terms of the basic genetics of crop populations and their interactions with growing environments (genetic variation, environmental variation, variation due to genotype-by-environment interaction [$V_{G\times E}$], and response to selection[R])[7,9] (Table 1).

FARMERS AND FVS IN TRADITIONALLY BASED AGRICULTURE SYSTEMS

TBAS are characterized by integration within the household or community 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; this production is essential for feeding the population in TBAS now and in the future, even with production increases in industrial agriculture.[10]

TBAS are also characterized by marginal growing environments (relatively high stress, high temporal and spatial variability, and low external inputs), and by the continued use of FVs, even when MVs are available.[11] 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).

TBAS farmers value FVs for agronomic traits, such as drought resistance, pest resistance, and photoperiod sensitivity. Because farmers grow some or most of the food they eat, storage and culinary criteria are frequently important; for example, families who make the traditional maize beverage *tejate* maintain more varieties of maize than families who do not, using them in preparation of that drink.[12]

The V_G of farmer-managed FVs is often much higher than that of MVs, and is presumed to support broad resistance to multiple biotic and abiotic stresses.[13,14] This makes FVs valuable not only for farmers, because they decrease the production risks in marginal environments especially with climate change,[15] but also for plant breeders and conservationists as the basis for future production in industrial agriculture.[8,16]

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

Farmers classify and value traits in their crops, and this can vary between women and men,[7] and between households in a community.[17–19] This variation affects their definition of varieties and populations, and thus the degree of intraspecific V_P (and V_G) they are willing to accept, as a result for example of intravarietal gene flow. These definitions in turn affect farmers' choice, such as which crops, varieties, and populations to adopt or abandon and thus the total V_G they manage, and the number of populations from which they select plants. Experimental evidence indicates that farmers can choose among large numbers of genotypes. In Syria, farmers were able to effectively identify high yielding barley populations from among 208 entries, including 100 segregating populations.[20]

Farmers' choice of varieties and populations without discriminating between individual propagules when adopting or abandoning them from their repertoires, saving seed for planting, and in seed procurement, does not change the genetic makeup of those units directly, and there is no evidence that farmers expect to change them. However, genetic structure may be altered due to sampling error, if the number of seeds required to plant an area is small, and many of these may be half sibs in a crop like maize, with <143 ears ha^{-1} in the case of Oaxaca, Mexico and many farmers planting much smaller areas.[21]

FV crop mating systems in combination with farmers' propagation methods are important determinants of inter- and intraspecific V_G. These also affect differences in phenotypic consistency over generations and therefore farmers' perception and management.[22] Apart from low-frequency somatic mutations, V_G in asexually propagated outcrossing crops, such as cassava, is unchanged between generations, and discrete, fixed types (clones) or groups of types are maintained as distinct varieties[23,24] that may be either homo- or heterogeneous. Intrapopulation V_G increases and genetic structures become more variable and dynamic with the intentional inclusion by farmers of sexually propagated individuals into clonal populations based on morphological similarity or heterosis.[24]

The same increase in dynamism occurs with increasing rates of outcrossing in 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 much change in V_G between generations. In highly 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 retaining distinguishing varietal characteristics requires maintenance selection[25] (see below). 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.

Genetic—Keystone

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 ways 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, Guyana; 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; seed lots in cross-pollinating crops	↑ or ↓ intravarietal diversity	Common bean, East Africa; maize, Mexico
Agronomic, storage, culinary, esthetic 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

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

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 (V_E) in these growing environments interacts with V_G ($V_{G\times E}$) 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 choice criteria for different environments, as in Rajasthan, India, where pearl millet farmers realize there is a trade-off between panicle size and tillering ability. So, farmers in a less stressful environment prefer varieties producing larger panicles, whereas those in a more stressful environment prefer varieties with high tillering.[26]

