Plant breeding for harmony between agriculture and the environment

E Charles Brummer, Wesley T Barber, Sarah M Collier, Thomas S Cox, Randy Johnson, Seth C Murray, Richard T Olsen, Richard C Pratt, and Ann Marie Thro

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Plant breeding programs primarily focus on improving a crop’s environmental adaptability and biotic stress tolerance in order to increase yield. Crop improvements made since the 1950s—coupled with inexpensive agronomic inputs, such as fertilizers, pesticides, and water—have allowed agricultural production to keep pace with human population growth. Plant breeders, particularly those at public institutions, have an interest in reducing agriculture’s negative impacts and improving the natural environment to provide or maintain ecosystem services (e.g., clean soil, water, and air; carbon sequestration), and in creating new agricultural paradigms (e.g., perennial polycultures). Here, we discuss recent developments in as well as the goals of plant breeding, and explain how these might be connected to the specific interests of ecologists and naturalists. Plant breeding can be a powerful tool to bring “harmony” between agriculture and the environment, but partnerships between plant breeders, ecologists, urban planners, and policy makers are needed to make this a reality.

In a nutshell:

- Plant breeding has played a vital role in the successful development of crops to meet the food and material needs of society
- Plant breeders are continually improving the ability of crops to withstand various environmental conditions, including those associated with global climate change
- Reducing agriculture’s impact on the environment while maintaining sufficient production will require the development of new crops and production practices
- Partnerships between ecologists, urban planners, and policy makers with public and private plant breeders will be essential for addressing future challenges

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are better adapted to environmental stresses, productivity can be maintained in the face of increasingly variable weather patterns and suboptimal conditions, as well as pest and disease pressures; and (2) by developing plants that can alter and “improve” environments, sustainable solutions to ecological dilemmas may be provided.

### Plant breeding

The domestication of staple crops – for example, rice (Oryza sativa) and soybean (Glycine max) in eastern Asia; wheat (Triticum aestivum) in the Middle East; sorghum (Sorghum bicolor) in Africa; maize/corn (Zea mays), beans (Phaseolus spp), and potatoes (Solanum tuberosum) in the Americas (Harlan 1991) – began independently, in multiple locales, 5000–12,000 years ago. For thousands of years, these crops were grown and morphologically altered by farmers, who selected the most desirable and adaptable varieties to plant in the next growing season. After the discoveries of Darwin and Mendel, scientific knowledge was applied to plant breeding in the late 1800s (Borlaug 1983). With the implementation of hybrid crop breeding beginning in the 1920s, yield per unit land area rapidly increased in the US (Pratt 2004; USDA-NASS 2009; Figure 1). In the US and throughout the world, improvements in yield have been a function of both plant breeding and improved management practices (Tilman 1999). However, more food could be produced – with less land and effort – to meet societal needs.

Modern plant breeding is the science of improving plants to achieve these needs and better fit production environments, but is a long-term proposition. Each released cultivar represents a culmination of a decade or more of work, from initial crosses through final testing. The rate of improvement is a function of the amount of heritable genetic variation present in a population, the time it takes to complete a breeding cycle (from seed production through selection to seed production again), which can range from multiple generations per year (eg, corn on field sites in both hemispheres) to decades (some trees require 8 years of growth before flowering). In hybrid crops, several years (multiple breeding cycles) are necessary to develop inbred lines that must then be tested in hybrid combinations. Many years of testing under various environmental conditions must be conducted to ensure that the new cultivar (inbred, hybrid, or population) will perform well for the farmer, consumer, or end-user before any substantial additional investment is made to increase production and distribution of the cultivar. After such a lengthy selection process, therefore, the greatest genetic variation – the raw material essential for crop improvement – is found not in the few elite cultivars that reach farmers’ fields but in breeding programs, genetic repositories, and the wild.

In general, plant breeding consists of controlled hybridization of plants within the same or closely related species and selecting the most desirable plants based on phenotype – any characteristic of the plant that can be measured. However, new technologies and techniques, such as “marker-assisted selection”, use molecular genetics and statistical techniques to characterize, identify, and select favorable, naturally occurring trait variants. Marker-assisted selection is particularly important for improving complex, quantitatively inherited traits that alter yield, and for speeding up the breeding process. In a growing number of species, genetic engineering is an additional tool that can accelerate improvement rates, but only a few genes can be altered (or added) through transgenic events, based on the current science and expensive regulatory approval process (Bradford et al. 2005). Transgenic breeding involves the introduction of foreign DNA and is almost exclusively used in the commercial private sector. Diverse and polarizing opinions on transgenic tools have detailed more important agreements on goals to scientifically improve plants that can better harmonize agriculture with the environment.

