

Plant Breeding and Genetics

A paper in the series on The Need for Agricultural Innovation to Sustainably Feed the World by 2050

ABSTRACT

The art and science of plant breeding is directed to one of humanity's greatest challenges: the need to feed, clothe, and nourish a growing world population in the face of climate extremes, decreased water availability, demands for renewable energy, and the imperative for environmental stewardship. Innovation is critically important to continued progress in providing food and nutritional security to humankind in the decades ahead. There is an urgency to plant breeding and the need for innovation because our increasing population and increasing prosperity will require genetic improvements in our crops at twice the current rate of improvement globally.

The ultimate goal of plant breeding is to develop improved crops. Improvements can be made in crop productivity (e.g., grain yield; adaptation to a specific region; disease and pest resistance; tolerance to drought, heat, cold, or salinity), crop processing and marketing (e.g., milling or baking/cooking/fermentation quality, biofuel yield, visual appeal, postharvest storability, shelf life), and/or consumer quality (e.g., flavor, protein content, oil profile, fiber quality, nutritional value).

The process of developing an improved *cultivar*¹ begins with intercrossing lines with high performance for the traits of interest, then evaluating and selecting outstanding progeny that demonstrate superior performance, and finally, confirming performance stability across the potential market region.

Given the goals and steps in the plant breeding process, innovation provides the means to achieve greater gains, increase efficiency, and accelerate time-to-market for improved

¹ Italicized terms (except genus/species names and published material titles) are defined in the Glossary.



Given the focus and investment devoted to technological innovation in crop improvement, it is vital that maximal value is derived. (Photo from PAN KBOON/Shutterstock.)

cultivars. The innovation can come in the form of new genetic technologies that may involve creation or assembly of genetic diversity, production of the progeny to be evaluated, structures and schemes to facilitate selection of superior *genotypes*, and even systems to enable delivery of superior performance to farmers. Several significant examples of innovative technologies are presented to demonstrate what has

been done to date.

Crop improvement through technological innovation is facilitated, empowered, leveraged, and maximized in a number of ways. Partner technologies, multidisciplinary collaboration, technology transfer, financial investment, governmental biosafety accreditation, protection of intellectual property, farmer adoption, and consumer acceptance all play a role in

CAST Issue Paper 57 Task Force Members

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enabling genetic technological advancement and effective realization of food security goals. Aspects and influences to these empowerments of technological innovation are discussed in detail.

Given the focus and investment devoted to technological innovation in crop improvement, it is vital that maximal value is derived; this often means fitting improved cultivars and the process to create them with other features of the agricultural production system and the value chain. Integration with farmer-implemented agronomic practices; delivery options for crop protection; and machinery used for planting, harvest, and postharvest storage are important to realizing the full genetic potential of improved cultivars and deriving maximal value and impact from innovation. Likewise, further innovation in production systems and value chains will sustain and leverage genetic advancements.

Past success in devising innovative plant breeding solutions to develop improved crop cultivars to nourish, fuel, and beautify the world while mitigating climate change and enhancing the environment has been impressive. Success to date should provide the motivation and confidence to sustain and intensify efforts in the decades ahead to eliminate human hunger and malnutrition while preserving our environment. The scale of innovations that needs to be made and broadly implemented globally within the next few decades in the many and diverse crops that sustain humanity reinforces the urgency and call to action for innovation in plant breeding if a

global population of more than 9 billion by 2050 is to be fed and nourished.

INTRODUCTION

Grand Challenges

Human life depends on plants for food, feed, fiber, fuel, aesthetics, and environmental services such as recycling carbon dioxide (CO₂). Some of humanity's grand challenges are met, at least in part, through improved plants: feeding and nourishing a growing human population, supporting a biobased economy, coping with and helping mitigate climate change, and sustaining the environment. Looking pragmatically at the past and strategically to the future, this paper focuses on the role and critical importance of innovation in plant breeding to meet the grand challenge of being able to provide food and nutritional security to humankind in the decades ahead. Improved crops are also used for sources of fiber, wood, and amenity plants such as flowers and turf grasses.

Feeding and Nourishing Humanity

The U.S. population has grown from 76 million in 1900 to 321 million in 2015 (USDA–ERS n.d.) (Figure 1). Having many more mouths to feed necessitates increases in crop production, which can be achieved through higher crop yields per land area unit (increased productivity) or through more land devoted to crop production. In addition, as people become more prosperous, they eat more food and have a more diverse diet.

Per-unit area yields of the three major field crops in the United States—corn, soybean, and wheat—have increased dramatically since the late 1800s or early 1900s (USDA–ERS n.d.) (Figure 1). Approximately 50 to 60% of this increase has been attributed to improved crop cultivars (varieties), with the remainder of the yield improvement attributable to improved crop production practices (Fehr 1984).

Despite yearly fluctuations, the total U.S. acreage (1 acre=0.4047 hectares) devoted to these three major crops increased from 160 million acres (65 million hectares) in 1926 to 225 million acres (91 million hectares) in 2015 (USDA–ERS n.d.) (Figure 1). Hence, increases in total crop production from 1900 to the present have been due to a combination of higher yields per acre as well as more acres cultivated. The amount of U.S. and global arable land, however, is limited and decreasing because of urbanization, salinization, limited irrigation water, and soil erosion (Tester and Langridge 2010). Hence future increases in crop production will need to come from increased productivity, often on less desirable land.

Future demands for increased crop production will be high because of population increases. The U.S. population is projected to increase to more than 450 million in 2050. The world population is projected to increase from 7.3 billion in 2015 to approximately 9.6 billion in 2050 (Godfray et al. 2010). Staple crops such as wheat, maize, and rice account for a high proportion of the caloric intake in the human diet

(approximately 60% globally [FAO n.d.]), and a nutrient-sufficient diet for a growing population will have greater demands for vegetables, fruits, oilseeds, and nuts (FAO 2009). At the same time, increasing affluence will lead to a greater demand for meat and dairy, which in turn will drive demand for crops used as animal feed (e.g., corn, soybean, alfalfa, and forage grasses). Finally, to combat the various forms of undernutrition globally, a generally more diverse and nutritious diet is critical. Improving nutritive value is a major breeding goal in many crops.

There is an urgent need to increase agricultural productivity to meet the grand challenges facing humanity. Simply stated, current improvements in crop production through genetics and agronomy are not sufficient (less than half of what is needed) to support the human activities predicted due to population growth and increased prosperity by 2050 (e.g., the predicted 9 billion people of 2050 will consume the agricultural products equivalent to 12 billion people of today [Godfray et al. 2010]). Furthermore, while great progress is being made in some crop plants, not all crops currently share equally in these advances, which may greatly lessen the diversity of choices that humans will have in the future. Simply imagine a salad of the future with its diverse vegetables, fruits, and nuts if most of the scientific advances are made only in the major crops of the world (e.g., maize, wheat, rice).

Will plant breeding end hunger? No. The causes of starvation and malnutrition are inextricably linked with poverty, lack of markets, poor political leadership, wars, etc. It is understood that today nearly one billion people live in poverty and are malnourished or food insecure despite global crop surpluses. The urgent goal of plant breeders is to ensure that hunger, malnourishment, and food insecurity are never due to lack of agricultural production, despite the possibility that other factors may limit food availability and quality.

Biobased Economy

Reserves of fossil energy like oil and coal are currently used to meet the majority of needs for fuel, plastics, and other industrial products. These fossil resources are nonrenewable, whereas biobased resources—which

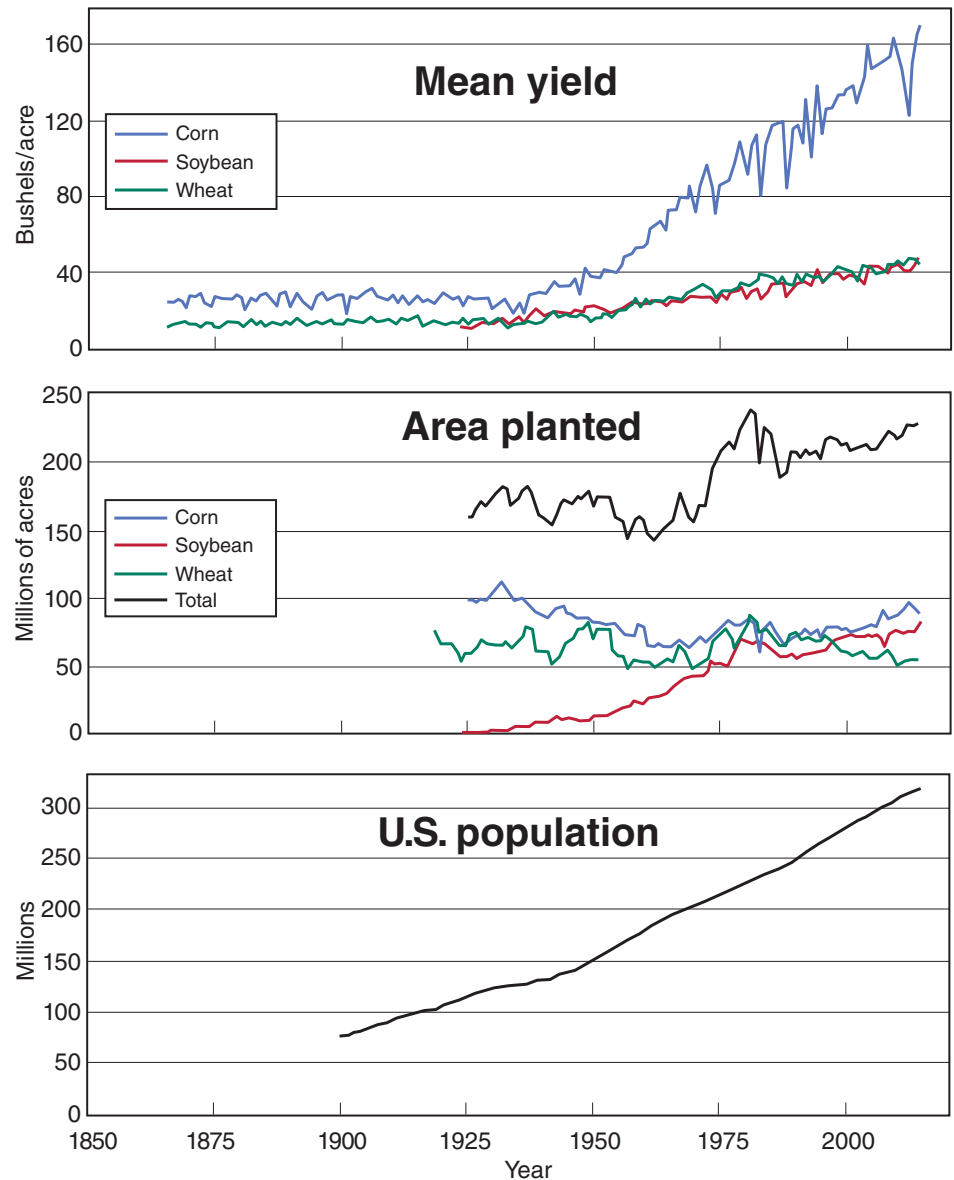


Figure 1. Average yields of corn, soybean, and wheat per acre through time; acreage in the United States planted to these crops; and U.S. population growth (USDA-ERS n.d.).

are dependent on plants, animals, and microorganisms—are renewable and can contribute to rural economy. More than 40% of the U.S. corn crop is currently used to produce fuel ethanol, yet coproducts from ethanol production (such as distillers dried grains with solubles) make their way back into the food/feed chain, substantially offsetting corn and soybean requirements in livestock diets (Mumm et al. 2014). Ethanol and biodiesel produced from leaves and stalks (instead of grain) or from nonfood crops, as well as plant-derived plastics and industrial products, are projected to become increasingly important. These new uses for plants will create a demand not only for

greater quantities of plant material, but also for plant biomass that has specific chemical and physical characteristics that make it more amenable to bioprocessing. Plant breeding will be important in developing these significant new characteristics in crops.