Patterns of variation in yield affect farmers' choice of crop variety via their attitude toward risk. In response to scenarios depicting varietal $V_{G\times E}$ and temporal variation, farmers from more marginal growing environments were more risk averse compared to those from more favorable environments. The former preferred a crop variety with low but stable yields across environments while the latter chose a variety highly responsive to favorable conditions but with poor performance under less favorable conditions.[27] Sorghum farmers in Mali tend to choose varieties to optimize outputs in the face of variation in rainfall, level of striga infestation, and availability of labor and other production resources, especially cultivator and seeder plows.[28] As a result, they choose combinations of long- and short-cycle sorghum varieties to optimize yield, yield stability, and post-harvest traits like taste. For example, when rains are better, farmers choose a greater number of long-cycle varieties.

FARMER SELECTION: HERITABILITY, PHENOTYPIC SELECTION DIFFERENTIAL, AND RESPONSE

Phenotypic selection, operating on V_P, is identification of the 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.[29] Whether or not farmer selection does change the genetic makeup of the population (i.e., effects genetic response between generations [R], or cumulative multigenerational microevolution [E_V]) 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 in mean between parental population and sample selected from it: $R = h^2S$.

$S > 0, R \approx 0$. Heritability is often understood by farmers who distinguish between high and low heritability traits, consciously selecting the former, while often considering it not worthwhile or even possible to select the latter, especially in cross-pollinating crops.[27] When farmers' selection criteria center on relatively low heritability traits such as large ear and seed size in maize, they may achieve high S, and little or no R. However, they persist with that selection because their goal is high-quality seed for planting.[25,30] A study across four sites, each with different crops, found that often a majority of farmers at a site did not see their seed selection as a process of cumulative, directional change.[27] However, intentional phenotypic selection for goals other than genetic response was practiced by nearly all farmers in that study. Selection exercises with maize in Oaxaca, Mexico[30] found farmers' selections to be significantly different from that of the original population in their selection criteria, resulting in high S values. However, R values were zero for these as well as other morphophenological traits. The reasons documented to date are for seed quality (germination and early vigor) and purity, and because of "custom," that is, not to change or improve a variety. 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, improvement).

$R > 0, E_V \approx 0$. Farmers also select seed to maintain defining, desirable, heritable varietal traits that change as a result of gene flow and indirect selection by environmental factors in fields and storage containers, especially in allogamous species. When successful, this results in R and, over time, prevents unwanted E_V. Selection exercises with maize in Jalisco, Mexico, found that farmers' selection served to diminish the impact of gene *flow* and maintain varieties' morphological characteristics, but not to change the population being selected on. Indian farmers were able to maintain the distinct ideotypes of introduced FVs of their allogamous crop pearl millet via intentional selection of panicles for their unique phenotypes.[31]

$E_V > 0$. In seeking cumulative genetic response or E_V, farmers may practice intentional selection either to create new varieties, best documented in vegetatively propagated and self-pollinating crops,[32] or for varietal improvement, although much evidence for this is anecdotal. Most often this is selection for heritable, qualitative traits; for example, 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.[33]

CONCLUSIONS

Selection and conservation in TBAS contrast substantially with industrial agricultural systems. Therefore, understanding farmers' practices, and the knowledge and goals underlying them, is critical for supporting food production, food consumption, crop improvement, and crop genetic

