What Is Plant Breeding?

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"The great power of this principle of selection is not hypothetical."

Charles Darwin, On the Origin of Species

My assigned task this morning is to provide some background on the practice of plant breeding, providing a common foundation for the participants. Given the breadth of the subject and the range of experiences of the participants I will concentrate on the key biological features of plant breeding. In addition I will spend some time discussing what makes plant breeding different from other crop improvement technologies and some of the implications of these differences. Numerous excellent texts on plant breeding are available and these should be referred to for specific methods and practices (Allard, 1999; Fehr, 1987; Simmonds and Smart, 1999)

It is not my intention to compare plant breeding and genome engineering (transformation and developing genomic applications). However, genome engineering is now the dominant paradigm, and engineering and breeding are frequently compared, especially in literature promoting engineering. So there are occasions, especially when dealing with common misstatements regarding plant breeding, when I have found it necessary to compare the two processes.

What Plant Breeding Is

Key feature:

Distilled to its essence, plant breeding is human directed selection in genetically variable populations of plants. Selection based on the phenotype is the key feature of plant breeding programs. The reliance on selection, both artificial and natural, differentiates plant breeding from other technologies. The target population must be genetically variable, otherwise no change can occur. If successful, selection results in a population that is phenotypically and genetically different from the starting population.

Principles and Implications of Selection.

The power and implications of selection cannot be over emphasized. Earth's biological diversity is due to natural selection, and diversity of our domesticated plants and animals is due to artificial selection. Darwin, in developing the theory of natural selection, relied heavily on the knowledge and experiences of plant and animal breeders. Darwin used examples from plant and animal breeding to demonstrate the feasibility of natural selection (Darwin, 1859). Given the familiarity of Victorian England's intellectual class with domesticated species, these examples were persuasive. Today, most people in the industrial world are distant from both agriculture and nature; thus, it is unsurprising that few understand the power of selection and its role in our world.

The raw material for selection is the genetic variation created by mutations. As selection is applied, plants with favorable alleles are chosen. If the non-selected individuals are removed from the population, the remaining population will have a different gene frequency from that of the original population and selection will have been effective in improving the average performance of the population. But, no new individuals or genotypes were created. Everyone, including anti-evolutionists, understands and accepts this eliminatory aspect of selection.

What Darwin recognized, and plant breeders harness is the creative power of selection. If only the selected plants are allowed to sexually reproduce, new genotypes will occur in the

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following generation many of which have never existed before. If the process is repeated for a number of generations, then favorable alleles at many loci affecting the selected trait will accumulate in the population. Through sexual reproduction, those alleles will be recombined, often resulting in completely novel and unexpected individuals. As Darwin (1859) said

> "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds."

It is crucial to recognize the creative aspect of selection. It is my opinion most scientists, including many biologists, still do not recognize Darwin's key insight - the creative power of selection.

The creative power of selection is the key feature of plant breeding and what makes plant (and animal) breeding unique among human technologies. It is this power that distinguishes plant breeding from genomic engineering and, in the long run, makes breeding so powerful.

Frequently, critics of plant breeding (proponents of engineering) suggest that the products of plant breeding are random and unpredictable. Usually these allegations occur when people are defending the safety of genome engineering and suggest that, in comparison to plant breeding, genomic engineering is precise and scientific. The concept of randomness and imprecision is due to a misunderstanding of the process of plant breeding and confusion of biological levels of organization. Genetic recombination is random, but the effect of selection is not. If we select for resistance to rust we get rust resistance. If we select for higher yields we get increased yields. If we select for more tender sweet corn we get tender corn. The direct effect of selection is remarkably predictable and precise.

The direct effects of selection are highly predictable. However, what makes selection immensely interesting and valuable are the unpredictable correlated or indirect effects. Such effects result in novel, useful, and sometimes wonderful changes that could not have been predicted prior to the beginning of the selection program. The retrospective studies of the changes in Corn Belt Dent maize hybrids by Duvick et al (2004) provide many excellent examples.

Selection for harvestable yield has resulted in some correlated changes that one might have predicted at the outset. Since harvestable yield includes only those ears that can be harvested by a machine, one would predict that standability (root and stalk strength) would be improved and indeed this is the case (Duvick et al, 2004). One might also have predicted that ear and kernel size, leaf number, and photosynthetic capacity would increase. However, these traits changed only slightly if at all (Duvick et al, 2004; Tollenaar and Wu, 1999). It is unlikely that one would have predicted that tassels would have become much smaller or that leaf angle would have changed, but these changes were strongly correlated with years the hybrids were released. One may have predicted that stress tolerance would increase, which it did, but one would have been even more likely to predict that yield capacity and heterosis would have increased, which haven't.