Regardless of method, breeding objectives can be

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**Figure 1.** Plant breeding and agronomic improvements have greatly increased yields of important crops. Five-year moving averages of US yield scaled to each crop’s historical minimum were calculated from available data (USDA-NASS 2009). The yield of seven important annual crops shows that yield per unit land has increased from three- to 11-fold, meaning that between one-third and one-eleventh as much land is needed today to produce the same amount of food as in the past. This increase confounds improvements from breeding and from agronomic practices, which are extremely difficult to separate. Two of these crops – sugarcane and coffee – are perennial, resulting in fewer breeding generations over the same period and substantially less investment. Increasing yield per unit land area and yield per unit input (eg water and nutrients) results in greater production to feed a growing human population without increasing the amount of land under cultivation.
Native germplasm is being used to improve staygreen cultivars that are more tolerant to drought conditions (Figure 2). The increasing cost of water to farmers places a value on corn cultivars that are more tolerant to drought conditions, and the value of these drought-tolerant cultivars will be captured by the private seed sector, farmers, and society.

Figure 2. As a result of breeding with native maize germplasm, increased staygreen (delayed leaf senescence) is shown in the hybrid on the right under drought conditions.

Panel 1. Private plant breeding

The ability to maintain high yields under low water stress, often one component of broadly defined “drought tolerance”, is critically important for increasing agricultural production while minimizing agricultural inputs. Because corn is the most productive grain crop and has the highest acreage in the US, it is an important target for improvement. Because the corn industry is well developed and highly profitable, most commercial breeding and seed production occurs in the private sector. Pioneer Hi-Bred International is using native diversity in corn, combined with advanced measurement technologies and statistical analyses, to develop corn lines that better resist periods of drought (Figure 2). The increasing cost of water to farmers places a value on corn cultivars that are more tolerant to drought conditions, and the value of these drought-tolerant cultivars will be captured by the private seed sector, farmers, and society.

Figure 2. As a result of breeding with native maize germplasm, increased staygreen (delayed leaf senescence) is shown in the hybrid on the right under drought conditions.

Breed to adapt plants to the environment

Producing more with less

In the coming century, fresh water suitable for irrigation is expected to become increasingly scarce and the costs of fertilizer and other agricultural inputs will increase as fossil-fuel costs rise. Nevertheless, continuing gains in production per hectare must be realized to offset the loss of premium agricultural lands (e.g., from suburbanization) while supplying a growing population. By developing plants that use resources more efficiently, plant breeders continue to improve the sustainability of agriculture as well as urban and forest ecosystems. Plants that require application of fewer off-farm inputs—specifically water, pesticides, nitrogen, phosphorus, and other nutrients—decrease the cost of production, lower fossil energy use, and reduce contamination of water systems, which help to improve public health and stabilize rural economies (Tilman 1999; Robertson and Swinton 2005). Additionally, world supplies of phosphorus—a critical plant nutrient—are dwindling and may limit future crop production. Although modern plant breeding efforts initially focused on improving uptake of inputs, recent efficiency gains have been made in physiologically increasing yield and biomass production without further increasing inputs. Many crops already have genetic variation in nutrient use efficiency, utilization, and uptake; plant breeding will further improve these traits (e.g., Hirel et al. 2007; Foulkes et al. 2009; Korkmaz et al. 2009).

Adapting to global climate change and breeding for abiotic and biotic stress tolerance

Extreme weather events—such as the recent recurrent flooding in the Midwestern US, a center of world food and animal feed production—are expected to increase in both number and severity in coming years (IPCC 2009). The 2010 flood was ranked as the third extreme flood event within the Midwestern US over the past 20 years, and offers a glimpse of possible future patterns (Takle 2010). In addition to physically destroying crops, changes in climate have altered host–pathogen relationships and resulted in increased disease incidence and insect-pest-borne stress in crop plants. To maintain productivity in the face of increased climatic variability, plant cultivars and populations will need to be continually developed to withstand “new” climatic extremes and the stresses that these will entail (Ortiz et al. 2008).