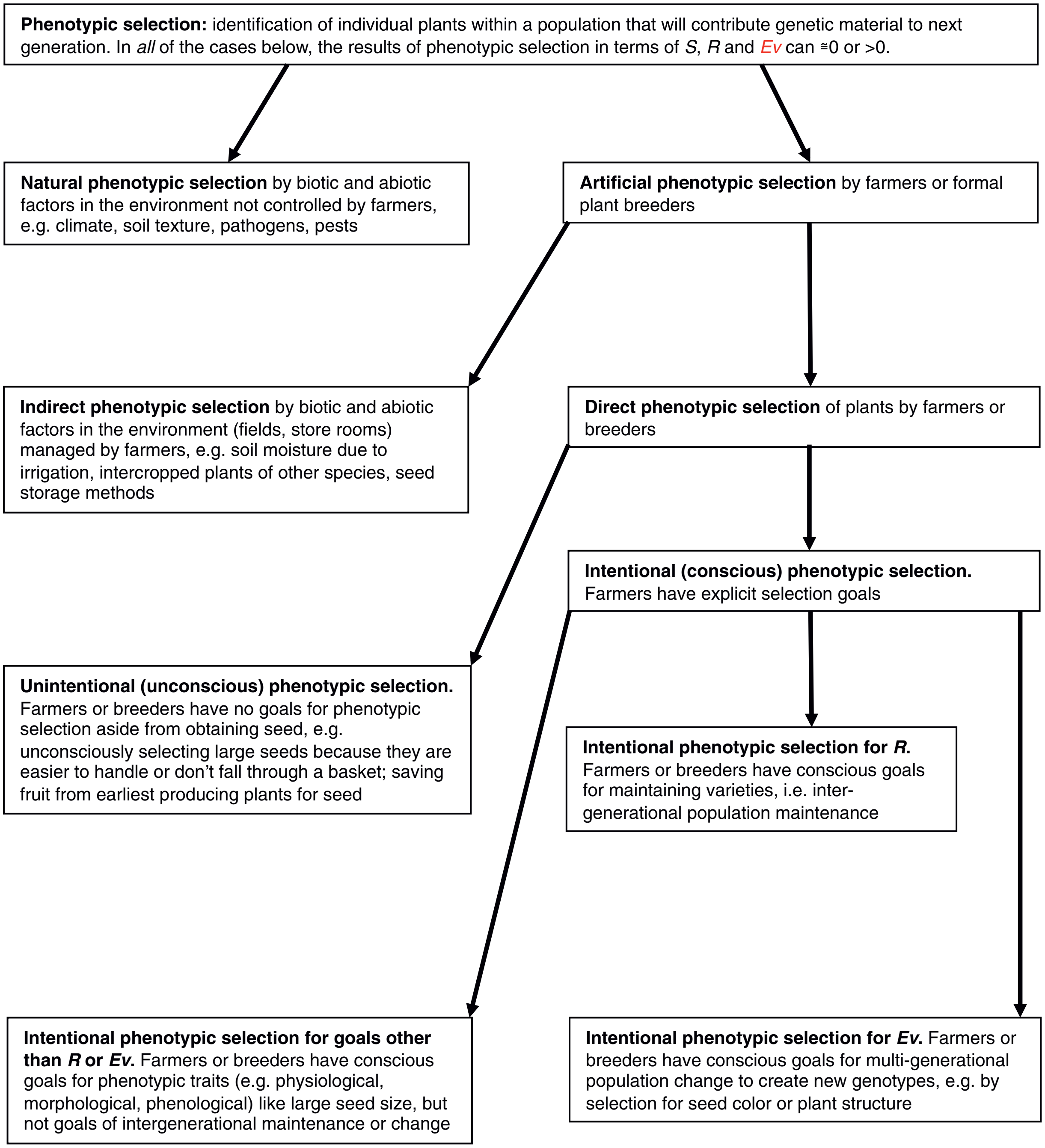

Fig. 1 Phenotypic selection classified according to the agent of selection, and intention of the farmer or plant breeder as agent. See text for definition of abbreviations. © D. Soleri & D.A. Cleveland, 2013.

resource 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 ongoing 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.