Climate Change

Plants use energy from the sun to convert water from the soil and CO₂ from the air into sugars and oxygen. Human use of fossil fuel continues to increase the concentration of CO₂ in the atmosphere, which is favorable to crop productivity. Because plants have an optimum temperature for productivity (less than approximately 33°C [91°F])

for many plant species), however, the expected increase in productivity due to a higher CO₂ concentration will be offset by a lower productivity due to higher temperatures caused by higher atmospheric CO₂ concentration.

Of greater concern, climate change is expected to cause a higher frequency of climate extremes—too hot or too cold, or too dry or too wet. Therefore, plants need to be bred to respond to such extremes in climate, as well as to new insect and disease pressures that may arise from such variability in climate. In addition, several studies have shown that rising CO₂ levels will lead to reduced nitrogen, iron, and zinc content of grain crops (Loladze 2002), which will impact nutritional quality. On the positive side, plants can help mitigate climate change by sequestering carbon—i.e., converting CO₂ from the atmosphere into roots of perennial herbaceous plants or into woody plant material, which is not quickly degraded, so that carbon is “stored” in the form of plant material for a period of time.

Stewardship of the Planet

Agriculture originated through selection of native plants and wild animals by hunter-gatherers who began to cultivate land, leading to the development of new strains of domesticated plants and animals that are the basis of modern agriculture. Agriculture provided for the conduct and growth of civilized societies. The origins of agriculture some 8,000–10,000 years ago marked a cardinal change in how humankind would interact with the physical environment and ecosystems. Agriculture is a dominant form of land management and often involves major regional disturbances of natural ecosystems (Dale and Polasky 2007). Excluding desert as well as rock- and ice-covered lands, 50% of the remaining global land area is now used for agriculture (Tilman et al. 2001). Zhang and colleagues (2007) describe agriculture as “representing humankind’s largest engineered ecosystem.” As such, well-established cultivated farmland is now recognized as a distinct ecosystem (Heinz Center 2002; MEA 2005).

There are many concepts and definitions of “sustainable agriculture.” In this paper, the definition developed by the U.S. Environmental Protection Agency (EPA) will be used: “development that

meets the needs of the present without compromising the ability of further generations to meet their own needs” (USEPA 2010). Plant breeding can play a large role in developing sustainable agroecosystems (Brummer et al. 2011).

The Royal Society (the United Kingdom’s equivalent of the U.S. National Academy of Science) (2009) warned of a “stark choice” to either “expand the area of agricultural land to increase gross production, or increase yields on existing agricultural lands.” The response to meet this grand challenge has been a call for “sustainable intensification” founded on scientific and technological innovation (Fish, Winter, and Lobley 2014; The Royal Society 2009; Tilman et al. 2011). Agriculture must be considered in the wider ecological context of sustainable landscapes and biodiversity, where “food is not against the environment per se, but rather one of interlocking services provided by the environment which sustains and enhances life” (Fish, Winter, and Lobley 2014).

The term “ecosystem services” (ES) was first coined by ecologists to demonstrate the diversity of processes that support human well-being (Daily 1997; Daily et al. 1997). Negative effects on other ES are termed “ecosystem disservices.” Agriculture both provides and receives ES. For example, the net value of services from wild insects to U.S. agriculture has been estimated at US\$8 billion per year (US\$9.8 billion at 2015 valuation) (Losey and Vaughan 2006) and €153 billion (€162.5 at 2005 valuation or US\$188.5 at 2015 valuation) per year globally (Gallai et al. 2009). As a further example, cumulative benefits of \$6.8 billion over 14 years in suppression of European corn borer (*Ostrinia nubilalis* [Hubner]) were estimated to have accrued from the use of maize varieties engineered to include a gene from *Bacillus thuringiensis* (Bt). Of this total, \$4.3 billion in benefits accrued to growers who did not plant Bt varieties because corn borer populations were significantly depleted across the whole growing area. A Chinese study carried out over 16 years (Lu et al. 2012) showed an increase in abundance of arthropod predators (ladybirds, lacewings, and spiders) along with fewer aphid crop pests where there was widespread adoption of Bt in cotton.

Whether agriculture impacts ES positively or negatively depends on farm management practices and on the surrounding landscape (Tilman 1999). For example, land use changes to agriculture may result in habitat loss, irrigation can divert rivers and deplete aquifers, overgrazing will cause erosion and desertification, and nutrient runoff can lead to river and marine eutrophication (Swinton et al. 2007). On the other hand, agriculture can be managed to conserve soil and contribute to more sustainable use of water, nutrients, and energy (Australia 2.1 2012; Mati 2005; Robertson et al. 2014; Swinton et al. 2007) while contributing to the needs of humanity. Kesevan and Swaminathan (2008) likewise advocate for a more holistic approach with the goal of transcending the Green Revolution with an “Evergreen Revolution” by taking a comprehensive farming systems approach that considers land, cultivar improvement, water, biodiversity, and integrated natural resource management.

The Path Ahead: Breeding Targets for the Future

The continued transformation to make agriculture a major contributor, not detractor, to ecosystem integrity while feeding the world is the grand challenge for the 21st century (Scherr and McNeely 2008). Foley and colleagues (2011) conclude that food production can be doubled while greatly decreasing the negative environmental footprint of agriculture by the adoption of four strategies: (1) halting agricultural expansion; (2) closing yield gaps on underperforming lands; (3) increasing cropping efficiency; and (4) shifting diets and lessening waste. High levels of innovative research, including basic research in plant physiology and genetics, will be required to deliver on these strategies (The Royal Society 2009). Plant breeding has a critical role in increasing cropping efficiency of food, feed, and fiber crops, as well as developing more nutritious food.

Beyond improving crops to meet the basic caloric needs for humans and livestock, plant breeders must collaborate with food and health scientists to develop more nutritious, healthy foods. Given the lack of nutritional security in both developing and developed countries, some attention to genetic

improvement of the nutritional value of crops is globally warranted. Protein-energy malnutrition, vitamin A, iron, and iodine are primary shortfall nutrients globally (IFPRI 2014). Shortfall consumption is also relatively common in the developed world, but incidence is lower and symptoms rarely are extreme. Vitamins A, C, E, magnesium, calcium, and potassium are shortfall nutrients in the United States (Dietary Guidelines Advisory Committee 2005). Of these shortfall nutrients, crop plant sources account for all of the vitamin C; more than 50% of the vitamin E, magnesium, and potassium; and more than 40% of the vitamin A in the U.S. diet (Simon et al. 2009).

Several global efforts have targeted genetic improvement of nutritional quality primarily in staple crops, sometimes referred to as biofortification. One such program directed to small shareholder farmers, HarvestPlus (<http://www.harvestplus.org/>), has led to the development of new cultivars with elevated levels of iron in beans and millet; increased zinc in rice and wheat; and an improved source of vitamin A in cassava, sweet potato, and maize (e.g., see Palmer et al. 2016). Determinations of optimal levels of particular nutrients are necessary before a major breeding effort is undertaken.

Consumer scientists will play a role in deployment of nutritionally improved crops, because consumer acceptance must be at least equivalent to available unimproved cultivars and identification of the improved cultivars in the marketplace can be a difficult consumer education challenge. Average daily vegetable and fruit consumption in the United States is less than 40% of that recommended, and the Centers for Disease Control and Prevention (CDC 2011) has developed strategies to encourage higher consumption to counteract the rising rate of obesity. Improving flavor and other aspects of consumer appeal have been proposed to encourage increased vegetable and fruit consumption.

In addition to consumers, other stakeholders in the value pathway (e.g., food processors) are also important in determining breeding targets and cultivar development goals. For example, malting quality is critical for barley cultivars used for beer production, whereas wheat is bred for a variety of end uses including bread, cookies and cakes, and

pasta. In many cases, the biochemistry of end-use traits is well known and specific genes can be targeted in selection. In the case of malting and brewing, genes encoding a range of enzymes involved in mobilizing starch are key selection targets whereas the genes for grain hardness and the high-molecular-weight glutenin proteins play key roles in the end uses of wheat.

How Plant Breeding Works

The domestication of crop plants has provided a sustainable food and feed supply to meet the challenges of a growing global population as civilization developed during the last 8,000–10,000 years, and plant breeding has continued and expanded that process to address modern challenges. The process of improving crop traits, with regard to a given species, typically involves several steps: (1) defining the traits to be improved; (2) identifying *germplasm* with desired traits and favorable genes that can contribute to an improved cultivar (i.e., identifying parents); (3) crossing/intermating chosen parents; (4) evaluating and selecting the outstanding progeny of intermated plants (which may be repeated for several generations); and (5) field testing in the potential market region to determine if the performance of any selected progeny is sufficient to warrant release of an improved cultivar. Depending on the breeding or propagation system for the crop, a new high-performing line may be used directly as a new cultivar, as a component parent in a hybrid crop or population, or as parental breeding stock to develop further improved *germplasm*.

The ultimate goal of plant breeding is to improve crop performance for traits or defined characteristics of a plant that are under genetic control. Traits contributing to a particular product target might include those important for crop productivity (e.g., yield; adaptation to a specific regional environment; disease and pest resistance; tolerance to abiotic stress factors like drought, heat, or cold), for crop processing and marketing (e.g., milling or baking/cooking/fermentation quality, biofuel yield, visual appeal, postharvest storage ability, shelf life), and for consumer quality (e.g., flavor, protein content, oil profile, fiber quality, nutritional

value, health benefits), to name a few.

Classical plant breeding relies on naturally occurring genetic variation (the raw material underlying traits evaluated and selected by plant breeders) in the *germplasm* pools from which cultivars were developed. Crop species typically have originated in one global geographic region, often where domestication was initiated. This concept of a “center of origin” for a crop was first described by Nicolai Vavilov in the 1920s (Vavilov 1987). As regional and global trade and migration expanded during the Middle Ages and Renaissance, not only did new crops come to new geographic regions where they were previously unknown, but also new types of known crops came from regions beyond local populations. With the introduction of these new plant types came additional genetic diversity.

The *germplasm* pools for a given crop currently include improved cultivars grown regionally and across the globe, cultivars grown in the past, wild progenitor species from which crops were domesticated, and other wild or cultivated relatives of a crop that can be intercrossed to the crop. With the advent of genetic engineering (crops that result are often described as genetically modified crops, synonymous to genetically modified organisms), the biosphere becomes a source of new genetic resources.

The ability for a plant breeder to improve a trait depends on the crop and the particular trait. The ability to improve traits in *diploid* or diploid-like crops, such as maize or tomatoes, is generally more readily achieved than in polyploid crops, such as alfalfa or potato, which have more complex genetics. Because crop improvement in a breeding program advances with each generation of sexual reproduction, crops with rapid reproductive cycles allowing several generations of seed production and selection in one year can be advanced much more rapidly than crops that only reproduce annually, or in the case of some perennial crops, after several years. Similarly, selection for traits controlled by variation in one or two genes often is easier than for traits controlled by multiple genes.

Regardless of the crop reproduction system and genetic control of a trait, the ability of a breeder to effectively select among progeny from breeding crosses

also depends on the magnitude of nongenetic factors in the environment that introduce variation among plants in a population (i.e., “noise”), preventing easy identification of genetically superior individuals. Even for simply inherited traits in rapidly reproducing diploid crops, the gain from selection can be low or nil if nongenetic factors have a large influence on the genetic expression of a trait.

Before the recent advances in molecular and *genomic* techniques, plant breeders had to select solely on the plant *phenotype*. The phenotype of a crop is defined as the observable and measurable characteristics of that crop. The reliability of phenotyping is important for plant breeding because efficient phenotyping translates to efficient selection in breeding populations. Essentially the phenotype is made up of anything we can measure. These measurable traits, however, will vary in their importance to the breeding program and also in the reliability or accuracy of the measurements.