The point is we know what is biologically important after the fact. If in 1930, genomic engineers had chosen to improve yield capacity and increase ear size, would they have made the same gains as plant breeders did simply selecting for yield? If, in 2003, genomic engineers view the results of Duvick et al. (2004) and decide to decrease tassel size and increase stress tolerance, are these the best decisions for the new environments and germplasm of the new century? The beauty of selection is that humans don't make those choices and retrospective information isn't needed. We simply select the phenotypes we want and let the genome interact with the environment to give us new organisms that yield more, taste better, and are healthier.

Selection also results in changes the genetic base of the crop in unpredictable ways. In the 1930s, at the beginning of the hybrid corn era, there were hundreds of open-pollinated corn cultivars. It would have been impossible to predict which ones would be most successful in the future. Indeed by the 1970s, many were surprised that a relatively obscure cultivar "Lancaster Surecrop" was apparently the most important germplasm source (Sprague, 1972; Zuber, 1976). And who would have predicted in the 1970s that Lancaster would be relatively unimportant in 2000 (Troyer 2000)? Overtime, selection for increased yield changed the germplasm that contributed to high yields. The environment and gene pool favored Lancaster in the first half of the hybrid era, but changes in crop management made Lancaster germplasm less favored in the last 30 years.

If genomic engineers had been able to engineer the corn plant in 1970 they would have devoted much of their resources to Lancaster germplasm. This decision would have been based on a retrospective look at what had occurred between 1930 and 1970. However, it now appears that heavy investment in Lancaster would have been the wrong choice and severely limited potential gain.

The key thing to recognize is, while selection predictably has resulted in high yields, the ways in which the changes occurred were entirely unpredictable. And it is important that plant breeders were ready and able to capitalize on these unpredictable occurrences. Henry A. Wallace the founder of Pioneer Hi-Bred said

> ”There is no substitute for the man who can observe and who lives so closely with his material that he can recognize a lucky break when he sees it.” (in Smith et al, 1996)

Selection results in adaptation to the local environment while selecting for the trait of interest. This may be obvious for a trait strongly influenced by the environment, such as yield. But this is true for any trait as long as the breeder also selects for overall performance. Since the breeding process is repeated each growing season, selection identifies genotypes that are adapted to the current abiotic and biotic environment. If the climate is becoming warmer over time then genotypes adapted to warmer temperatures will be selected. Likewise, if a new race of a pathogen becomes prevalent, the newly selected individuals will be relatively more resistant, than plants not developed under those conditions. This presumes that the original germplasm had genetic variability for temperature response or disease resistance.

Selection also results in adaptation of the internal environment (genome) to a new trait. For example if we wish to develop a high sugar, high yielding sweet corn line, we would cross a source with the high sugar gene by a high yielding, low sugar line. We know from experience that the high sugar gene is nearly lethal in the high yield background. But by selection for high sugar, high yield, and high viability at the same time over a number of generations, selection and recombination will result in gene combinations that produce a viable product.

The contrast between selection and engineering regarding adaptation to the internal or external environment is stark. Given adequate genetic variability, selection adapts the evolving genome to the environment. Engineering needs to know in advance what the coming climate or pests will be. Likewise, the engineering approach to develop high sugar high yield lines would be to simply transform the high sugar gene into a number of high yield lines until a viable combination is found. This could hardly be considered more precise or predictable than selection.

Critics of plant breeding often suggest that plant breeding is slow, requiring great patience and persistence and that plant breeders are stolid creatures, doggedly sorting through material. While these misperceptions are traceable to the internal mythology of plant breeding, they are false. If it were true how could the life span of modern corn hybrids be between three and five years? Selection rapidly changes populations and creates phenotypes that have never before existed. Plant breeders are impatient, anxiously awaiting the products of an exciting cross, the latest trial data, or the opening of a flower for pollination. Speed does depend on a number of factors including life cycles, genetic variation, and intensity of selection. Very intense selection can produce dramatic changes in a few generations, but may deplete genetic variation for the trait of interest. Mild selection will result in more gradual but sustainable change.