At present, attention and investment in transgenic genetic engineering dominate crop improvement globally. Yet, schemes that are to some extent modeled on and make use of farmer management and the V_G of their FVs show good potential for increasing yields, conserving genetic resources, and supporting adaptation to growing environments that are changing at an accelerating pace.[34] Farmer management and conservation of crop varieties developed in situ is a form of precision agriculture that, when combined with formal scientific methods and research support, may be the strategy most

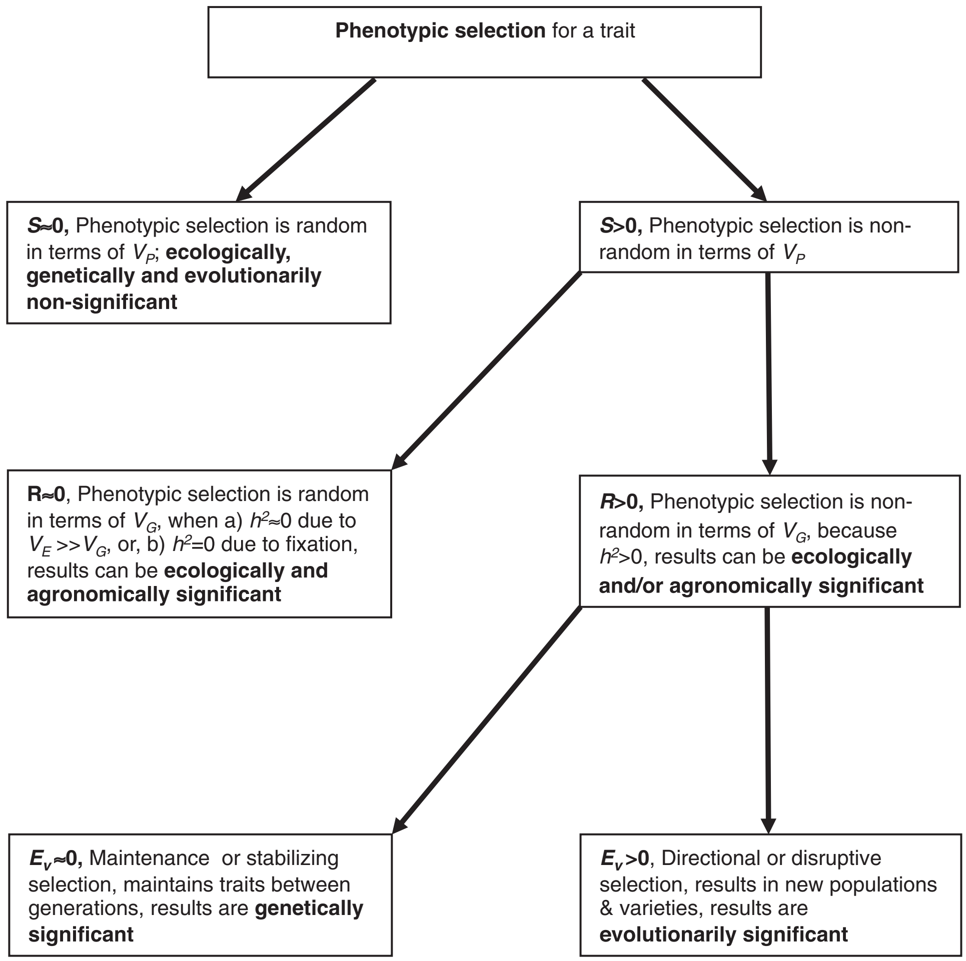

Fig. 2 Phenotypic selection classified according to outcome of selection. See key to symbols below. © D.A. Cleveland & D. Soleri, 2013. Abbreviations: FV, farmer developed crop variety; h^2, heritability in the narrow sense; MV, modern crop variety, product of formal breeding system; R, response to selection; V_E, environmental variation; V_G, genetic variation; $V_{G\times E}$, genotype-by-environment interaction variation; V_P, phenotypic variation; ↑, increase; ↓, decrease.

likely to address multiple criteria of environmental, economic, and social sustainability in the global food system.[35]

ACKNOWLEDGMENTS

This entry is an update of an entry in the *Encyclopedia of Plant and Crop Science*.[36] The research on which some of this entry is based was supported in part by NSF grant nos. SES-9977996 and DEB-0409984, and a grant from the Wallace Genetic Foundation.

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