Breeders seek to improve the characteristics of the crop to reach the genetic potential of the crop. Understanding the genetic expression of the phenotype is important. For some traits, such as susceptibility/resistance to certain diseases, this is not difficult to assess; if the plants are exposed to the pathogen, they will either show disease symptoms or not. The genetic basis of a characteristic is not always easy to determine, however, because many traits will vary greatly depending on the environment; in the case of disease susceptibility/resistance, the symptoms may be more severe if the plants are growing under stress. A trait such as plant height can vary greatly depending on the growth conditions of the plant—with abundant nutrients, sunlight, and water, the plant can be quite tall but may be less than a tenth of the size if it is nutrient starved and stressed.

The interaction between the genetic makeup of the plant (genotype) and the environment is referred to as *genotype-by-environment interaction* (GxE). For breeders to make progress in the genetic potential of the plant, they need to know what proportion of the observed trait expression (i.e., phenotype) is determined by the genotype relative to the environment and GxE. This is referred to as the heritability of the trait; the higher the heritability, the more the trait is under

genetic control and the more effective screening and selection among progeny will be for more favorable combinations of genes from each parent. Heritability can be measured by growing a series of cultivars or lines under diverse conditions and determining the proportion of the genetic, environmental, and GxE variation that changes across sites.

Different genotypes interact with environments differently, and hence the magnitude of GxE is of considerable interest to breeders and ultimately to farmers. Breeders would ideally like to develop cultivars that are superior to all others throughout the entire range of production environments in which they will be grown, yet this is rare. By evaluating breeding germplasm under diverse environments representative of the possible production environments, genotypes with superior performance overall may be identified. This is generally expensive and for many smaller-acreage or lower-value crops impossible to achieve using standard methods. By coupling genomic information with environmental information, breeders gain a better understanding of GxE than in the past (Heslot et al. 2014). Crop modeling can similarly play an important role in attempting to understand GxE, thereby helping to predict performance under future climate scenarios (Parent and Tardieu 2014).

In crop improvement, breeders are screening for plants with outstanding performance for all the traits of interest associated with the particular product target. Because most traits of interest are controlled by many genes, individual plants with most of the favorable genes from each parent are rare, making it critical to evaluate a large number of progeny. The more plants that a breeder observes, the more likely truly superior individuals with new combinations of favorable genes from each parent will be present in breeding populations and can be identified through screening. For this reason, plant breeding is often referred to as “a numbers game.”

GENETIC TECHNOLOGIES

Given the objectives and steps in the plant breeding process, innovation provides the means to achieve greater gains, increase efficiency, and accelerate time to market for improved cultivars. The innovation can come in the form

of new genetic technologies that may involve creation or assembly of genetic diversity, production of progeny to be evaluated, structures and schemes to facilitate selection of superior genotypes, and even systems to enable delivery of superior performance to farmers. Some examples are discussed below.

Technologies to Introduce New Genetic Variation

Several genetic technologies have been developed to expand the range of genetic variation beyond that found in the allelic variation of native genes in diverse germplasm. The mutagenic effect of x-rays, ionizing radiation, and certain chemicals discovered in the early to mid-twentieth century have led to the use of mutagenesis as a tool in plant breeding programs. Most mutations tend to have negative consequences from the perspective of crop improvement, but dedicated efforts in mutation breeding have led to the release of hundreds of improved cultivars (Maluszynski 2001). Notably, semi-dwarf stature has been developed through mutation and utilized in a number of crops—including barley, rice, sunflower, and wheat—to prevent plants from falling over prior to harvest, a condition that results in grain yield loss (Maluszynski 2001; Rutger 1992).

More recently, *TILLING* (targeting induced local lesions in *genomes*) has been developed to identify induced point mutations in specific genes of interest in populations of individuals chemically mutagenized by traditional means (Till et al. 2003). High-throughput *TILLING* allows the rapid and low-cost recovery of plants with induced point mutations in key genes. Furthermore, *TILLING* facilitates the evaluation of diverse plant germplasm resources for mutant *alleles* that may influence trait performance.

The development of genetic transformation techniques late in the 20th century has provided an opportunity for plant breeders to introduce transgenes—i.e., genes from other organisms—into crop species, thereby greatly expanding the gene pool otherwise limited to species that cross-pollinate with the crop. Transgenics have revolutionized plant breeding in several major crops—including maize, soybean, cotton, and canola—by facilitating access to genetic

variation contributing to disease, pest, and weed management not present in native gene pools. Transgenes to confer improved abiotic stress resistances, nutritional qualities, and other key traits are being developed (USDA–APHIS 2016). Current use and benefits of transgenes, however, is limited or nonexistent in some crops because of regulatory policy and consumer acceptance.

Gene editing (CRISPR [clustered regulatory interspaced short palindromic repeats]) (Svitashev et al. 2015) is a new technique capable of expanding mutation breeding by generating specifically designed alterations in the deoxyribonucleic acid (DNA) sequence of characterized genes and consequently altering trait expression. The most encouraging system at the current time is CRISPR/Cas9 (CRISPR-associated), and it appears to function in most organisms (Belhaj et al. 2015).

Technologies to Identify and Track Genes for Key Traits

Although breeding can be conducted without any knowledge of the actual genes causing trait variation, understanding the genetic basis of a trait

can lead to more effective selection. Classical genetic analysis pioneered by Gregor Mendel in the late 1800s can establish the nature of gene action and the number of genes controlling traits. In addition, knowledge about the location of specific genes on chromosomes enables breeders to identify molecular markers to tag the trait. Molecular marker tags can track genes for specific traits at numerous locations throughout the genome and are useful in identifying progeny that have desirable alleles, even for important traits that are controlled by many genes.

Use of molecular markers to tag and track genes relies on a phenomenon called linkage. Two genes are considered “linked” when they are close to each other on the same chromosome so that they tend to be inherited together. A molecular marker close to a favorable allele for a trait of interest tends to be inherited with that favorable allele. Through laboratory analysis, the marker can be used to track the favorable allele for the trait. Linkage can be broken if recombination occurs between the genes. How often the gene of interest and the linked marker

segregate together varies and depends on the proximity of the linked genes and the level of recombination. The more often they cosegregate, the better.

The ideal situation involves a “perfect” marker, in which the tag is situated within the gene itself rather than simply nearby. Thus, the technology of molecular markers to track genes for traits of interest has been revolutionary, and because markers can be screened even in seeds or in seedling plants, evaluation and selection can be done before the plant is grown and measured. Because the evaluation is based directly on genotype, selection is not affected by GxE, which affects the phenotype. Selecting on the genotype, rather than the phenotype, increases the likelihood of identifying truly superior progeny present in the breeding population. Of course all selections must be phenotypically validated (see Figure 2).

Expression of the *Fhb1* gene in wheat



No linkage					Complete linkage				
	MR	Mr	mR	mr		MR	–Mr	mR	mr
MR	MMRR	MMRr	MmRR	MmRr	MR	MMRR			MmRr
Mr	MMRr	MMrr	MmRr	Mmrr	–Mr				
mR	MmRR	MmRr	mmRR	mmRr	mR				
mr	MmRr	Mmrr	mmRr	mmrr	mr	MmRr			mmrr

Figure 2. Association between a marker (m) and disease-resistance gene (r), and wheat lines with and without the *Fhb1* gene for resistance to *Fusarium* head blight (see textbox).

Textbox 1. Explanation of Figure 2.

Suppose *r* is a gene that controls resistance to a particular disease in a diploid crop (which has a pair of each chromosome with one inherited from each parent), and *R* is the corresponding gene that confers susceptibility. In other words, *RR* and *Rr* plants are susceptible whereas *rr* plants are resistant. Suppose *M* and *m* are the contrasting forms of a molecular marker. If the marker and the resistance genes are unlinked, all four pairwise combinations of genes (*MR*, *Mr*, *mR*, and *mr*) will be produced at the same frequency in a plant’s gametes. As depicted in a Punnett square (Figure 2, No linkage), the progeny will show no association between resistance and the marker, because resistant plants (with the *rr* genotype) would have the *MM*, *Mm*, or *mm* marker genotypes.

Now suppose the marker is perfectly linked to the resistance gene. An *MMRR* parent is crossed with an *mmrr* parent to produce *F1* plants that are all *MmRr*, and the *F2* generation is produced from the *F1*. Because of perfect linkage, no *Mr* or *mR* gametes are produced. This leads to resistance always being associated with the *mm* marker genotype in the *F2* (i.e., *mmrr* plants; Figure 2, Complete linkage). Instead of spending much time, labor, and money to identify *rr* plants, a plant breeder can extract seed or seedling DNA and screen for the presence of *mm* plants. If linkage is imperfect, some *Mr* and *mR* gametes will be produced and some—but not many—of the resistant plants will have the *MM* or *Mm* marker genotype. This approach of finding marker-gene linkage in the cross between two parental lines has become known as linkage mapping.

Linkage mapping has been successfully used to identify markers linked to the *Fhb1* gene for *Fusarium* head blight resistance in wheat and to track susceptible plants (Figure 2, left plant in photo) and resistant plants (Figure 2, right plant in photo). The black marks in the Figure 2 photo indicate where artificial inoculation for the disease was done to evaluate the plant’s response. (Photo courtesy of James A. Anderson, University of Minnesota.)

Markers are now available to track a large number of traits. For example, analysis of wheat seedling DNA can tell the breeder when the plant will flower, how tall it will grow, which diseases it can resist and to which it is susceptible, if the plant will be tolerant to environmental stress, and the likely end-use quality of the flour (MAS Wheat 2016).

There has been a continual development and advancement of marker technologies since the introduction of isozymes during the late 1970s, with resultant significant improvements in the ability and precision to genotype line at a much greater throughput capability. The technological advances in DNA sequencing have extended to methods for detecting and monitoring genetic variation at the level of the single base pair, the lowest level of sequence differentiation possible (Ganal et al. 2012). Single base pair changes between individuals are called single nucleotide polymorphisms or SNPs. Because many SNPs can be easily identified, SNP markers can provide saturated coverage of the genomic . In addition to their abundance, SNPs are particularly attractive because of their high-throughput capacity, low cost, and high repeatability.

Molecular markers can be applied to make plant evaluation quicker, cheaper, or more precise. For example, traditional methods for evaluating soybean resistance to cyst nematode (phenotypic selection) took 30 days at a cost of \$1.50 to \$5 per soybean line. In contrast, the availability of molecular markers that tag genes for soybean cyst nematode resistance has decreased the evaluation time to one or two days and the cost to less than \$1 per soybean line (Hyten, D. Personal communication). Furthermore, temperate regions such as the United States are typically limited to only one growing season per year; a breeder working with corn or wheat or rice, therefore, grows field trials only once a year, selects the best candidates, and needs to wait for the following year to conduct the next round of testing.

In contrast, the ability to predict the yield of a plant based on molecular markers allows breeders to select for multiple generations each year in a greenhouse or in a nontemperate location such as Hawaii, where multiple growing seasons per year are possible. Marker-based selection works because

although corn yield performance in Hawaii is not predictive of yield performance in the U.S. Corn Belt, the molecular marker profile of a high-yielding line and of a plant remain constant regardless of where the plant is grown.

Just as marker technology has advanced through innovation, the applications to which markers are directed have become more sophisticated and the approaches more refined. For example, *genomic selection* is a breeding approach based on the availability of marker sets providing saturated coverage of the whole genome. For traits such as grain yield that are controlled by many genes having mainly small effects, effects associated with the nearby markers are also small and can be difficult to detect. With genomic selection, marker effects are estimated without the need for tests of statistical significance of the marker effects. The markers are then used to predict the performance of individual plants or to estimate breeding value of prospective parents in creating breeding populations (Heffner, Sorrells, and Jannink 2009).

In situations where a broader sweep of the germplasm is desired or when making a controlled cross between two parental lines is not possible (e.g., in banana, which does not produce seeds) or is too difficult or time consuming, marker-gene linkages can be found via association mapping. Collections of diverse lines or clones can be analyzed for molecular markers and the trait of interest, and the correlation between marker genotypes and trait expression is used to infer linkage. Care must be taken, however, because the nonrandom nature of the diverse lines or clones and rare recombinants can lead to false associations.

