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Prediction in Plant Breeding*

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I. INTRODUCTION

For the past 10,000 years, plant and animal breeding have been associated with continued increases in food production and the sustenance of a growing world population (Borlaug 1999). Despite systematic gains, many aspects of the breeding process during this period have been considered artistic and experiential rather than predictive and scientific (Smith 1995; Harlan 1992; Duvick 1996). The process of plant breeding has developed through several key phases, including unconscious selection in Neolithic times, empirical art during the development and expansion of agriculture, and a predictive science-based approach practiced today. Did the turning point from empirical to scientific plant breeding reflect a gradual transition from an art to a science during the late 19th and early 20th centuries, or was there a key element that paved the way for this transformation? Throughout much of this chapter, I will argue that the development of predictive models, based initially on the progeny test, during the mid-19th century signaled the dawn of a scientific era in plant breeding.

Natural and artificial selection are similar in many fundamental ways, and the process of plant breeding has often been compared to selection in nature, albeit with a human-guided directionality. Despite the similarity, most models of natural selection are based on random mating, while artificial selection is based on mate choice. Darwin suggested sexual selection as an explanation for certain types of mate choice in nature, based on predictive signals presented by potential mates. In this chapter, I will suggest that the natural selection analog traditionally associated with the breeding process is perhaps better represented by the process of sexual selection, which incorporates predictability. Finally, I will suggest that the introduction of predictive systems to plant breeding has defined the last half-century of strategies, practices, and successes in crop improvement.

A. Art and Science in Plant Breeding

Art and science are often interposed and presented as a dichotomy. Artistic impulses are often considered in the context of a search for beauty, while scientific impulses are connected with a search for rational truth or explanation of phenomena. Although each term is clearly distinct, there is at least one area where the two overlap. Certain definitions of art and science concern themselves with that skill or knowledge gained from study, practice, or observation. The similarity between art and science has been a subject of discussion since at least the 18th century, when Immanuel Kant wrote that the search for truth was the same as the search for beauty (Beck 1959). The intersection between art and science is often exemplified in superior artistry or craftsmanship. Examples of this kind of mastery, such as the "baker's art," derive from continuous experience and observation. When scientists or artisans gain mastery of their work through sustained observation and first-hand experience, it is indeed difficult to determine how their activities could be separately explained by traditional definitions of art and science. Since the definition of art and science coincide with respect to this principle, how do they differ when it comes to experiential learning?

What differentiates art from science in this all-encompassing definition is the goal of the activity. A scientist may pursue knowledge gained from practice and experience in an effort to develop and codify fundamental principles on which such observations can be based. On the other hand, an artisan may pursue wisdom gained from practice and experience in an effort to create works of beauty. While it is certainly possible that both scientist and artisan may uncover fundamental principles and generate beauty, in general the scientist explains and the artisan creates. Today, the practice of plant breeding includes both art and science, as it is both a creative enterprise and a means for gaining insight into biological phenomena. The art of the plant breeder, an indefinable quality brought about by experience and observation, is closely connected to the breeder's "feeling for the organism," a phrase used to describe the deep level of understanding Nobel laureate Barbara McClintock exhibited for her experimental organism, the maize plant (Keller 1983). Writing about the connection between artistic impulse, based on experience and observation, and plant breeding success, Duvick (1996) stated:

> Breeders universally depend on experience and art more than on genetics. The best plant breeders are the best artists. They may or may not be the best geneticists.

Domestication and its reliance on mass selection allowed early agriculturists to select phenotypes suited to local conditions, using a mechanism nearly identical to the process of natural selection (Darwin 1868). These efforts may best be described as visual selection for characters with agricultural suitability. As agriculture was introduced and the adaptive landscape was altered, mutations resulting in phenotypes favorable to cultivation would have been selected and preserved regardless of their suitability or neutrality in nature. This type of selection has been described as "unconscious selection." Although the act of choosing is certainly deliberate, the stated reason behind the choice is not to increase the frequency of a particular genotype in a population; however, in the case of unconscious selection, that outcome will often result.