Regarding the contention that plant breeding is unscientific. This appears to be due to a general discomfort with the fact that plant breeders do not need to understand how a trait works (biochemically or physiologically) to successfully alter the trait. What this ignores is that plant breeders are experts in the science of selection and allied disciplines, especially statistics. If the definition of science is a way of knowing based on the process of proposing and testing hypotheses, plant breeders may be world champions. Each yield trial consists of dozens of hypotheses, tested in highly replicated, well-designed experiments in multiple environments. Plant breeding is a science-based technology.

Mechanics of plant breeding:

Methods, tools, time frames, and types of cultivars vary widely depending on the lifecycle, reproductive biology, and level of domestication of a particular species. In maize, which is relatively easy to cross pollinate and emasculate, US breeders use the inbred/hybrid breeding method and complicated mating designs, while in soybeans, which are much more difficult to hand pollinate, breeders develop pure line cultivars and use methods that minimize mechanical crossing. Wheat breeding is highly mechanized, while the breeding of flowers such as the day lily is almost completely unmechanized. Snap bean breeders may be able to get five generations per year, and elm breeders may not get that many in their entire career.

While life cycles and resources (greenhouses, winter nurseries) determine the number of generations per year, the number of growing seasons per year in the intended area of release determines the speed with which new cultivars may be evaluated. Traditionally plant breeders have been conservative in their evaluation of new products emphasizing multiple years and locations of evaluation prior to the release of new cultivars. This emphasis makes good business sense because risk adverse growers will stop buying failed products and avoid companies that have marketed failed brands. Most plant breeders believe extensive testing is important, because implicit in their Land Grant University education was a sense of service and the concomitant duty to protect the growers. Unfortunately, as investment in plant improvement has increased, the testing process has sometimes been cut short in a rush to get new products to market. Usually public breeders are not under the same pressure to rush new products to market. However, as public support has decreased, the pressure on public breeders to get products to market has increased.

Objectives:

Objectives vary widely. Take, for example, a single species; maize. The sole objective of many US maize breeders is harvestable yield; maize breeders in Mexico are concerned with yield and also quality factors for making tortillas. Sweet corn breeders need to be concerned with many quality factors including flavor, texture, and tenderness, as well as ear and husk appearance and even how easily the silks are removed from the ear. Popcorn breeders are interested in popping volume, tenderness, flavor, and flake shape. Maize silage breeders work on forage quality and may measure yield as "milk per acre".

The main objective of private corporations is to make profit for the owners/investors. This is generally done by developing cultivars that sell large volumes of seed. Public breeders are generally less concerned about sales volume and may be more interested in developing cultivars that actually reduce seed sales, such as long lived perennials or cultivars from which the farmer may save seed such as pure lines and open-pollinated cultivars. Private corporations invest resources in a few major crops, which are most profitable. This along with regulatory and economic factors contributes to the decline in on farm crop species diversity. Less-favored crops are left to public breeders who are often responsible for multiple crops and have very limited resources. Many crops have a fraction of a full time equivalent responsible for their improvement (Frey, 1996). Improved cultivars of these less-favored crops are needed to increase on-farm species diversity (along with changes in US farm programs.)

Adaptation:

All cultivars must be adapted to the environment in which the cultivar will be grown. New cultivars need to tolerate the normal range of pests and climatic conditions. This requirement is the basis for one of the most basic principles from introductory plant breeding classes **- Breed in the area where the new cultivar will be grown.** At the very least, cultivars should be evaluated for multiple years and in numerous environments prior to release. Sometimes, due to financial considerations, breeders attempt to breed in an environment different from the target region and/or short cut testing, usually with very negative results for both the farmer and seed producer.

The size of the intended area of adaptation varies greatly. Large hybrid corn companies target widely adapted hybrids that, within a maturity zone, may be grown from Nebraska to Delaware. Farmer-breeders in western Mexico may target a specific altitude in a single valley. Widely adapted cultivars tend to be more stable over a wide range of environmental conditions, but may not suit the needs of specialized market niches or environments. Size of the target area is a function of economics, both in terms of sales and costs. Large companies prefer wide adaptation to gain efficiencies in inventory management, marketing, and seed production. But breeding for wide adaptation requires greater investment in breeding programs. Small seed companies and farmer-breeders can develop cultivars well suited to local conditions, but the size of the market may not support even a small breeding program. Public plant breeding programs tend to focus more on local or regional adaptation and local markets and production systems. As consolidation continues in the seed industry and companies abandon markets and regions, the need and opportunities for serving local communities increase. But at the same time, the number of public breeders declines, and seed production and distribution infrastructure are lost.

What Does a Plant Breeder do?