In another important application, markers are used to generate “DNA fingerprints,” such as are commonly used in forensics and in human genetics, to characterize plant materials and protect finished line intellectual property. Hence, DNA-based information and resources are being creatively applied to maximize effectiveness and efficiency throughout the entire process of cultivar improvement and protection. Through innovation focused on discovery of DNA sequence and function, more is known about genetic architecture of key traits and this information is used in

creative ways to enhance the process to develop improved cultivars (Moose and Mumm 2008).

Doubled Haploidy

For many crops, evaluations are done using *homozygous* lines developed by several generations of self-pollination. Such homozygosity “fixes” the genotype to stabilize trait expression, allowing a line to breed true. Developing homozygous lines from a cross between two different parental lines, however, requires six to eight generations of selfing, which can take a long time. *Doubled haploidy* offers a fast means to develop homozygous lines. Haploid plants may occur spontaneously in nature or through various innovative methods, using either maternal or paternal gametes (for an example of in vivo maternal haploidy via gynogenesis, see CIMMYT n.d.). Further innovations enable breeders to double the genome of a haploid via in vitro or in vivo means, resulting in homozygous lines with sufficient seed for testing in a matter of two to three generations. This technology is now routinely implemented in corn and wheat; many commercial corn breeding programs have shifted to nearly 100% doubled haploids. The reduced development time results in cost savings, more precise field testing, and faster time to market with improved cultivars.

Precision Phenotyping

Evaluation of plant performance remains a critical aspect of plant breeding. Phenotyping involves assessment of performance for the traits associated with the breeding target. New and innovative approaches and technologies have been developed to facilitate these evaluations. These approaches do not take the place of yield performance testing to finalize decisions about the release of new cultivars; however, novel approaches to phenotyping enable the collection of additional information that serves to enhance and make better selection decisions. The primary features of new phenotyping technologies involve automation enabling more measurements through time or faster data collection, a focus on secondary traits that are strongly associated with target traits yet easier or less expensive

to measure, and/or collection of information to facilitate insights into the environmental conditions impacting phenotype.

A range of new technologies allows the measurement of diverse crop and plant characteristics in an automated fashion. In particular, the cost and weight of cameras has come down to a level at which several cameras can be attached to drones or unmanned aerial vehicles and can take large numbers of images of a developing crop. From the images, a number of parameters can be measured. Using normal visible light cameras, the growth rate of the crop can be measured and plotted (Grieder, Andreas, and Achim 2015). These images also allow detection of abnormal color of the crops due to factors such as nitrogen deficiency or disease outbreaks. Long-wave infrared or thermal cameras can also be used to determine if plants are under stress or suffering from disease. For example, under drought stress plants are less able to cool themselves via transpiration and tend to show an increase in canopy temperature.

It is now possible to use hyperspectral, visible, and near-infrared cameras that capture hundreds of images over the whole electromagnetic spectrum (Araus and Cairns 2014; Fahlgren, Gehan, and Baxter 2015). Proximal (ground-based) sensors can be used to measure moisture availability in the soil (Araus and Cairns 2014), assess canopy temperature to help identify drought-tolerant genotypes (Andrade-Sanchez et al. 2013), or predict ultimate traits like biomass yield (Pittman et al. 2015). All of these data can be fed into models of crop performance.

To improve plants, the breeder selects for the traits he/she wants—to get high yielding plants, measure yield; for plants high in protein, measure protein; and so on. Directly measuring phenotypes, however, can be time consuming, difficult, or simply not feasible for some traits, even with advanced machinery. Alternatively, breeders can practice “indirect” trait selection; that is, they can measure another trait correlated with the trait of interest that is easily and accurately measured, e.g., measuring plant height as a proxy for yield. Techniques such as near infrared reflectance spectroscopy (NIRS) have been used for decades to predict parameters such as grain or forage composition (Roberts,

Workman, and Reeves 2004) to avoid laborious wet laboratory or in vivo procedures. More recently, on-harvester NIRS equipment (Montes, Melchinger, and Reif 2007) has been developed to measure these traits “on the fly,” further increasing throughput by not requiring separate lab analyses.

Other opportunities for indirect trait selection can be determined by observing relationships between phenotypic traits—e.g., total biomass of the plant is often associated with leaf area and the duration of vegetative growth. Some of the associations between traits can be quite complex—e.g., canopy temperature can be linked to heat tolerance because a plant that is cool is able to transpire more water than a hot plant and this protects it from high temperatures. This trait, however, is also associated with root depth because a plant that can track water down the soil profile late in the growing season is better able to access water (Reynolds and Langridge 2016). Therefore, canopy temperature can be used to select plants that have deep roots.

Selection for drought tolerance has taken on greater importance with climate change scenarios, yet this is a very complicated trait because the timing and severity of the drought stress can have very different effects on yield and other economically important traits. In maize, at moderate drought stress initiated near flowering time, grain yield is associated with the anthesis-silking interval (ASI) (the period between pollen shed [male flower] and emergence of the silks [female reproductive structure]), which in turn is a stress-response indicator. Therefore, ASI can be used to screen for improved drought tolerance (Ribaut et al. 2004).

Some technologies are also directed to the collection of information related to the impact of the environment on phenotype. For example, automated facilities have been designed to screen plants under particular conditions (e.g., temperature, moisture availability levels, soil conditions) that may be associated with the target traits (e.g., heat resistance, drought tolerance, low soil-nutrient tolerance). Such facilities generally use single plants grown in pots in a greenhouse or growth chamber. The plants can be moved via a conveyor belt to imaging stations where they are photographed using a diverse set of

cameras (visible, infrared, near infrared, fluorescence). At a fine level, information can be generated on parts of the plant, leaf area and structure, leaf surface, flower size and number, and many other features. Still finer analysis can be made of the composition of plants, such as the levels of metabolites (metabolomics) or proteins (proteomics) and levels of gene expression (transcriptomics).

Crop models integrate these physical measurements into biologically relevant measures such as transpiration being modeled from temperature, wind speed, and soil moisture content. New techniques for root analysis have added further to the long list of plant characteristics that can be measured (Downie et al. 2015). In field situations, sensors can be deployed to collect data on rainfall, temperature, humidity, soil properties, and other environmental conditions that can affect phenotype but are not heritable. Such information, which provides a better understanding of the environment, is useful in positioning improved cultivars in the marketplace as well as understanding and dissecting GxE.

Ultimately these measurements are aimed at supporting selection for traits that will be of importance to farmers and end users of the harvest crop. Breeders are seeking tools from precision phenotyping datasets that

- offer high heritability (and repeatability) and consequently rapid genetic gain through selection (i.e., high control of environmental variation);
- correlate highly with traits of importance to their programs so they can replace difficult, unreliable, time-consuming, or expensive measurements;
- feature assays that are low cost and high throughput so they can screen large populations at reduced cost compared to conventional screening methods; and
- facilitate high accuracy in measurement.

The higher-throughput opportunities afforded through precision phenotyping technologies offer many possibilities for modifying breeding methods, plot numbers, or other aspects of the breeding process to increase selection accuracy. Furthermore, the intersection

of high-throughput phenotyping and high-throughput genotyping could lead to even broader successful application of genomic selection, greatly enhancing genetic gains (Cabrera-Bosquet et al. 2012).

Hybridization Systems

Experimentation into hybrid vigor, or heterosis, was conducted as early as 1761 by Joseph G. Kölreuter, a German botanist (Kölreuter 1761–1766). Exploitation of this phenomenon to increase grain yield in maize has a long history. American Indian tribes planted different types of corn in close proximity to increase yields (Obolensky 1958). Because hybridization can translate to yield increases of as much as 20–50% in self-pollinated or open-pollinated crops (Tester and Langridge 2010), it is not surprising that many crops are grown either significantly or predominantly as hybrids (maize, rice, canola, sunflower, tomato) and that hybridization plays some role in cultivars of cotton, barley, wheat, and triticale. Capitalizing on hybrid vigor, hybridization can be a straightforward way to increase yield per land unit. The expression of heterosis requires the use of genetically dissimilar parent lines; however, it also demands complementarity between the parent lines in terms of favorable alleles. Currently, higher-yielding hybrid crops account for a limited portion of global cultivated area—e.g., less than 1% of the total world wheat area is planted with hybrids (Longin et al. 2012). Thus, increased use of hybridization has tremendous potential for increasing agricultural productivity.

To use hybridization as a means to boost crop productivity, a way to create the F1 seed is needed and this system must be practical and economical. If the crop species is *dioecious* (i.e., there are separate male and female plants), seed production can be easily arranged to produce the F1 farmer seed, because both pollen distribution and seed set can be well controlled. Other approaches involve a means to control pollen exposure to ensure that only pollen from plants intended as males is involved in seed production on plants intended as females. This includes physical removal of male reproductive plant parts through mechanical means

(e.g., detasseling), use of a cytoplasmic or nuclear genetic system to elicit male sterility in the female parent plants, and chemically or transgenically induced male sterility. Furthermore, a means to transfer the pollen from the desired male parent to the desired female parent plants is needed.

Innovative technologies have been developed to accomplish these objectives and facilitate hybrid seed production economically and in large scale. In U.S. hybrid maize production fields, physical detasseling has been the predominant method to control pollination (Wu et al. 2015) despite the fact that removal of vegetative material can decrease seed yield by up to 40% (Wych 1988). Cytoplasmic male sterility (CMS) systems have been employed, but they are not effective in all maize germplasm and can fail to maintain sterility under environmental stress conditions (Wu et al. 2015). Cytoplasmic male sterility is very reliable and used to produce new cultivars of several horticultural crops—including all hybrid cultivars of table beets, carrots, onions, and petunias as well as some hybrid cultivars of vegetable *Brassicas*. It is also used to produce all hybrid cultivars of sugarbeets as well as some hybrid canola and alfalfa (Havey 2004).

For crops where manual emasculation is not feasible and CMS is not an option, commercial quantities of hybrid seed may be produced using male-sterile plants created by chemical or genetic manipulations. Nuclear genetic male sterility occurs spontaneously in flowering plants (Kaul 1988), providing many potential candidates for achieving emasculation in several crops, including maize, rice, wheat, and sorghum. One of the first biotechnological approaches to achieving male sterility included tapetal-specific expression of a ribonuclease gene barnase (Mariani et al. 1990, 1992). Timely application of herbicide and compliance with global regulatory requirements was required using this method.

A biotechnology-based process, *seed production technology* (SPT), has been devised to propagate seed of homozygous male-sterile female inbred lines (Wu et al. 2015). This process requires no detasseling, works across all maize germplasm, results in increased

seed production yield and purity, allows for reliable restoration of fertility in the hybrid plants grown in commercial maize fields, eliminates soil compaction and fuel that would be used in mechanical detasseling equipment, and lessens the need to hire numerous part-time employees to assist in detasseling. Seed production of the inbred parent lines does not result in inheritance of the SPT construct. Consequently, neither hybrids made using the SPT process, nor commodity grain produced from such hybrids, are transgenic as acknowledged by regulatory agencies in Australia (FSANZ 2012), the United States, and Japan (Wu et al. 2015). The SPT process can also be applied in other crops, including rice, sorghum, and wheat, which may contribute to increased crop productivity.

Other innovation has focused on hybridization technologies using herbicide-mediated sterility systems (Feng et al. 2014; Whitford et al. 2013). In the future, *apomixis*, an asexual method of reproduction through seed that occurs naturally to some extent in more than 400 species (Bicknell and Koltunow 2004), may be harnessed to facilitate multiplication of clonally propagating material in the form of seeds. This process would aid in eradication of plant pathogens, especially viruses, in support of increased global germplasm distribution and could cut costs of propagules, storage, transportation, and planting of many clonal crops (Kandemir and Saygili 2015). Spillane, Curtis, and Grossniklaus (2004) estimate that use of true seeds in potato and cassava could save \$3.2 billion worth of tubers annually. Use of *apomixis* has the potential to revolutionize the face not only of plant breeding but of agriculture in general (Grossniklaus et al. 1998; Kandemir and Saygili 2015).