Many breeding programs are already developing plants that can tolerate extreme weather conditions, including drought, heat, and frost (Araus et al. 2008; Cattivelli et al. 2008). Plant breeders are also beginning to address expected changes due to increased climate variability, by increasing genetic diversity sources and by adjusting selection and testing procedures (Ceccarelli et al. 2010). A specific example is breeding for in-field diversity (WebPanel 1). More frequent weather extremes will likely affect the existing ranges of not only agronomic cultivars but also local native plant species (Burke et al. 2009). Because some genetic variation useful for climate...
Harmonizing agriculture with the environment

Panel 2. Public plant breeding

The goal of breeding projects for forages, which include several species, is to produce a high yield of leaf and stem biomass, as opposed to grain, for ruminant animals. Many forages are perennial, providing year-round erosion control, improving water infiltration as compared with that from annual cropping systems, and, in some cases, sequestering carbon. Most forage cultivars have been developed by university or government breeders. The forage breeding program at the University of Georgia (UGA) has developed cultivars in several species and has been proactive in developing agreements with private-sector commercial partners to oversee seed production and marketing of new cultivars. Among the cultivars developed at UGA is “Jesup MaxQ” tall fescue, a cultivar carrying a non-toxic endophytic fungus that was both highly persistent under grazing and greatly improved animal weight gain and feed efficiency over standard cultivars.

In addition, this program developed the first true dual purpose – grazing and hay – alfalfa cultivar “Alfagraze” (Figure 3), followed by several further improved cultivars. These cultivars and others – such as the ecotypic white clover selection “Durana” – are highly persistent in the southeastern US piedmont and coastal plain regions, which have typically not been the target of private breeding programs (Bouton 2007).

Figure 3. A plot of the UGA-developed alfalfa cultivar – Bulldog 805 (center) – has persisted through summer under cattle grazing in Tifton, Georgia, while other plots on all sides show stand loss and lower production. This cultivar survives substantially longer in the southeastern coastal plain of the US under hay and grazing management than any other currently available cultivar.

Change adaptation will be found only in wild plant relatives of cultivated species, preserving genetic diversity is essential so that breeders can select plants that will be well-suited for future environmental conditions (Jarvis et al. 2008).

Global climate change notwithstanding, additional stress tolerances in crop species are needed to maintain productivity and survival. In the near term, tolerance to various soil conditions – including acidic, aluminum-rich soils (particularly in the tropics) and saline soils (especially those resulting from irrigation) – will be increasingly important for production on marginal agricultural lands or as the salt content of irrigated lands increases (Witcombe et al. 2008).

Globalization has, among other consequences, led to the rapid spread of plant diseases and invasive pests. Developing resistant cultivars reduces the need for expensive and environmentally damaging pesticides to be produced and applied. Tree breeding efforts, for instance, are sometimes the only means to ensure the successful survival and establishment of important species in both urban forests and native habitats. Current tree breeding programs are developing elms (Ulmus spp), chestnuts (Castanea dentata), hemlocks (Tsuga spp), and other species that are resistant to introduced diseases and insects (Jacobs 2007; Santini et al. 2007). As compared with natural selection, artificial selection via plant breeding has overcome these stresses more effectively by rapidly incorporating diverse exotic genetic sources of resistance, hybridizing to include multiple, different genetic resistances into the same plant, and making use of off-season locations or artificial conditions to shorten generation cycles.

Breeding plants to improve the environment

An early report evaluating ecosystem services suggested that agricultural systems ranked lower in terms of contributions in comparison with other systems, such as forestland (Costanza et al. 1997). This suggests that – despite providing food, feed, fiber, and fuel – current agricultural systems could also supply additional essential ecosystem services, or supply them more efficiently. Plant breeders need to understand the various valuation strategies (Robertson and Swinton 2005) very early in the breeding process if they are to direct long-term selection toward reducing agriculture’s negative environmental impacts and achieving greater sustainability while maintaining productivity. New crop cultivars developed by plant breeders must help improve soil health, reduce soil erosion, prevent nutrient and chemical runoff, and maintain biodiversity. Informed plant breeding choices – based on the needs of the overall cropping system – present opportunities to improve environmental conditions if ecosystem-service valuation (conducted by ecologists and land-use planners) is disseminated and adopted by society at large.