A plant breeder develops and implements a program designed to produce improved crop cultivars. Depending on the organization in which the breeder works, the breeder may be responsible for managing a research station, raising funds, and even selling seed. I will concentrate on the plant breeding aspects of the breeders job.

The plant breeder a) chooses germplasm to form the basis of the breeding program, b) plans crosses to create genetic variation, c) manipulates the plant reproduction, d) develops and applies selection protocols, e) plans and implements a cultivar testing program, f) collects and analyzes data, and g) decides which cultivars should be advanced. All of these functions are important for a successful plant breeding program but some functions can be quickly picked up by any novice, while other functions including decisions on parental germplasm, selection protocols, and germplasm evaluation require years of experience. It is this experience that is often called the "breeder's art" or "eye". "*Breeders universally depend on experience and art more than genetics*." Duvick (1996). But it is art in the sense of skill. Experience becomes art (skill) when knowledge becomes subconscious. The experienced plant breeder has observed hundreds or thousands of germplasm sources and crosses and develops an understanding of how certain germplasm sources perform in specific environments and crosses. Experienced breeders have seen tens of thousands of phenotypes and develop a set of selection criteria that become subconscious. An experienced breeder will make a decision based on a quick look at a plant, a plot, or even an entire trial. When asked what criteria are being used for such decisions it may take some time for the breeder to fully articulate the key traits, but those traits have become key based on repeated experience. Darwin (1859) summed it up by writing

> "Not one man in a thousand has accuracy of eye or judgment to become an eminent breeder. If gifted with these qualities, and he studies his subject for years, and devotes his lifetime to it with indomitable perseverance, he will succeed, and may make great improvements: if he wants any one of these qualities he will assuredly fail."

None of this is to suggest that plant breeding is unscientific. I do suggest that successful breeders spend years in the field with their crop and they develop "a feeling for the organism" as has been said of the maize geneticist Barbara McClintock (Keller, 1983).

Education:

Plant breeders are educated as biological scientists. In the past, most plant breeders received their undergraduate education at Land Grant Colleges of Agriculture, with training in crop and soil sciences, entomology, plant pathology, genetics, chemistry, botany, and some agricultural economics. In graduate school they would take plant breeding, cytogenetics, advanced genetics, plant physiology, quantitative genetics, and statistics. Of these courses, statistics and plant breeding would have been of the greatest direct use for the breeder, with other areas being more or less important depending upon the crop and the breeding objectives.

Today the situation has changed. Graduate students are entering from a wider array of institutions. Fewer students have a solid background in agricultural science from their undergraduate programs and there is not enough space in the graduate curriculum to correct these deficiencies. Furthermore, molecular biology and biochemistry courses have become a standard part of the curriculum. With new additions to the curriculum and no additional time, something has to give and these may be the traditional plant breeding core courses such as statistics, quantitative genetics, and cytogenetics. The courses that graduate students take depends on their interest, that of their advisor, and the academic strength of the institution but the trends remain. Clearly the decline in quantitative/population thinking does not bode well for a discipline that is based on manipulation of gene frequencies in genetically variable populations over multiple environments.

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Will Plant Breeders Continue to Exist?

In any discussion of the impact of plant genomic engineering on plant improvement, it will be asserted that plant breeding will continue to be extremely important and that without plant breeding genomic engineering cannot be successful. Unfortunately I disagree. The world will not come to an end if traditional plant breeders disappear and it is clear the disappearance is well underway. Don't misunderstand, the planet will be poorer for the loss of plant breeders, but it will keep on spinning.

To explain my belief, a definition of plant breeder is required. I could use Darwin's description, but I will be more concise. Based on the discussion above I define a plant breeder as one who develops and implements phenotypic selection programs and spends enough time with the plants so as to gain a feeling for the organism. Scientists with the title "plant breeder" may continue to exist but, unless trends change, professionals who meet this definition will continue to disappear.

There are a number of reasons to believe the disappearance of "selectionists" will come to pass.