ENABLEMENT

Crop improvement efforts resulting in better crop cultivars are facilitated, empowered, leveraged, and maximized in a number of ways. The next section touches on some of the most important of these.

Partner Technologies

Plant breeding is a highly integrative area of work—never more so than

today, when engineering and biology are intimately connected. Satellites provide data on crop health and productivity, and this information is combined with ground data and used as the basis for farm management decisions. Scientists now know the detailed genetic makeup of many crop species, and they can deploy knowledge of the association between genotype and phenotype to predict performance under a wide range of environmental conditions. Armed with this diverse information, plant breeders can make decisions that optimize the use of available resources while minimizing the environmental impact of farming. A modern breeding program typically has access to a broad range of expertise: molecular and cell biologists, engineers, entomologists, pathologists, physiologists, statisticians, bioinformaticists, computer scientists, crop agronomists, and nutritionists. Moreover, breeders will need to collaborate with climate scientists so that they understand the future production environments and determine the characteristics that future cultivars will need.

Molecular Biology

For plant breeding, molecular biology is particularly important because it includes the study of the raw material for breeding—genes and their regulation and ultimate expression. Previously the authors discussed the importance of molecular markers. Molecular biology, however, also provides the means to understand and change the expression of the traits selected by breeders. Gene expression is controlled, at least partially, by genes and allelic (sequence) variation at those genes. Variability in the regulation of those genes provides scope for trait improvement.

Advances in molecular biology have greatly expanded understanding of gene regulation and the processes that operate in plants. Methods to modify gene expression in a highly targeted fashion (Boettcher and McManus 2015) can therefore be useful to alter phenotypes. The technologies include ribonucleic acid (RNA) interference that inhibits gene expression, usually by causing the targeted destruction of messenger RNA. Genes can even be silenced (i.e., turned off) entirely. Nonbrowning apples in which the gene encoding the enzyme polyphenol oxidase has been silenced represent the first plant cultivar pro-

duced through this technology (Arctic Apples 2016), but many more are being developed.

The ability to identify genes controlling specific traits has improved dramatically in recent years, driven by changes such as a 10,000-fold drop in DNA sequencing costs over the past decade (Sims et al. 2014). If a gene controlling a trait has been identified, geneticists can screen thousands of germplasm accessions for DNA sequence variants that may cause useful phenotypic changes and that could be used as molecular markers.

In addition to molecular biology, other technologies can greatly impact plant productivity. For example, nanotechnology offers tremendous potential for plant improvement, both through high-throughput DNA sequencing and RNA expression profiling and through delivery systems to promote plant health and nutrition. For example, Pratim Biswas and his research team at Washington University in St. Louis found increased yield and a higher level of the antioxidant lycopene in tomatoes through application of zinc oxide and titanium dioxide nanoparticles to leaves using novel aerosolization spray techniques (Raliya et al. 2015). The nanoparticles are credited with boosting chlorophyll content, promoting light absorption and photosynthesis, and increasing nutrient uptake by the plants.

Engineering

The rapid advances in DNA sequencing technology have come through the development of very sophisticated and highly automated sequencing platforms and laboratory information management systems that have driven down the costs and opened new options for cheap, reliable genotyping of germplasm. Because of these advances, phenotyping, not genotyping, has now become the rate-limiting step or bottleneck in crop genetics (Fiorani and Schurr 2013; Furbank and Tester 2011). Engineering is now driving improvements in phenotyping technologies (see earlier discussion on precision phenotyping).

Several sophisticated and automated platforms for screening individual plants grown under controlled conditions are now available to researchers, and public research networks have been established to facilitate access to these

facilities. At the international level, a network of researchers and facility operators has been formed to develop standards and protocols to provide scientists and breeders from both the public and private sectors with phenotyping information (IPPN 2016). Regional organizations offer more specific access to facilities; for example, the European Plant Phenomics Network “offers European scientists transnational access to 23 experimental plant phenotyping installations, at 7 different institutions, in 5 countries across Europe” (EPPN n.d.) and, in Australia, “The Plant Accelerator” offers professional consultation on plant phenomics and experimental design, backed by dedicated bioinformatics support with data management and analysis (APPF 2016).

The phenotyping arena is changing rapidly as technologies continue to improve. These changes have meant that plant geneticists and breeders need to maintain linkages to groups that are actively engaged in developing new systems for high-throughput plant analysis. Indeed, several companies have been established over the past decade that offer sophisticated engineering solutions for plant analysis. The key areas have been around imaging systems, using a diverse array of cameras capable of imaging across a wide range of spectra from visible to long-wave infrared (Fahlgren, Gehan, and Baxter 2015), and, more recently, terahertz radiation (Gente and Koch 2015) and measurements of the light reflected back from the crop (i.e., spectral reflectance) (Pavuluri et al. 2015).

Advances in imaging technology have also led to the development and deployment of drones to rapidly capture detailed images from field trials. At the controlled environment level, the development to robotic platforms to move plants to watering, imaging, or spraying booths under a range of growth conditions has allowed breeders to expand the pool of lines under selection and analysis, capture differences over time in great detail, and measure plant characteristics with high accuracy.

Computing Power

The ever-expanding capacity to generate information about individual plants and crops requires simultaneous improvements in computing capacity to capture, store, analyze, and visualize

data. Advances in data storage mean that it is no longer a great problem to capture and accumulate very large datasets, although it can be costly. Likewise, increased computing capacity has enabled advancements in statistical methodology to facilitate data analysis and data mining. There are now major bottlenecks in analyzing terabytes or petabytes of data, however (Ma, Zhang, and Wang 2014). These problems are inherent to many areas of biology, and generally medical research is credited with developments that pave the path for plant science. Machine learning systems may be the best route to extracting useful information from large and complex datasets that may originate from photos or multispectral images, for example. Machine learning is itself a multidisciplinary area of computer science involving information theory, statistics, and artificial intelligence.

Data Management (Big Data)

Integrated research approaches, which combine data and information from various areas of crop research, require systems that can provide simple access to information via channels from field testing, laboratory analysis, genotyping, crop modelling, and even weather data. Currently, relevant information may be dispersed across multiple databases around the world and this often limits effective exploitation of the available information by the crop improvement community. The development of single-access web-based systems that link existing and new databases and support sharing and integration of data resources in addition to providing a common platform to host available bioinformatics tools has become a high priority for many crops. To achieve the full potential of the information systems, efforts need to cover a wide range of areas.

An important starting point is the development of defined standards, protocols, and processes that facilitate the integration of data. For phenotyping, the international networks described earlier are taking the lead in developing standards and ontologies for trait measurement. Similar activities have been under way for molecular data for some time. Standard processes are being developed for the creation of platforms that support the exchange of data files and associated metadata (i.e., underly-

ing definition or description) between different data repositories, and again there are several international initiatives that have been established to achieve this outcome, most notably CyVerse (CyVerse n.d.), originally the iPlant Collaboration. These platforms provide a structure for researchers and breeders to access internationally available data and data analysis tools while also being able to maintain proprietary data and analysis outputs.

Statistical Analysis

Statistical analysis has underpinned many advances in plant breeding methodology for the last century. Through the application of advanced experimental designs and statistical principles and techniques, the quality of data generated from both field and controlled-environment trials can be greatly improved. Recently, the development and widespread adoption of methods that adjust data for spatial variation across a trial site, greenhouse, or growth chamber have been a great improvement. Further developments in experimental designs and their analysis will result in more efficient data collection and in better data quality.

Many of the genetic analysis tools now in routine use have come from deployment of new statistical techniques enabled by increased computing power. The identification of genomic regions associated with complex traits depends on this combination of statistical analysis and computing, fueling methods such as quantitative trait loci mapping, association analysis, and genomic selection.

In the past, linear regression and correlation analysis were key drivers for the extraction of meaningful genetic information from datasets. Now, the sheer magnitude of datasets and the complexity of biological systems has in many cases reached a stage in which these standard statistical analysis tools are no longer adequate. This concern has triggered a move to the use of techniques that are data driven and make no presumptions about the structure or distribution of the source data—for example, nonparametric statistics such as reproducing kernel Hilbert spaces (e.g., Gianola and Rosa 2015). In addition, approaches that make use of all the available information (e.g., Bayesian statistics) help to maximize value of

collected data and efficiency in decision making.

Modeling

A wide range of crop modeling tools has been developed for breeders and researchers to support decision making, planning, and process optimization. For example, well-constructed models can provide an idea of what might happen in the future under a range of environmental scenarios. Whereas modeling can provide guidance on crop management practices to maximize yield in improved cultivars, it also can aid breeders in determining changes that may impact their breeding objectives for the future (Ramirez-Villegas, Watson, and Chalinor 2015). This aspect has become particularly important as models for climate change become more robust, so that breeders can assess future climate scenarios for their crops and regions. The research needed to develop reliable models spans many areas of science, including characterization of the different environments and likely future climate scenarios where changes in diseases and pests, elevated temperature, increased atmospheric CO₂, and variable water and nutrient supply are expected. Efforts are also being directed to improve understanding of the impact of environmental changes on physiological traits that in turn affect yield, quality, and resource utilization. Several international programs have been organized to help develop these models, such as the European MACSUR program (MACSUR 2012–2015).

Modeling is also important to develop breeding strategies that optimize speed and efficiency in product development through targeted use of genomic technologies. For example, to maximize the probability of success in the integration of value-added traits to improve an elite line, modeling can be used to simulate the outcome of genetic recombination in large populations of progeny (Peng, Sun, and Mumm 2014a,b; Sun and Mumm 2015). As with deployment of new statistical methods, advances in modeling have co-evolved with increases in computing power.

Health and Consumer Sciences

The nutritional quality of food crops is clearly a key objective for many breeding programs, and here again scientific advancements in health

and nutrition shape breeding targets and support screening and selection. A prime example is the clear evidence of the effect of trans-fatty acids created through partial hydrogenation of liquid vegetable oils such as soybean oil (Ascherio and Willett 1997), which led to modification in lipid profiles of soybean cultivars used in food and industrial purposes (Clemente and Cahoon 2009).

Vegetable breeding to improve nutritional value has also been successful, leading to the development of cultivars that are richer sources of vitamins A, C, and E. Furthermore, there is a wide range of genetic variation in nutrient content and composition in diverse germplasm of many crops, suggesting that future prospects for plant breeders to improve nutritional quality are bright (Simon et al. 2009). Whereas nutritional value is of interest for consumers, flavor is also important (Drewnowski and Gomez-Carneros 2000). Like nutritional value, flavor often varies widely across diverse germplasm (Pattee 1985), suggesting an important role for plant breeders in flavor improvement. Breeding to increase consumer appeal and consequently stimulate consumption of a moderately nutritious crop by improving flavor, convenience, or shelf life, for example, can also be an effective approach to increasing intake of shortfall nutrients.

Industrialized societies are enjoying the cheapest and safest food in history. In addition to production, the transport, processing, and retail aspects of food also can impact breeding objectives. For example, the ability to effectively screen and detect mycotoxins such as deoxynivalenol in wheat has resulted in new sources of resistance to *Fusarium* (the disease that produces the mycotoxin in wheat) and more *Fusarium*-resistant cultivars have been developed (McMullen et al. 2012). Anti-nutritional (e.g., toxic) compounds occur naturally in a number of crop species—for example, potato may contain toxic levels of glycoalkaloids (Korpan et al. 2004) and durum and common wheat can accumulate cancer-causing cadmium (Guttieri et al. 2015). The development of rapid, reliable assays for use in crop improvement greatly facilitates the development of healthier foods.