In a modern sense, plant breeding may be defined as systematic crop improvement by genetic change and a plant breeder may be defined by his or her participation in activities related to this process, such as generation of segregating populations, selection, and recombination of selected individuals. Despite the modern emphasis on conscious efforts to manipulate the genetic makeup of plant populations, plant breeding activities predate the invention of agriculture itself. Thus, the first plant breeding activities involved unconscious selection for agricultural suitability. In the millennia that followed, plant breeding developed into an empirical art and ultimately into a modern scientific enterprise characterized by predictive methods. The objective of this paper is to present the argument that the adoption of predictive methods brought about this transformation from unconscious selection to predictive science.

B. Unconscious Selection, Empiricism, and Agriculture

The first plant breeding efforts involved selection of individual plants from wild or weedy populations. A classic example of a phenotype associated with cultivation is the reduction in lateral branching and ear number in modern maize (*Zea mays*) compared to its wild ancestor, teosinte. Teosinte possesses many lateral branches terminating in male inflorescenses (tassels). As a result, teosinte was more prolific (i.e., produced more ears) than modern maize because female infloresences and small ears were formed in axils of these lateral branches. Selection during the domestication and evolution of modern maize has been practiced for fewer lateral branches and an overall reduction in ear number (Maita and Coors 1996). The desire to select for fewer ears was probably due to the fact that maize was harvested by hand and a single ear with much grain was more easily harvested by hand and stored than multiple, smaller ears with fewer grains. Molecular genetic studies (White and Doebley 1998) have shown that selection has been effective in modifying the expression of the *tb1* allele (*teosinte branched-1*), a transcription factor involved in lateral branch suppression. Large modifications in phenotype, centered on allelic configurations at a single locus and enhanced by modifying genes, are a common theme in crop evolution (White and Doebley 1998). Development of novel phenotypes during the process of changing branching habit in maize resulted in selection of an ideotype. Although these changes are of a fundamental genetic nature, they were brought about by early agriculturists practicing visual selection for traits of agricultural suitability.

Many traits important to early agriculturists were heritable and, therefore, could be reliably selected. However, this phase of breeding was empirical and generally not considered scientific in the modern sense because changes in these plant and animal populations were not analyzed in an attempt to explain biological phenomena. At this stage of agriculture, the focus was on the practical goal of producing food rather than finding rational explanations for nature (Harlan 1992). Ideas about heredity during the period when many early crops were domesticated ranged from mythological interpretations to near-scientific notions of trait transmission. In his Presidential Address to the American Society for Horticultural Science in 1987, Janick (1988) stated:

> The origin of new information in horticulture derives from two traditions: empirical and experimental. The roots of empiricism stem from efforts of prehistoric farmers, Hellenic root diggers, medieval peasants, and gardeners everywhere to obtain practical solutions to problems of plant growing. The accumulated successes and improvements passed orally from parent to child, from artisan to apprentice, have become embedded in human consciousness via legend, craft secrets, and folk wisdom. This information is now stored in tales, almanacs, herbals, and histories and has become part of our common culture. More than practices and skills were involved as improved germplasm was selected and preserved via seed and graft from harvest to harvest and generation to generation. The sum total of these technologies makes up the traditional lore of horticulture. It represents a monumental achievement of our forbears—unknown and unsung.

The Biblical passage concerning Jacob's sheep, goat, and cattle breeding (Genesis 30:32–42) describes a program designed to identify brown, speckled, and spotted segregates in a population of white animals. These non-white animals were to be Jacob's to keep in return for managing the herd for his father in law, Laban. Presciently anticipating a trait governed by a single gene in a heterozygous condition, the story suggests a proportion of the offspring of white animals crossed with speckled animals will possess colored offspring. In addition, Jacob suggests feeble animals will be removed from the breeding pool so as to improve the strength of the herd. While clearly a breeding program designed to produce a certain phenotype, Jacob relies on supernatural phenomena to explain the appearance of speckled progeny in the crosses. Jacob exposes the inner white bark of poplar, hazel, and chestnut trees and places these before the flock when watered in order to promote mating and ultimately the formation of speckled progeny.