1. This has happened to other disciplines dealing with the whole plant, physiologists, anatomists, pathologists, and to a lesser extent agronomists and horticulturalists. If the titles still exist the disciplines have morphed into essentially new disciplines. I am not opposed to this. It is the way science and culture evolve. But let us not kid ourselves and think it can't happen to plant breeding. Each of these groups believed they were necessary and eventually the "new folk" would figure out how important their knowledge was and come looking for advice or expertise. Wrong! These groups became marginalized in terms of funding and science. Today if a molecular geneticist is interested in the anatomy of the coleoptile, they pull Esau (1965) off the shelf and cobble together what they need to know. The results may not always be pretty or efficient but they will be successful as far as peer review goes, because none of the reviewers will be anatomists.
2. As outlined above, professionals trained in plant breeding today do not have the same background or advanced classes as that of the selectionists of the past. They are weaker in agricultural sciences, quantitative thinking, whole plant biology, and selection theory.
3. Supervisors may sincerely believe that plant breeders are needed. But what is the supervisor's background? How do they define plant breeder? Do they understand the power and role of selection? Do they know what it takes to gain a feeling for the organism?
4. The reigning engineering paradigm is in direct opposition to the selectionist paradigm. Engineering suggests that we can find out what all the genes do and then put them together in the optimal way. Selectionists apply selection and let nature and the organism create an array of solutions any number of which will be useful, some in unique and unexpected ways.

Plant improvement can and will occur following the engineering paradigm. Gains may not be as rapid, cost efficient, successful, or to my mind interesting as those made via selection, but gains will be made. Plant breeders will exist as technicians for engineering programs.

Why should plant breeding be supported by taxes?

Why should plant breeding be supported in the public sector? Or, how does plant breeding differ from other industries? If we attempt to convince taxpayers that they should support plant breeding we need to have good answers for these questions.

- Food Security: Plant breeding decisions determine the future of the world's food supply. Placing the responsibility for the world's crop germplasm and plant improvement in the hands of a few companies is bad public policy. The primary goal of private corporations is to make profit, and even in the case of the most civic-minded corporations, this goal will be at odds with certain public needs. Even if we assume that the one or two companies controlling a crop were completely altruistic, it is extremely dangerous to have so few people making decisions that will determine the future of a crop. Even well intentioned people make mistakes. The future of our food supply requires genetic diversity but also demands a diversity of decision makers (plant breeders).
- Sustainability: Diversity at multiple levels leads to a more sustainable agriculture. Genetic diversity, crop diversity, cropping system diversity, farming system diversity, community diversity, and intellectual diversity are needed. The merger-acquisition model of late 20th century economics continues today. Justification for such activity includes efficiency of scale, which by

definition works against diversity. As acquisitions occur in the seed industry, large geographical areas are abandoned. Farmers in these regions are left to use old cultivars or ones that were developed elsewhere and just happened to fit their needs. This has negative effects on the future of those farms, thereby decreasing diversity at the level of community. Numerous public breeders working in diverse ecosystems with diverse crops needed to increase diversity at all levels.

- Independence: Ideally, public plant breeders do not have an economic interest in the results of their breeding program. Therefore decisions should be made in the public interest. Public breeders should be able to focus on solutions that do not necessarily result in high seed sales volume, such as long-lived perennials and pure line and open-pollinated cultivars, or in unique and original ideas such as supersweet corn and afila pea.
- Public service: Plant breeders actually developing cultivars adapted to the local environment must be familiar with the needs and challenges of the local farmers and consumers. Academic plant breeders (no cultivar development) can operate independently of the local community responding only to grant and manuscript reviewers.
- Education: Actual cultivar development programs at Universities with complete plant breeding curricula offer the best opportunity for training the next generation of plant breeders. If the next generation is to consist of selectionists then we need to reemphasize the role of population/quantitative thinking as the foundation for the education of plant breeders
- Continuity and efficiency: Successful plant breeding programs require long-term continuity. Plant breeding requires cycles of selection and recombination. Plant breeding, unlike other types of research, cannot be started and stopped based on three year granting cycles. Plant breeding is rapid only when programs are continuous. Plant breeding programs that suffer interruptions are slow and inefficient. If society requires rapid gains, plant breeding programs require continuous support.

Summary

Plant breeding is a technology that harnesses the creative power of selection. It is powerful, precise, and predictable. Selection and genetic recombination create new organisms. Plant breeders must be concerned with adaptation of new cultivars; however, the area of adaptation is an economic decision. As for many professions it takes many years of experience for a plant breeder to develop the requisite skill (art or eye) to be most effective. While plant breeding (selection) is a useful and efficient technology, the continuation of this discipline is by no means assured. The paradigm for crop improvement has shifted from selection to engineering. It is not clear whether selection can survive the competition from this new paradigm. Even if plant breeding survives as an idea it is unclear that it will survive as a function of the public sector despite clear public benefits. These benefits including food security based on diversity of decision makers, crops, and cropping systems must be demonstrated to stakeholders if plant breeding is to survive. Plant breeding is one of humanities most successful and benign technologies, but its future depends on whether society elects to continue its support.

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