Broad Educational Requirements to Prepare and Sustain the Supply of Plant Breeders

Given the breadth of science and technology that underpins crop improvement, multidisciplinary interaction and collaboration with a broad range of expertise are clearly essential in crop improvement. To interact with this diverse range of expertise and assimilate valuable technologies, plant breeders must receive broad-based training. Individual breeding programs typically interact with numerous other disciplines (Morris, Edmeades, and Pehu 2006; Repinski et al. 2011). Training in statistics is universally considered important for plant breeders (Repinski et al. 2011). Expertise in high-throughput and analytical phenotyping to complement traditional field phenotyping is also important.

For public and private sector breeders in the developed world, stakeholders emphasized a need for expertise in molecular biology, biotechnology, and data management. Both developing world breeders and public sector breeders in the developed world need expertise in plant genetic resources and germplasm as well as soft skills in communication and collaboration. Perhaps not surprisingly, the private sector also viewed training in business and program management as important. Furthermore, a modern plant breeder needs not only traditional knowledge of cropping systems, fertilizer regimes, and field pathology, but also new techniques for assessing crop health based on data from images captured by a diverse set of cameras mounted on drones or satellites. Because students often decide late in their education what sector they will enter, they need to be broadly trained for future career flexibility. As pace of scientific advancements in plant breeding and partner technologies accelerates, there is a growing demand for continuing education for plant breeders.

Transfer of Technologies to Specialty Crops and Developing Regions of the World

Crop improvement strategies, breeding methods, field testing

approaches, genotyping technologies, and even equipment and facilities to some extent can and must be utilized quite broadly across crop species to retain the diversity that our food, fiber, and biobased economy needs. Often the development of new innovations originates in a few key crops of economic importance. For example, maize has been a primary focus because of the vast amount of knowledge already available on the genetic, molecular, and cytogenetic levels, but also because it is the most valuable crop for the seed industry, a principal cash crop, and a key export of the United States. The necessary transfer of technologies for use in other crops requires specific tailoring to the reproductive biology and propagation system as well as the “process” of new line development for the diverse crops of interest. Likewise, because of the financial investment necessary for innovative research, technology transfer typically originating in developed countries, much of it in the private sector, must be transferred to the public sector and the developing world.

Cross-industry partnerships enhance technology transfer across crops. Multi-national seed companies are successful in transferring technologies across crops and from the developed world to developing world markets, often relying on human capital and programmatic resources they have based globally. For crops associated with smaller or less profitable markets that may not support the private expenditure on new genetic technologies, not-for-profit centers such as the CGIAR (Consultative Group for International Agricultural Research) are effective in facilitating technology transfer from the developed world to the developing world and aiding with associated requirements for effective operation such as personnel training, access to essential tools and software, and governmental policies (Delannay, McLaren, and Ribaut 2012). Furthermore, the CGIAR and other not-for-profit centers can be very effective in making long-term, high-risk investments that may not have obvious commercial benefit (e.g., quality protein maize or hybrid rice).

The transfer of genotyping technologies from model species and key crops involves one particular caveat—molecular markers specific to the species of application must be developed. This

need has been greatly facilitated by exploitation of synteny among species (Ramu et al. 2009). More recently, genotyping-by-sequencing (Elshire et al. 2011) approaches enable development of species-specific markers without a great deal of up-front work to create a baseline sequence reference (Melo, Bartaula, and Hale 2016). Thus, not only is innovative technology transferable from crop to crop, innovative approaches to facilitate that technology transfer are emerging.

Science-based Government Regulation

Governments implement regulatory policies with goals to protect human health and promote a clean and diverse environment. Therefore, regulatory oversight necessarily extends to agriculture (including prevention of the introduction of new pests, diseases, or noxious weeds) to ensure the health and safety of food and feed, to ensure the safe use of chemicals and pesticides, and to maintain biodiversity and a sustainable environment.

Various basic research techniques and technologies (tissue culture, gene cloning, cell-to-fertile-plant regeneration, transformation) commenced during the 1970s and early 1980s, cumulating in the development and commercialization of genetically modified (GM) crop cultivars as early as the mid-1990s. It was understood that regulatory oversight would be required to evaluate the effects of GM crops on human and environmental health through scientifically based risk assessment prior to their use in agriculture. In the future, innovation will generate other products of DNA manipulation that must be considered for regulatory oversight; policies will need to anticipate such products—e.g., traits facilitated by gene editing and other forms of “precision plant breeding.”

Different Approaches to Regulatory Oversight Taken by Different Countries

Approaches to regulatory oversight have varied by nation. As the first to approve commercialization of a GM crop, the United States adopted a product-based approach. The U.S. National Research Council concluded that risks should be based on the nature of the organism and the environment into which it is introduced, not on the method by

which it was produced (NRC 1987) (see Pew Initiative 2001), a position supported by the U.S. Office of Science and Technology Policy (OSTP 1992) and the Organization for Economic Co-Operation and Development (OECD 1986) (Kershen and Parrott 2014). The U.S. government established a coordinated framework for regulation of biotechnology as a formal policy for risk assessment in 1986 (OSTP 1986). The framework was based on existing laws to protect public health and the environment with additional regulations, policies, and guidance to make them applicable to biotechnology (Hoffman 2014).

Three government agencies comprise the United States framework: the U.S. Department of Agriculture–Animal and Plant Health Inspection Service (USDA–APHIS), the EPA, and the Food and Drug Administration (FDA) within the Department of Health and Human Services. The USDA–APHIS regulates organisms that are known or suspected to be plant pests. For example, APHIS reviews biotech crop plants resulting from transformation, including events produced using *Agrobacterium*, a known plant pest, or containing DNA sequences derived from plant pests. The EPA oversees growth regulators and pesticides, including plants that produce pesticides (e.g., cultivars containing the Bt gene). A product may therefore be subject to regulatory oversight by one or both of these agencies. The FDA is primarily responsible for safety and proper labeling of food and feed, and FDA oversight of agricultural biotechnology is in the form of voluntary consultation with the technology developers.

In contrast, most countries that are signatories of the Cartagena Protocol (CBD 2015), including those in the European Union (EU), have implemented a regulatory framework that uses a process-based approach to regulatory oversight. The EU approach gives attention to the process of creation and production of food in adherence to the precautionary principle, a principle enshrined in EU treaties and legal decisions (Male 2005). (Readers are directed to M. Victor [2001] for a comprehensive history of the “Precautionary Principle.”) The Rio Declaration (UNCED 1992) formulated the precautionary principle: “Where there are threats of serious or irreversible damage, lack of full scientific certainty

shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation.”

Article 26 of the Cartagena Protocol on Biosafety (Cartegena Protocol 2000) also establishes the right of parties to take into account socioeconomic considerations in reaching a declaration on whether or not to import biotech seeds or crops. Definitions of the precautionary principle, however, are partial and incomplete (van den Belt 2003). The principle can be interpreted narrowly or broadly such that “these accounts should be seen not as fixed types but rather as points on a continuum, or even as dynamic tensions within regulatory procedures,” thereby mixing value-based decisions with issues to be addressed in a scientific inquiry (Levidow, Carr, and Wield 2005).

Consequently, the precautionary principle has been invoked to provide widely different conclusions. For example, Taleb and colleagues (2014) argue that uses of GM crops “represent a public risk of global harm, while harm from nuclear energy is comparatively limited and better characterized.” In marked contrast, Goklany (2000) concludes, “A comprehensive application of the precautionary principle indicates that a GM crop ban, contrary to the claims of its advocates, would increase overall risks to public health and to the environment. Thus it would be more prudent to research, develop, and commercialize GM crops than to ban such crops, provided reasonable caution is exercised.” Van den Belt (2003) notes that often the principle is “reduced to an absurdity” because “normally, no minimal threshold of plausibility is specified as a ‘triggering’ condition, so that even the slightest indication that a particular product or activity might possibly produce some harm to human health or the environment will suffice to invoke the principle . . . leading to an outright ban.”

Alternatively, some countries (e.g., Mexico, China, and South Africa) developed distinctive regulatory systems integrating various elements from the United States and European Union approaches rather than focus on a single model (Falkner and Gupta 2009). As an example, for GM crops to be authorized in Argentina, the National Advisory Committee on Agricultural Biotechnology first must conclude that the GM crop is as safe as its conventional counterpart

for human and animal health and for the environment. The National Service on Agricultural Food Health and Quality then evaluates food safety. And finally, the Directorate of Agricultural Markets examines the commercial impact of the GM crops. More than 20 countries plus the EU have developed fundamentally different organizations and mechanisms for regulatory review (Rowe et al. 2012). The varied approaches to global authorizations have resulted in asynchrony and, as such, can put producers and the entire global commodity value chain at high risk of noncompliance. Under those circumstances, countries at most risk are unfortunately often those most in need of commodity imports to address food and feed needs (Gruere 2011; Kalaitzandonakes, Kaufman, and Miller 2011).

Regardless of the approach, the financial and labor resources required to obtain regulatory authorizations are significant. Phillips (2014) reported the mean cost of discovery, development, and authorization of a new biotechnological crop trait in the time period 2008–2012 was \$136 million, with \$35 million (26%) being regulatory costs. Furthermore, a data package for a new commercial trait may take up to three to four years to develop (Rowe et al. 2012).

At the same time, more applications are filed every day as new potential trait products are discovered.

Toward an Improved Future for Decision Making in Agricultural Biotechnology

Now is a critical time to re-examine the scientific regulatory review process and to better understand more holistically the decision-making processes that determine whether or not GM crops, as well as the next generation of precision plant breeding tools, will be deployed. All available breeding tools will be required to develop the broad base of genetic diversity necessary for food and nutrition security across the globe contributing to environmental sustainability. Yet the current trend is for regulatory compliance procedures to slow development and increase trade barriers (Goodman 2014). Increasing resource burdens attached to additional regulatory authorizations will inhibit or at least delay accessibility of improved cultivars, including those with positive health benefits, to resource poor

farmers and smaller markets (De Greef 2011; Phillips 2014).

Despite having a quarter century of accumulated experience and history of safe use of GM crops on farms with no documented cases of an approved GM crop causing harm to animals or humans (Goodman 2014), the trend is for regulatory reviews to become more costly and to take up more time (De Greef 2011; Phillips 2014). It is also no longer practical to think that any domestic food system can act in isolation; markets are global. There is a critical need for synchronized and transparent regulatory systems that facilitate global trade in food, feed, and processing commodities. D. G. Victor (2001) raised concerns that the continued use of existing systems will lead to gridlock and gaps in regulatory assessments because the technology is continuing to expand at a faster rate than many developing countries can implement policies.

With regard to the asynchronicity of authorizations, in 2012, 170 million hectares of GM crops (approximately 11% of global arable land) were grown among a total of 28 countries (Roser 2015), with the United States, Brazil, Argentina, Canada, and India having the majority of acreage (ISAAA 2012). These data indicate that current regulatory systems provide a legal basis for GM crop cultivation and are working in many countries with diverse agriculture and histories (Devos et al. 2014; Ramessar et al. 2009). On an international basis, there are critical needs for synchronized import authorizations to replace the current global patchwork of systems (Rowe et al. 2012). Serious economic dislocation can result due to asynchronous authorization of GM crops among countries putting producers and the entire global commodity chain at unreasonable economic risk with significant upward impacts on commodity prices (Gruere 2011; Kalaitzandonakes, Kaufman, and Miller 2011). Synchronized regulatory systems would feature harmonization of data collection and testing procedures, means for information exchange, and cooperation at a regional level to develop and implement a sustainable strategic framework (De Greef 2011; Goodman 2014; Ramessar et al. 2009). Global harmonization or cooperation does not imply that each country or region has to agree on policy. Indeed, experience shows that a diversity of poli-

cies will need to be accommodated.