Breeding alternative crops and crops for new uses

Perennial crops have environmentally “beneficial” properties not present in annual crops, such as helping to prevent erosion in agricultural systems, providing wildlife habitat, and acting as sinks for carbon and nutrients. Cover crops are annual species planted in rotation with crops specifically to improve soil conditions and to control weeds, soil-borne diseases, and pests (Pimentel et al. 2008).
1987; Glover et al. 2007; Jackson et al. 2009). Many current perennial and cover crop cultivars are essentially wild species bred from germplasm collections and developed to increase success in managed agroecosystems or to eliminate undesirable traits, such as seed shattering. Alternative crops are also being bred for new uses, such as removing toxic chemicals (eg mercury) and excess nutrients and improving degraded soils, including mine spoils (Zhao and McGrath 2009).

New perennial crops and tree species (eg switchgrass [Panicum virgatum], poplar [Populus spp], Miscanthus, Arundo, etc) are being developed as improved cellulosic feedstocks for biofuels that will have a higher yield and energy content than was previously available (Rooney et al. 2007; Jessup 2009). Cellulosic biofuels provide one approach for mitigating the impacts of global warming associated with fossil-fuel combustion, but concerns over appropriate implementation and environmental impacts remain (Robertson et al. 2008). Simply developing more productive feedstocks does not necessarily lead to enhanced environmental health. Without crop rotation, further monocultures of grain maize or increased oil-palm production could have net negative environmental effects in the long term, but such efforts may be a necessary transition to facilitate infrastructure development for cellulosic feedstocks. However, the concern that energy crops might inadvertently compete for land currently allocated for food crop production, and thereby raise food prices, must be considered carefully. Breeding alternative crops needs to be undertaken in close consultation with agronomists, economists, ecologists, and the commercial sector or industry, to ensure that new cultivars have the proper traits that will make them both profitable and sustainable.

**Breeding for local adaptation**

A major goal of harmonizing agriculture with the environment is to “tailor” crops to individual landscapes. Plant breeding has always maximized production by selecting for adaptation in the target environments of interest, using local environmental forces for plant selection (Ceccarelli and Grando 2007). By selecting breeding germplasm growing under local environmental conditions, individual cultivars can be optimized for small regional areas of production that fit prevailing environmental and weather patterns. Likewise, plants could be tailored to provide specific ecosystem services to local environments, to address local needs. One cost-effective way to achieve this is through participatory plant breeding, which involves local farmers in the breeding process (WebPanel 2).

**Breeding for optimum cropping systems**

Alternative crop rotations, planting densities, and tillage systems may make production more environmentally benign but will require altering breeding targets and an understanding that systems biology is complex and rarely has simple solutions. For example, no-tillage systems used for soil conservation can lead to colder soils in spring and could change the prevalence and onset of various soil-borne diseases, thus requiring the addition of specific disease resistances in the breeding objectives (Cook 2006). Breeders must select under the conditions prevailing under new management practices to ensure cultivars will be optimally productive.

**Breeding for new agricultural paradigms**

Beyond changes in management or the use of alternative crops in conventional systems, entirely new systems must also be developed. On the basis of findings in ecology and agronomy, wholesale changes in farming methods have been proposed – for example, the development and implementation of perennial polycultures that closely mimic natural ecosystems (Glover et al. 2007; Jackson et al. 2009; Glover et al. 2010). These agricultural systems would have more in common with native prairies than industrialized

Panel 3. Non-profit plant breeding

The Land Institute, a non-profit organization based in Salina, Kansas, focuses on breeding crops to fit systems that mimic the natural ecology of the prairie (Jackson et al. 2009; Glover et al. 2010). Four specific traits being researched to accomplish this goal are: (1) perennial structures that allow overwintering of plants, which will minimize tillage and soil destruction; (2) deep roots that can access water and nutrients within the soil profile and thus thrive with minimal inputs (Figure 4); (3) the ability to grow in biculture or polyculture systems that include grasses such as perennial wheat, intermediate wheatgrass, sorghum, legumes such as *Desmanthus illinoiensis*, and/or composites such as perennial sunflower (*Helianthus* spp); (4) increasing yield through hybridization between perennial species and annual crops, as well as direct domestication of wild perennials. In all cases, improving grain yield per hectare will be essential because the perennial germplasm derives from wild or forage species that have not previously been selected for yield.