Despite the presence of rudimentary hereditary concepts more than 5,000 years ago, early agriculturists had not yet uncovered and systematically formulated basic concepts about the sexual process in plants and the hereditary laws underlying the breeding process. Babylonians manipulated reproductive structures in date palm in order to promote fruit set, although the degree to which the reproductive process was understood is not known. Biblical aphorisms such as “like begets like” suggested that early agriculturists knew something about trait transmission, but the fundamentals of heredity were to remain a mystery until the end of the 19th century and not generally accepted until the rediscovery of Mendel in the early 20th century.

Although plant breeding efforts have been continuous since the beginnings of agriculture, the breeding process retained its primarily empirical character during the discovery of many of the foundation concepts of biology (Sturtevant 1965). Codification of the breeding process as a scientific endeavor did not occur until the 20th century. In fact, up until the 20th century, most breeders were members of agrarian societies selecting crops to fit agricultural environments for the purpose of the production of food or fiber, or hobbyists known as “fanciers” interested in manipulating natural objects for esthetic goals (see Section II C). The existence of this latter group is an indication of the degree to which breeding was connected to artistic expression (Desmond and Moore 1991). This tradition continues today with breeders focusing on “ideal phenotypes” for participation in animal shows, flower judging contests, and the like. One of the most famous plant breeders of the modern era, Luther Burbank, was idolized for his prized selections of fruit and vegetable cultivars, despite eschewing the science of genetics. Burbank’s selection process was artistic and based on esthetic goals. Yet, when sought as a source of information on heredity during the period immediately following the rediscovery of Mendel’s paper, Burbank had little interest in the scientific foundations of his craft (Dreyer 1975). Despite this aspect of Burbank’s work, he was an avid follower of Charles Darwin and was certainly one of the “fanciers” whose work stood as a testament to the power of artificial selection.

C. Predictability and Progeny Test: The Turning Point

Mass selection was the dominant plant breeding procedure throughout the domestication of crop plants and through the millennia that followed. Mass selection may be defined as a process of simple phenotypic selection involving the identification of superior individual plants from a population, forming a bulk of these selected individuals, cross or self-pollination among individuals in the selected bulk, and re-evaluation of plants grown from seed saved from selected individuals. Mass selection is an effective method for changing allele frequencies in plant populations, and it is still practiced by many professional breeders, hobbyists, and agriculturists striving to improve crop plants. Mass selection generally does not involve record keeping of pedigrees because, in mass selection methods prior to the 20th century, selected plants are either recombined with pollen from the population at large or self-pollinated. The lack of a family structure in the selection process also obviates the need for recording lineages. Mass selection can therefore be effectively practiced with little, if any, recorded information.

During the 18th century in animal breeding and the 19th century in plant breeding, the practice of artificial selection by breeders began to include formal record keeping and detailed accounts of particular lineages. The development of pedigree records was helpful to animal breeding efforts because it was useful to know if a particular dam bred with a particular sire resulted in superior progeny (Troyer 1996a). Darwin (1868) discussed pedigree record keeping in animal breeding, citing examples from scores of different animals and the human cultures who bred them. The pedigree method of breeding makes use of performance in past crosses to predict performance in future crosses, based on the principle of heritability. Heritability is the degree to which a trait is passed from parent to progeny, or more precisely a ratio of the additive genetic variance to the total phenotypic variance. The pedigree method is essentially individual plant selection in segregating populations where the lineage of particular selections is known. Using the pedigree method, inferences can be drawn about the value of particular lineages and predictive patterns may emerge. Testament to the value of this approach is the simple fact that the pedigree method has been a mainstay of animal and plant breeding efforts for centuries.

In practice, however, the pedigree method allows for many twists and turns in parental choice, as individuals are mated generation after generation. Parent choice in this process is still highly intuitive and relies strongly on the breeder's experience. However, once pedigree records were regularly kept, plant breeders in Europe began to systematically value particular lineages. The introduction of a quantitative aspect to progeny evaluation was a key turning point in the development of modern scientific plant breeding. Lineages were chosen based on their overall performance, and performance patterns began to emerge. Coincident with quantification of progeny performance was the incorporation of error measurement techniques for biological investigation (Smith 1966). In his historical treatment of plant breeding, Smith (1966) mentions the work of Gauss on theory of least squares and Laplace's conception of the law of error in 1812, and Quetelet's description of biological phenomena in quantitative terms in 1846. It is likely that quantitative descriptions of biological subjects became commonplace in Europe during this period, perhaps paving the way for breeders to consider evaluating progeny performance in a systematic and quantitative fashion.