In addition, greater stakeholder engagement through research, development, and commercialization is vital to “demystify” GM crops and precision breeding tools, to help distinguish between value-based and scientifically based decision making, and to help correct misconceptions that may have arisen during the first quarter century of GM crop use. Stakeholder engagement is “critical to the long term success of biotech products in the marketplace, and also for realizing the full potential of new breeding innovations. Everyone along the value chain, including consumers, must have confidence in the safety of biotech products” (Rowe et al. 2012). Wickson (2014) argues that the cultural significance of agroecosystems is unrecognized, thereby marginalizing public participation in decision making, and further concludes that “these factors only work to amplify rather than resolve the entrenched debate in Europe.” Wickson (2014) also notes that such a direction could promote a forward-looking approach with respect to meeting food and environmental goals rather than to be fixed on comparisons to past practices, including those that might not have been sustainable.

International trade of agricultural products is crucial to spread the benefits of crop and animal production among consumers globally and to allow crop production to occur on land that is the most productive, thereby decreasing pressures to take more marginal or fragile lands into cultivation. Clear policies coupled with appropriate, efficient, and synchronous regulatory mechanisms will help ensure the safe and effective conduct of breeding and crop management that collectively enable farmers to make the most productive and sustainable use of plant and animal genetic resources and facilitate production of a safe and affordable food supply to the benefit of the consumer.

Financial Investment in Enablement of Plant Breeding

The shift over the past 50 years from the public sector as the main provider of new cultivars toward the private sector, as well as the growing trend to protect plant breeding germplasm and other innovations with revenue-generating

instruments, has generated considerable discussion; yet relatively little has been published about the financial investment necessary to enable plant breeding. Morris, Edmeades, and Pehu (2006) reported that governmental development assistance to agriculture, in terms of funds provided, declined internationally since the early 1990s as both a percentage of gross domestic product and on a per capita basis. Furthermore, agricultural research expenditures in the public sector declined in most of the developed and developing world in the same period. One study reported that plant breeding expenditures in the U.S. industrial sector rose from less than \$50M in 1960 to more than \$500M in 1995, whereas public sector plant breeding expenditures were relatively constant around \$300M in a similar period with some downward trend after 1980 (Heisey, Srinivasan, and Thirtle 2002).

The need to develop more human capital through capacity building has received more focus. The consensus is clear that the number of scientists trained in plant breeding has been dropping for 20 years, whereas at the same time the demand for trained plant breeders has been rising both in the developed and developing world (Baenziger 2006; Frey 1996, 2000; Guner and Wehner 2003; Traxler et al. 2005). Perhaps not surprising, based on these trends, the number of faculty training plant breeders has also been declining in the United States and other developed countries (Bliss 2006; Gepts and Hancock 2006). More information about the financial and human capital currently involved in plant breeding, and an analysis of expected future global needs, will be of great value as societies plan for the futures they want.

Intellectual Property Protection and Enforcement

New, improved cultivars can take seven to ten years to develop, or longer if “exotic” (i.e., unadapted) germplasm is also used. Basic and applied research, introduction of exotic germplasm, and development of GM crops plus regulatory evaluations may have horizons of 20 years or longer, extending timelines for development of improved cultivars. To justify research investments and foster new funding, the products of plant breeding and its related research need intellectual property (IP) protection. In

support of public sector plant breeding and technology development, the Bayh-Dole Act of 1980 allows U.S. universities to obtain ownership of an invention in preference over the U.S. government (Loise and Stevens 2011).

The John Innes Centre, a research organization with charity status in the United Kingdom, states that “our research innovations will often require substantial further investment to reach applications in the market place and that IP protection has an important role in creating favorable conditions for the uptake and use of such research findings” (JIC 2012). Likewise, the Brazilian Agricultural Research Corporation and the CGIAR use IP protection when appropriate and necessary to help accomplish specific goals supporting their mission statements (Cohen 2000; SGRP 2010). Similarly, the private sector must have IP protection to support their research and attract investments. Contributions by both the public and private sectors are essential to support agricultural advancement through plant breeding, both nationally and internationally. Readers are directed to a report by Lusser (2014) for an exemplary perspective of how both sectors can optimally contribute.

There are at least four ways plant breeders can pursue IP protection: (1) contracts; (2) trade secrets; (3) plant

variety protection (PVP) (also called plant breeders’ rights) (U.S. Congress 2005); and (4) utility patents (U.S. Congress 2011). Under the 1995 Trade-Related Aspects of Intellectual Property Rights (TRIPS) within the World Trade Organization, countries may exclude plants and animals from patentability. Most countries, including the EU, have chosen not to allow patentability of plant cultivars per se, although transgenic events may still be eligible subject matter (EPO 2015). Notably, the United States allows plant cultivars as eligible subject matter for utility patents. Any country that excludes plant cultivars from patent protection is obliged under TRIPS to provide an effective sui generis system of plant protection. Plant variety protection is a sui generis form of protection prescribed by the International Union for the Protection of New Varieties of Plants (UPOV 2011). The 1991 UPOV convention resulted in stipulations for PVP that are widely accepted globally. United States laws support PVP and additionally protect cultivars of asexually reproducing nontuberous species through a PVP-type protection enacted via the 1930 U.S. Plant Patent Act (U.S. Congress 2010). The important criteria and protections of PVP, including protections through the U.S. 1930 Plant Patent Act, and utility patents are presented in Table 1.

Table 1. Comparison of PVP and patent systems of IP protection.

Criteria	Plant Variety Protection		Utility Patents
	Per International Union for the Protection of New Varieties of Plants 1991	Per U.S. Plant Patent Act 1930	
Specificity	Varieties of all species	Asexually reproduced nontuberous plants	Plant genotype not normally found in nature
Requirements	Novelty Distinctness Uniformity Stability	Novelty Distinctness Stability	Novelty Utility Nonobviousness Enablement
Disclosure	Full morphological description	Complete as possible; Photographs and drawings preferred	Enabling disclosure that may be seed deposit of novel material
Claims	Single variety	Single variety	Specific to the patent
Exemption	Farmer and breeder exemptions	None	Some countries allow exemptions
Protections and Rights	Prevents others from producing for commercial purposes; Prevents import/export	Prevents others from using, reproducing, or selling	Prevents others from making, using, or selling claimed invention

Although IP protection offers benefits to innovators, the question arises as to whether or not innovation and development of new improved cultivars is thwarted by such practices. In accordance with the 1991 UPOV convention, PVP does not prohibit further breeding with protected cultivars and commercialization of resulting cultivars provided these are not “essentially derived.” This restriction helps prevent plagiarism, “me too,” or “cosmetic breeding” while enabling subsequent developers who make relatively minor genetic changes with agronomically useful consequences to share in the IP with the developer of the initial cultivar. In addition, an effective PVP system can provide important benefits in an international context by removing barriers to trade in cultivars; breeders are unlikely to release valuable cultivars into a country without adequate IP protection (UPOV 2005). Furthermore, PVP based on the 1991 UPOV convention does not restrict farmers’ use of traditional seed cultivars. All farmers—indeed anyone—can breed with protected cultivars so that the diversity of useful genetics already present in traditional seed systems can be enhanced by the introgression of new diversity from the formal seed system.

Countries can exempt subsistence farmers from obligations under UPOV. Further exemptions can be implemented that allow the use of farm-saved seed of protected cultivars depending upon farm size and commercial nature. Consequently, many countries have determined sufficient flexibility exists within the UPOV model for their implementation of plant breeders’ rights. Some countries have developed new unique systems. For example, India has enacted the Plant Protection Variety and Farmers Rights Act, which takes a more comprehensive approach to supporting investments in plant breeding while also recognizing the role farmers play in varietal improvement and seed production. Interactions between formal and informal seed systems allow introgression of new genetic diversity into informal seed systems (Coomes et al. 2015; Sthapit and Jarvis 1999). Helfer (2004) provides policy options for national governments on implementation of PVP.

Patent systems, the U.S. Patent and Trademark Office in particular, are designed to further industrial and technological progress and strengthen

the national economy through both protection and revelation of inventions that provide solutions to specific technological needs or problems. Some countries—e.g., France and Germany—provide patent exemptions to allow further breeding, including commercialization of the nonpatented germplasm, whereas the United States has no such exemption. Holders of U.S. utility patents on plant cultivars, however, agree to maintain seed in the public depository for 30 years, the life of the patent, or 5 years after the most recent request, thereby enabling the seed to be available to the public domain upon expiration of patent protection. The degree to which research is allowable under patents varies according to jurisdiction—e.g., very limited in the United States. Further breeding and commercialization of a plant cultivar that is either protected by a utility patent or includes a patented trait is not allowed in the United States unless specifically authorized under license by the owner.

Economic studies and empirical evidence show that IP protection does not lead to a zero-sum game in agriculture (Lence et al. 2005, 2015). Provided that subject matter of IP protection is placed into the public domain at the expiration of protection, the net result is to encourage more innovation from which the consumer is the major beneficiary. Plant variety protection and utility patents may be seen as complimentary in the type and amount of IP protection they provide (Hayes, Lence, and Goggi 2009; Lence et al. 2005, 2015). Patents provide more potential for optimal genetic innovation than does PVP because of the ability of patent holders to restrict unlicensed access for further breeding and commercial use during the life of the patent. For example, long-term high-risk projects—including to introduce and incorporate useful germplasm from cultivars that are exotic, relatively uncharacterized, and unadapted to the target breeding environment or to develop a GM crop—could not be undertaken by a commercially funded business without the ability to obtain utility patent protection (Lence et al. 2015).

Nonetheless, genetic gain and social welfare do not always continue to increase as patent length increases; in terms of contributing to social welfare, there is an optimal patent life (Lence et al. 2005).

In contrast, PVP has a breeder exception that does not prohibit further breeding and commercialization during the protection period. Consequently, the primary contribution of PVP to increased social welfare is through supporting a moderate level of optimal genetic innovation, but one that is coupled with faster horizontal diffusion of innovation (Lence et al 2015; Swanson and Goeschl 2005) via the breeder exception. Utility patents facilitate licensing that contributes positively to genetic gain and social welfare and that could likely not occur if innovations were maintained solely as trade secrets.

Intellectual property protection in the field of plant breeding, biotechnology, and seed production is necessary to attract private or commercial investments in order to stimulate innovative research that may have an element of risk in leading to delivery of high-quality and better-performing products to farmers and growers with consequent benefits to society as a whole. Providing plant breeders with a diverse choice of IP mechanisms probably remains the best option to encourage and fund innovation and expanded creativity for the greatest benefit to society, as is expected in all life-science-based or other businesses. Continued innovation is essential because global challenges relating to sustainable crop production will require agriculture to produce greater quantities of more nutritious food while also contributing more positively to ecosystem services.

Farmer Adoption

In general, farmers accept new technologies when clear evidence shows they increase profit or decrease risk. When the technology benefit is less clear to the farmer, adoption is slower. Historically, following passage of the Morrill Act in 1862 that established the land-grant college system across the United States, state cooperative extension services were charged with delivering information about agricultural advances from the academic research programs to the farm community. Today, information flows much faster and all farmers in the United States, and increasingly throughout the world, have numerous media sources readily available to provide recommendations for managing crop production. Furthermore, the seed and chemical industries have developed in-house consultation programs to advise their farmer clientele.

In the developed world, farmers typically have sufficient capital to purchase seeds annually. In the developing world, however, seed cost, quality, and access are significant problems; seed saving is more common. To the extent that new genetic technologies raise seed costs or prevent the saving of seed, their adoption could be affected in areas where these constraints are problematic.

Markets provide the context for both the development and the adoption of technologies, especially in agriculture where crops are globally traded. Markets are affected by policies—agricultural subsidies and trade priorities—and thus deciding what cultivars carrying which traits developed using which technologies is not always straightforward, particularly if international markets are considered.

The agricultural policy of the United States, and more generally throughout the world, affects crop production by subsidizing particular crops and/or production environments. To the extent that policy exemplifies a favored status to particular crops, those crops tend to be cultivated to a greater extent than they may be otherwise. Changes to crop subsidies, crop insurance programs, and food aid programs—to mention just three areas—will change market projections, thereby leading farmers to modify planting plans and ultimately affect targets for plant breeders.