The use of wild germplasm brings desired as well as undesirable traits into breeding populations; therefore, several decades are required to develop acceptable perennial food crops for large-scale production.

Figure 4. The difference in rooting between perennial wheat (large plant) as compared with annual wheat (small plant) in summer (left); in autumn (right), only perennial wheat is present.
monoculture systems. In addition to increased productivity, these systems could enhance ecosystem services, such as soil carbon and nutrient sinks, erosion control, and wildlife cover. Plant breeders have a major role to play in making these systems functional, by domesticating (or re-domesticating) key species. Traditionally, perennial crops have not been a major focus of breeding programs because they generally take more time and scientific knowledge to improve, and therefore products, such as new cultivars, are often not produced within the timeframe of funding cycles. Intermediate steps toward this vision could be achieved by improving individual crops that fill gaps in our current system. Perennial wheat, for example, may ultimately be a component of a perennial polyculture but – in the context of current US wheat systems – could serve to limit soil erosion when planted strategically in the landscape (Scheinost et al. 2001).

**Breeding for specific ecosystem services**

In general, plants are bred for their most obvious end products, including grain, fiber, sugar, biomass yield, fruit quality, or ornamental qualities. However, plants deployed across the landscape in agricultural, horticultural, or forestry settings affect the environment in measurable ways. Given the marked results in breeding staple crops for yield, we would expect to see similarly strong outcomes in selecting and breeding those crops for ecosystem services instead (if the latter were similarly valued by society). A near-term example is the simultaneous breeding for yield and nutrient use efficiency, which would improve water quality and reduce nutrient loading into surface waters and groundwater (Hirel et al. 2007; Foulkes et al. 2009; Korkmaz et al. 2009). A more complex example that may be feasible in the future is breeding for larger and improved root systems that could decrease soil erosion, sequester carbon, and improve soil quality by increasing soil organic matter.

Breeding is also needed to improve the ecosystem services provided by urban (including residential) ecosystems. For example, selecting and breeding urban trees for pest and drought tolerance improves the survival of these trees in harsh environments, reduces water, fertilizer, and pesticide inputs, and ensures that ecosystem-service benefits – such as stormwater management, evapotranspirational cooling, and improved air quality – are preserved (Sæbø et al. 2003; Jacobs 2007; Santini et al. 2007). Of particular recent importance to the tree nursery industry is the development of non-invasive urban trees and ornamentals, to limit negative impacts on natural ecosystems (Anderson et al. 2006). The breeding of ornamentals, urban trees, and turfgrasses will increasingly focus on alternative, underutilized native and non-native species. As compared with non-native vegetation, plant species native to a particular region are generally thought to survive on less water, use fewer nutrients, require minimal pesticide applications, and be non-invasive; however, counter examples for both native and non-native species are plentiful (Kendle and Rose 2000). As potentially valuable species are identified, breeding to improve them for traits of consumer importance will be needed to broaden available diversity in cultivated landscapes.

Managed “natural” ecosystems also benefit from plant breeding. The US Department of Agriculture’s (USDA’s) National Resources Conservation Service Plant Material Centers (http://plant-materials.nrcs.usda.gov/) have a long history of breeding and selecting material for conservation and erosion-control plantings (Kujawski and Ogle 2005). The USDA Forest Service has programs investigating disease resistance to both natural and introduced diseases and pests, in an effort to maintain productivity and species diversity in the nation’s forests. With a changing climate, species considered critical to the landscape may require human-assisted hybridization with distant relatives to better ensure survival from novel pests or diseases. This type of plant breeding further confounds distinctions between native and non-native species. Because of the currently limited market potential of many traits and crops, the public (typically land-grant universities and the USDA in the US) and non-profit (eg in the US: The Land Institute, The Samuel Roberts Noble Foundation, and the Michael Fields Agricultural Institute; internationally: the Consultative Group on International Agricultural Research) sectors have undertaken, or are likely to pursue, the initial breeding.

**The necessity of public plant breeding**

Agricultural plant breeding is typically commodity- or species-oriented and solves problems within a species, rather than making breeding choices based on system-wide needs. For example, maize breeders currently maximize the area in which maize can be grown, and maximize the amount of maize produced throughout that area. If environmental harmony is, in addition to food security, to be a key breeding objective, then a change in agricultural thinking – to appropriately value whole cropping systems – will be required; this is something the public sector is well positioned to do.