During the middle of the 19th century, a major proponent of lineage evaluation was the family Vilmorin, among the most important seed firms in Europe and influential plant breeders of the 19th century. During the period 1840–1880, Louis de Vilmorin began a program he called "geneological selection" or "selection of the seed-bearer." This approach, which was also independently discovered in plants by Svalof in Sweden in the 1890s and by Hallet in England in the 1860s (Gayon and Zallen 1998), became synonymous with pedigree breeding but contained an important difference. In Vilmorin's approach, the breeder assessed "an individual's capacity to transmit a character . . . to the lineage" (Gayon and Zallen 1998). He called this property "being a good stallion" (cited in Gayon and Zallen 1998), an obvious reference to pedigree breeding in animals. But in this case, "being a good stallion" meant more than just keeping pedigree records; it brought on a new way to evaluate lineages—namely, the progeny test.

The progeny test evaluates the breeding value of a particular parent or lineage by evaluating its progeny. Typically, parents are crossed in multiple combinations and the value of progeny populations are recorded. Because the progeny test places a value on an individual based on the performance of its progeny, the procedure introduces an element of predictability into the breeding process because it allows for estimation of genetic effects. Genetic effects, although unknown at the time, were of course the fundamental underpinning of the progeny test (see discussion below). In short, the pedigree method and progeny test brought about a way for plant breeders to *quantitatively separate* the heritable portion of variation from the non-heritable and thus make parental choices that were based on heritability.

During this period, Vilmorin also introduced quantitative and statistical aspects of evaluating progeny to the progeny test, thereby increasing its power and precision. Interestingly, in this same period, Mendel was conducting statistical evaluations of segregating populations of pea plants in his monastery garden (Orel 1996). It would take more than another two decades before any of the biometricians would analyze genetic data in a real statistical sense. Vilmorin may be viewed as a pioneer in heredity because he encouraged the use of statistical tools in assessing progeny performance. Vilmorin's approach marks the introduction of models designed to enhance predictability in breeding. To back up the value of his idea, Vilmorin maintained a very successful seed business and was known worldwide for his work on increasing sucrose content in sugar beet from 5% to 16% using progeny testing (Hopkins 1899). Models such as the progeny test allowed for data-driven parent choice in plant breeding, a new idea for the mid 19th century. Indeed, Vilmorin influenced breeders in the U.S. with his progeny test. Hopkins, (1899), a chemist who initiated the Illinois Long Term Selection experiment at the University of Illinois in 1896, wrote that he wished to emulate the work of Vilmorin in his own experiments on chemical composition in maize:

> That the chemical composition of corn can be changed seems reasonably probable from the changes which have been produced in some other plants—notably in the sugar beet . . . A small portion of a beet is analyzed and, if it is found to be sufficiently rich in sugar, the beet is then set out as a "mother," or seed, beet. From the seed produced beets are grown and another selection of seed beets is made on the basis of their sugar content.

That Vilmorin influenced Hopkins to begin selection for chemical composition in the maize kernel 50 years after Vilmorin popularized the progeny test is clear (Dudley 1974). More specifically, Hopkins continued Vilmorin's tradition of mass selection combined with a progeny test, merging the advantages of a cyclical selection process with a quantitative assessment of progeny performance. After Hopkins began his experiment at Illinois in 1896, breeders in the U.S. became well aware of the power of both methods to improve crop plants.