The regulatory status of new genetic technologies is not always clear, and this limits the development of new cultivars using these methods (Lusser et al. 2012). Policies influence the acceptability of advanced genetic technologies in various countries (and various areas within the United States). And although policies may or may not be useful in determining the legality of genetic technologies, the ultimate arbiter of the value and hence the use of these techniques, rational or not, is the consumer. Thus, policies need to be developed in a manner that inspires consumer confidence in the process.

Public Acceptance

Plant breeding innovation can originate from the application of new scientific breakthroughs to plant improvement or it can be motivated by consumers, processors, or farmers demanding particular products. Although the former is more common, particularly in commodity field

crops, the latter is increasingly important, particularly in vegetable and fruit crops.

Technologies are often developed and applied to plant breeding programs because they appeal to plant breeders and other scientists, showing promise at improving traits thought to be important. Whereas these traits may be of actual value to growers or processors, they may not be traits of the greatest interest to consumers. Greater involvement of consumers in the development of breeding targets would help breeders prioritize traits (Tesfaye et al. 2013).

Consumer and societal attitudes toward food and agriculture can present both problems and opportunities for plant breeders. Demands for the decreased use of pesticides and fungicides has placed greater emphasis on selection for resistant cultivars; pressure to lessen the use of fertilizers is driving selection for nitrogen- and phosphorus-efficient genotypes. In many industrialized countries, demand for food from alternative production systems, such as organic and biodynamic, has also led to the development of breeding programs aimed at producing cultivars of crops that are suitable for these production systems. Organic farmers require cultivars that are suited to low-input production with a particular emphasis on nutrient-use efficiency, disease and pest tolerance, and ability to compete with weeds and tolerate mechanical weed control (Lammerts van Bueren et al. 2011). Organic crops usually are sold at a premium, so the end-use quality is also expected to be high.

At one time, academic agricultural scientists were able to provide the public with unbiased information regarding new cultivars and the value of new technologies. Whether or not academics or extension personnel still have the public's trust is an open question, and at least some of the anti-GM crop sentiment from the public is due to a perception—rightly or wrongly—that (at least some) university personnel are tightly linked to the seed industry and therefore are not providing an unbiased opinion. When the products of genetic technologies are traits that primarily benefit the value chain stakeholders other than consumers—e.g., farmers—consumers may be wary because of a lack of insight into food production overall. As with many increasingly technical areas that impact everyday life, there is an emerging need for experts who can provide evidence-

based viewpoints and opinions that are also considered to be “trusted voices” among the public.

LEVERAGING GENETIC TECHNOLOGIES

Given the time, effort, and investment devoted to technological innovation in crop improvement, it is imperative that maximal value is derived, and this often means fitting improved cultivars and the process to create them with other aspects of the agricultural production system and the value chain.

Integration with Agronomic Practices and Inputs

Genetic advances per se are rarely sufficient for top on-farm performance of new cultivars. Typically, successful deployment of new cultivars requires an accompanying “management package” to ensure that the genetic potential of the cultivar is maximized when grown in the particular agricultural system. To optimally take advantage of a new cultivar, management may be significantly different from the common practice, so without adequate training, farmers may actually find the new genetics do not perform well for them. This is particularly true for the developing world where “best practices” in crop management may not be well known or cannot be practiced because of economics or unavailability—e.g., fertilizer application.

Likewise, best practices in crop management will influence the development of new cultivars and the production of a safe and healthy food supply. For example, evaluation of potential new lines is typically conducted under conditions representative of farmers' fields in the intended market region, reflecting practices involving planting date, tillage regimes, soil treatments, pesticide use, harvest methods, etc. Innovative genetic improvement must go hand-in-hand with best practices for crop management to facilitate manifestation and realization of the full genetic potential of the new cultivar and meet the expectations of a society for safe food and sustainable practices.

Agronomic practices are key to realizing the full genetic potential of the cultivar, in particular managing various plant stress factors (e.g., disease, insects, moisture deprivation) that might rob the yield potential and erode optimal

performance. Some control of stress factors may be included in the “genetic package.” For example, due to innovation, weed control can be achieved through breeding, mutation, or transgenic herbicide tolerance to broad spectrum herbicides; the herbicide-tolerant cultivar coupled with use of the associated herbicide can result in excellent weed control that protects yield potential from loss.

All yield-protective solutions, however, need not be genetic. Seed treatments are one example of an alternate mode to providing a suite of characteristics for crop management. And with the vast amount of research now being devoted to synergistic crop-microbe relationships, the future may bring a suite of microbiome products to facilitate optimal crop production. Thus, the overall product target for farmers will shape the breeding targets of plant breeders, yet a great deal of coordination is required to develop a clear picture of the overall product target.

Integration with Farm Machinery, Infrastructure Development

The design and development of farm machinery goes hand-in-hand with agronomic practices that maximize crop yields. The design of planters, for example, has followed research guiding row spacing in various crops to optimize yields in particular geographies and with specific cultivars. The foundational concept involves spatial arrangement of plants to increase plant density (number of plants per land unit) in conjunction with better light penetration into the plant canopy. Grain corn in the United States has gone from 0.9 meter (m)—1.0 m (36”–40”) rows to 0.75 m (30”) rows, and more narrow row spacing is now facilitated, including “twin rows.” Effects of row spacing not only involve plant density, but can depend on fertilizer regimes and other agronomic practices (Haegele et al. 2014).

Mechanized harvesting saves substantial time and labor compared to hand harvesting; yet for many crops, especially vegetables and fruits, much harvesting is still conducted by hand. In the future, machine harvesting will likely be required to keep food costs affordable. To at least some extent for some crops, breeders will be able to work with equipment manufacturers to tailor

new cultivars that can be harvested with modern machinery. As an example, the mechanized processing tomato harvester was developed by an agricultural engineer at the University of California—Davis in the 1950s and it, together with tomato cultivars suitable for mechanical harvesting, was released and rapidly adopted by the farm community in the early 1960s (Huffman 2012). In the future, as mechanization changes, breeders have opportunities to develop cultivars that can be suitably managed under those conditions. Likewise, breeders collaborate with engineers to develop postharvest equipment and storage facilities that minimize physical damage (spoilage and waste) and rapidly bring the harvested crop to optimal temperature for long-term storage.

These collaborative relationships have resulted in the delivery of high-quality produce that has been shipped long distances and/or stored for extended periods of time beyond harvest to supermarkets year-round, even though the crop harvest period may only extend a few months of the year. In developing countries, crop losses at harvest and during postharvest can be massive due to poorly developed infrastructure that includes lack of adequate harvest equipment, poor roads and transportation systems, and lack of a reliable system of electrical power to support the cold chain both postharvest and from cold storage to market. Mechanization may require more uniform crops for harvest, but the genetic diversity available to plant breeders can support the diversity of products (flowers, textures, flavors) that consumers want and expect.

SUMMARY

Plant breeding has been described as both an art and a science. The art is the vision, knowing what to select years in advance of the final outcome (population, cultivar, or hybrid). It is also the context of future agroecosystems and how the line will adapt to climate change, the ability to use nitrogen or other inputs including water, and the need to be resource efficient. Finally, the art is all the intangibles that science does not yet know how to measure or that are important in unforeseen ways. Much like the painter, the selection of colors and the brush strokes of their application create the painting; so too does

the plant breeder select new lines.

As for the science of plant breeding, the cornucopia of disciplines that nourish plant breeding has been described. From the physics of plant anatomy that determines if a plant lodges, to the chemistry of photosynthesis, to the biochemistry of vitamin and essential amino acid biosynthesis, to the genetics that control plant function, to the genomics that attempt to describe the symphony of plant genes in their fullest integrated detail that determine the plant’s productivity and use, and to the statistics that allow breeders to determine similarities and differences—plant breeders use them all. Plant breeders work with skilled scientists in entomology to lessen insect damage while enhancing beneficial insects; with plant pathologists to decrease the plagues and destruction of plant disease; with engineers to develop faster, better methods of measuring and understanding plant phenotypes; with nutritionists to make healthier and more nutritious foods and feed; and with bioinformaticians to collect, analyze, and create the linkages of science for plant improvement.

Plant breeding is an impact science that is helping to feed the world while creating global businesses. As such, it works within a legal and ethical framework of international law. Plant breeding plays a critical role in the citizenship of science—from the consumer who is nourished by the crops or enjoys the milk, eggs, and meat that are produced by animals that plant breeders help feed, to the ecologist trying to decrease soil loss or pesticide runoff, to the indigenous farmer who saves seed from this year’s crop to plant next year.

The urgent need for plant breeders and for innovation as the future is faced has also been described. Plant breeding science has been successful, but the rate of improvement (referred to as “genetic gain”) is insufficient to create the future that humanity wants, needs, and deserves. Complacency is unacceptable in the face of growing populations, malnutrition and under-nutrition, climate change, limited arable land, and a fragile biosphere. Innovation that will revolutionize agricultural productivity is critical to increase the rate of improvement. A step change in terms of genetic gain is demanded. What technologies of the future will deliver double rates of gain in production to

meet the forecasted needs? In the short span that this paper was written, new technologies such as gene editing have gone from novelty to product. Big data continues at an awesome pace to link genomics to phenomics to climate data in ways that were unimaginable only a few years ago. In the future, understanding the crop plant in context of its complex interaction with the microbiome may similarly revolutionize crop improvement and productivity. All of these, and certainly others to come, have the potential to be game changers in crop production. Furthermore, game-changing technologies must reach relevant crops that are important for the many and diverse regions and cultures of the world because realizing the gain needed in agricultural production will necessitate a broad sweep across global food production systems in grand scale.

Although the future is hard to predict and science will continue to evolve, humanity will increasingly rely on modern agriculture for food, feed, fiber, and fuel. And the detrimental aspects of human activities need to be remediated. It is possible to predict with absolute confidence that the future will need plant breeders and their skills. Investing in plant breeding is investing in the future or, as agriculturalists like to say, “growing our future.” Plant breeders’ track record for innovation in crop improvement to nourish, clothe, fuel, and beautify the planet while mitigating climate change and enhancing the quality of the environment is strong; this strength must be maintained and its durability supported.

GLOSSARY

Allele. An alternative form of a gene that arises by mutation.

Apomixis. An asexual method of reproduction through seed that occurs naturally in more than 400 species, resulting in offspring that are genetically identical to the parent plant.

Cultivar. A cultivated plant variety or hybrid produced by selective breeding.

Dioecious. Separate male and female plants within a species; literally derived from Greek for “two houses.”

Diploid. A plant, cell, or nucleus containing two complete sets of

chromosomes, one from each parent.

Doubled haploidy. The process of producing a completely homozygous plant by doubling the gametic contribution from one parent.

Genome. All the heritable traits of an organism.

Genomic selection. A breeding approach to improve plant or animal traits that uses a molecular marker set providing saturated coverage of the genome to predict performance.

Genomics. The branch of molecular biology concerned with the structure, function, evolution, and mapping of genomes.

Genotype. The genetic makeup of an organism.

Genotype-by-environment interaction. The interaction between the genetic makeup of a plant and the environments in which it is grown.

Germplasm. The genetic material available to a breeder to improve an organism (in this case, economically important plants).

Homozygous. The term used to describe the case wherein all alleles for a particular gene are the same.

Phenotype. An observed trait expression.

Seed production technology. A proprietary transgenic biotechnology-based technology that is designed to make hybrid seed production more efficient and reliable.

TILLING. The acronym for “targeting induced local lesions in genomes”; a mutation-based system to explore how specific genes affect phenotypes.

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Citation: Council for Agricultural Science and Technology (CAST). 2017. *Plant Breeding and Genetics—A paper in the series on The Need for Agricultural Innovation to Sustainably Feed the World by 2050*. Issue Paper 57. CAST, Ames, Iowa.



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