Achieving these goals will require collaboration among the private, public, and non-profit sectors, and with society as a whole. Programs within the private sector (eg Panel 1) excel at breeding major, profitable crops, and have economies of scale to increase the efficiency of production and ultimately provide farmers with seed. As a valuable complement to commercial breeding programs, public and non-profit breeding programs (eg Panels 2 and 3, respectively) focus on developing alternative crops, breeding for small target regions, tackling long-term and high-risk problems, evaluating diverse genetic resources, and, importantly, conducting basic research on breeding methodology to enhance efficiency. Only publicly funded breeding programs, and in particular those based at universities, can provide the necessary education and train-
ing in plant breeding and in specialized fields such as ecology. Without trained students from public programs, private commercial breeding programs suffer from an erosion of intellectual capital. Conversely, without the private sector to commercialize public-sector-derived products, beneficial traits and new varieties cannot easily and quickly be put in the hands of growers, as has been seen in developing countries without a developed seed industry (Delmer 2005).

Opportunities for new partnerships

Diverse groups – many not traditionally associated with plant breeding or even agriculture – have much to gain by interacting with and supporting plant breeders. Breeding is a powerful tool for meeting today’s environmental challenges because it can develop plant products that simultaneously improve food production and the natural environment. Ecologists and land-use planners may be interested in plant breeding objectives and increasing public and/or private support for improving plants to provide specific ecosystem services. Similarly, farmers and farm groups associated with organic and sustainable agriculture movements have supported publicly funded breeding as a way to ensure they have access to a diversity of crops that are not controlled by individual agribusinesses (Duvick 2003). Ideally, these partnerships should begin before the development and implementation of breeding objectives. The importance of plant breeding for achieving environmental sustainability makes it an attractive career for students and young scientists, and presents an excellent opportunity for tailoring research to provide high-impact, altruistic results (ie breeding is often not something done by the breeder for themselves; they often do not grow what they breed but instead give it to society, to improve farmer’s profits, peoples’ food security, or environmental quality).

Conclusions

Plant breeding is the science of improving plants to further improve the human condition. Here, we have sought to highlight advances and possibilities in various aspects of plant breeding. We hope that this will stimulate thought and discussion on how to use this approach to meet future food, feed, and fiber needs, while also having a positive impact on the natural environment. By working with ecologists, naturalists, and other scientists from related disciplines, plant breeders aspire to develop future products that positively affect both humans and the natural world, but success in doing so will require stable, long-term support from the public sector.

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WebPanel 1. Breeding for in-field diversity

Planting multiple species and/or cultivars of different genetic backgrounds in the same field more closely mimics what is found in native ecosystems. These approaches help agriculture to be more resilient to adverse environmental changes, ensuring that an entire crop will not be devastated by catastrophic events, such as disease outbreaks or periodic drought (Zhu et al. 2000). Currently, growers in developed countries often plant fields of differing monocultures to spread the risk associated with adverse weather events but have rarely incorporated in-field diversity because it reduces the efficiency of management practices that require crop uniformity. Plant breeders have recently developed “multi-lines”, a mixture of phenotypically similar varieties grown together to increase within-field genetic diversity. Like polycultures (mixtures of different crop species), multi-lines help to ensure a wider coverage of environments and broader resistance to pathogens than is possible with monocultures (Li et al. 2009). Cultivars bred for in-field diversity might be part of a strategy to help farmers reduce risks of crop failure as a result of increased climate variation.

WebPanel 2. Participatory plant breeding

Breeding for localized microenvironment adaptation can be very expensive. A participatory breeding strategy, which often involves a professional breeder who generates variable germplasm and provides it to individual farmers, can be used to avoid high costs. The farmers then help to evaluate and select breeding lines for their own farms or regions, focusing breeding efforts on specific traits and local needs (Ceccarelli and Grando 2007). Participatory breeding has been successful in generating cultivars that meet the unique needs of growers, leading to rapid adoption, especially in the developing world (Witcombe et al. 1996). Growing demand for locally produced food will expand interest in locally adapted plant breeding programs. Public land-grant institutions and other non-profit groups can work with local communities to initiate and sustain these programs. However, production for niche markets alone cannot feed the entire world.

WebReferences