D. Progeny Testing and the Exploitation of Additional Genetic Variance

Genetic gain is predicated upon the existence of genetic variation, often quantified in terms of additivity, dominance, and epistasis. Additive genetic variance is the variance among breeding values or that variance due to the sum of allelic substitutions (Falconer 1981, p. 115–119). Additive genetic variance and additive × additive epistatic interactions (including higher order additive interactions) are the only type of variances transmissible from parent to progeny. Mass selection would have preferentially identified and taken advantage of additive genetic variance. By contrast, the progeny test evaluates individuals on the performance of their crossed progeny, thereby allowing breeders to identify and exploit both additive and dominant genetic variances. Depending upon the type of progeny produced, genetic variance due to dominance deviations can be exploited in crossed progeny. Shull (1952) pointed out in 1908 that a population is actually a complex mix of genotypes, some of them hybrids and some of them selfed individuals. Even though a mass-selected population will in any given generation reveal both additive and dominance genetic variance, from generation to generation only the additive component will be transmitted. Although genetic variances were unknown to de Vilmorin, Hallet, and Svalof, their method allowed for identification of an important source of variation.

This previously unstated advantage of the progeny test resulted in the exposure of a reservoir of genetic variation previously masked by the process of mass selection. Unknowingly, breeders using the progeny test revealed and began to manipulate genetic variance due to dominance through systematic evaluation of the first generation crossed progeny, or the hybrid. This evaluation paved the way for the inbred-hybrid method, which quickly became the predominant paradigm for plant breeders in the 20th century (Kloppenburg 1988; Goldman 1998; Duvick 1999). As modern scientific breeding has moved inexorably toward predictive systems, exploitation of additive genetic variance during the inbreeding process and dominance variance during the testcrossing phase, when assessing performance across multiple testers, has become standard for cross-pollinated crop plants.

II. PREDICTION AND PLANT IMPROVEMENT

A. The Birth of Scientific Plant Breeding

Virgil (1st century BCE) in the *Georgics* (Dryden translation) clearly indicates a predictive element in cattle breeding:

> When she as calved, then set the dam aside,
> And for the tender progeny provide.
> Distinguish all betimes with branding fire,
> To note the tribe, the lineage and the sire;
> Whom to reserve for husband of the herd;
> Or whom shall be to sacrifice preferred;
> Or whom thou shalt to turn thy glebe allow,
> To smooth the furrow, and sustain the plough;
> The rest, for whom no lot is yet decreed,
> May run in pastures, and at pleasure feed.

These predictive elements are echoed in Shakespeare's *A Midsummer Night's Dream* from the remarks of Theseus on dog breeding:

> My hounds are bred out of the Spartan kind;
> So flew'd, so sanded; and their heads are hung
> With ears that sweep away the morning dew;

> Crook-knee'd and dewlapp'd like Thessalian bulls;
> Slow in pursuit; but match'd in mouth like bells,
> Each under each. (4.1.119–124)

It is clear that Shakespeare, who wrote more than 400 years ago, recognized that the breeders sought and maintained certain traits from particular lineages. However, this information appears to be from an empirical source rather than from strictly scientific foundations. One measure of a scientific enterprise is the degree to which fundamental laws or concepts are uncovered, applied, and repeated. Nineteenth-century biology had reduced stature as a science because of the inability to establish fundamental laws compared to those of physics and chemistry. Indeed, the probabilistic nature of biology made the search for unswerving laws a great challenge for many early naturalists (Mayr 1997). Up to the discovery of DNA and advances in molecular genetics, biology has been defensive for appearing to possess fewer immutable laws than other scientific disciplines.

However, another crucial aspect of a scientific discipline is the development and application of predictive models, presumably based on fundamental laws that have not yet been discovered or understood. Such models allow for data gathering and pave the way for interpretation of experimental results. Often, these models are the precursors to fundamental principles or concepts. When the progeny test was developed for plant breeding in the mid 19th century, its discoverers saw it as a way to improve breeding progress and parent selection. Since Mendel's work had yet to be published and understood and hereditary concepts were murky at best, the progeny test represents a predictive model that helped pave the way for the determination of hereditary laws. Certainly with centuries of pedigree breeding, many breeders confirmed that "like begets like." However, the mechanism for this transmission remained a mystery. With progeny testing, breeders began to recognize that progeny performance could be forecast from cross performance of combinations of parents. With the progeny test, it would become possible to identify lineages that performed well in cross combinations regardless of whether the lineage itself possessed useful characters. Even though the progeny test did not enable explanation of trait transmission across generations, quantitative analysis of progeny from the first cross-pollinated generation resulted in a fundamental change in plant breeding. It was precisely at this point that plant breeding took on one of the key characteristics of a scientific discipline: predictability.

Progeny test-based prediction and hereditary laws are related in a simple but fundamental manner. Understanding of the genetic basis of heredity arose from the work of Gregor Mendel at the Monastery of Augustinians in Brno, Czechoslovakia, in the 1850s and 1860s. Coincident in discovery with the era of progeny testing in Western Europe, Mendel's fundamental concepts of heredity were so revolutionary that they remained poorly understood at best until their re-discovery in 1900. The reason the progeny test was successful was of course that it exploited the laws of heredity, though they were unknown at the time. Later in the 20th century, biometrical geneticists would develop detailed models allowing for more precise partitioning of variances and estimation of the covariance among relatives. These two ideas were crucial in assessing the degree to which the relationships among relatives, such as half or full sibs, were due to genetic causes.

Thus, the predictive and scientific aspect of practical plant breeding first came about via the adoption of the pedigree method and progeny test, both of which relied on unknown laws of heredity. The progeny test thereby unknowingly allowed breeders to gain a better estimation of genetic effects, particularly for quantitatively inherited traits. In practice, it allowed breeders to place a value on a particular parent based on its contribution to a particular trait in its progeny. The progeny test was developed from the knowledge gained by the experience of crossing parents and evaluating progeny; thus it fits definitions close to both art and science. However, because of its predictability (founded on the fundamentals of genetics), discovery of the progeny test became a turning point for the adoption of the scientific method to the practice of plant breeding.

Interestingly, another plant breeding procedure known as the backcross may also be considered highly predictive, in the sense that a simply-inherited trait can be transferred through backcrossing to a recurrent parent with a high probability of success. Like the progeny test, the predictive aspect of the backcross is of course related to Mendelian principles. However, unlike the progeny test, the backcross did not become part of the standard repertoire of the plant breeder until after the turn of the 20th century. By this time, predictive aspects of quantitative trait manipulation introduced from the progeny test had already become commonplace in the practice of plant breeding.

B. Connection Between Natural and Artificial Selection

Artificial selection in plant breeding shares many similarities with the process of natural selection in nature. Natural selection and artificial selection may both be defined by differential reproduction and survival in populations where fecundity and heritable variation are present. However, natural selection occurs mainly in nature and is non-directional (in the sense that different phenotypes are selected in response to different environments and that such changes oscillate with a fluctuating environment), while artificial selection is practiced by humans and is often directional. It is important to note that both natural and artificial selection may be operative in breeding populations. Respect for the process of artificial selection paved the way for acceptance of the idea of natural selection. Moreover, Darwin was fundamentally inspired by breeders to consider the power of selection when thinking about evolution in nature (Desmond and Moore 1991). After his fabled trip to the Galapagos, Darwin wrote:

> I often asked myself how these many peculiar animals and plants had been produced: the simplest answer seemed to be that the inhabitants of the several islands had descended from each other, undergoing modification in the course of their descent; and that all the inhabitants of the archipelago had descended from those of the nearest land, namely America. . . . But it long remained to me an inexplicable problem how the necessary degree of modification could have been effected, and it would have thus remained for ever, *had I not studied domestic production, and thus acquired a just idea of the power of Selection.*

Ever since Darwin formulated natural selection as the primary mechanism of natural evolution, many breeders have commented on the similarities in artificial and natural selection. The primary similarities between the two systems are the presence of heritable variation, fecundity, and differential reproduction and survival. The primary difference between the two processes is the human goal-driven aspect of plant breeding and the lack of linear directionality in natural selection. Except for this important difference, the process of plant breeding prior to the advent of predictive methods such as the progeny test is in many ways analogous to the process of natural selection.

However, Darwin did not use natural selection to explain all kinds of evolution. In the *Origin of Species*, and later in *The Descent of Man*, Darwin invoked a process he called "sexual selection" to explain the evolution of traits that promote success in competition for mates. One type of sexual selection is the struggle between males for mates, whereby females choose mates based on displays of strength, visually appealing morphology, or elaborate courtship rituals. A classic example of this type of sexual selection is tail size in male peacocks (*Pavo cristatus*). In this case, female peacocks (peahens) choose males for mating based on the elaborate nature of their tail display. Such selection results in showy feather displays in male, but not female peacocks. In many cases studied to date, it has been difficult to determine what females gain from choosing elaborately colored males in cases where males provide no obvious material resources to the female or her offspring. Recently, carefully controlled studies where females were allocated to males for breeding at random and offspring were reared under the same conditions have been conducted. These experiments demonstrate that offspring of peacocks with the most elaborate trains (as measured by the total number of eyespots on the tail feathers) grow and survive better than offspring from peacocks with less elaborate trains (Petrie 1994). Improved growth and weight of offspring sired by peacocks with greater ornamentation translates into an improved chance of offspring success under natural conditions. Thus, mate choice based on sexual selection of males with elaborate trains is correlated with offspring survival and/or success in the peacock.

Because these male displays are selected based on offspring success, sexual selection offers a degree of predictability to the selection process that is not present in natural selection. In its predictability, sexual selection is akin to the progeny test, allowing females to choose superior phenotypes, and thus, at least partially, genotypes, to sire their progeny. Interestingly, progeny testing was introduced to plant breeding at around the same time Darwin began to think, although not explicitly, about sexual selection. In this way, sexual selection, whereby females choose among males to enhance offspring success, takes on some of the elements of a natural progeny test. It is important to note that the sexual selection model offered here focuses only on female mate choice, rather than male-dominated systems where individual males, based on their dominance of a group of females, may mate with multiple females in their group.

The analogy between natural and artificial selection, with the exception of directionality, has served well as a mechanism for explaining the processes of plant breeding and evolution in nature. A limitation of this analogy is the randomness of mating assumed in the natural selection model, which is not accurate in describing the non-random mating accompanying artificial selection. The presence of non-random mating in animals may be better described in certain cases by use of a sexual selection model. Therefore, since mate choice (or the choice of parents for breeding populations) is taken into account in certain sexual selection models, the analogy between artificial and natural selection may be better explained by the analogy between artificial and sexual selection.

C. Charles Darwin's Inspiration Derived from Breeders

Darwin was raised in the agricultural heartland of England and was very familiar with the process of "domestic breeding" (Desmond and Moore 1991). His uncle, Josiah Wedgewood, was among the leading breeders of sheep in the country and was responsible for introducing the shorthaired Spanish merino sheep to England. His mother bred and kept pigeons and another uncle (John Wedgewood) bred dahlia.

Darwin looked to landowners as a source of vital information about the process and power of selection, because it was they who possessed the necessary practical experience with "molding" breeds to fit their particular agricultural situations. During this period, Darwin acquired a pamphlet from one of the leading bird breeders, Sir John Sebright, which contained the following commentary on selection:

> A severe winter, or a scarcity of food, by destroying the weak and the unhealthy, has all the good effects of the most skilful selection. In cold and barren countries no animals can live to the age of maturity, but those who have strong constitutions; the weak and the unhealthy do not live to propagate their infirmities (Desmond and Moore 1991).

Despite the connection often drawn between natural and artificial selection, Darwin did not view domestic breeding as mimicking nature. He viewed the agricultural landscape as full of oddities of nature, saved by the breeders for their own purposes. It is revealing that the 19th-century name for many of these professionals was "fancier," suggesting the artistic vision and whim that was perhaps the primary aspect of their efforts. Capturing Darwin's view at the time, Desmond and Moore (1991) wrote that "transmuting nature and producing an ornamental duck were asymmetrical acts." Darwin himself wrote that the ornamental duck was a "mere monstrosity propagated by art." Darwin was able to see that the process of artificial selection resulted in the creation (and perhaps extinction) of thousands of intermediate forms between wild progenitor and modern derivative form, such as between the otter and its land ancestor. "Opponents will say, show me them, I will answer yes, if you will show me every step between bulldog and greyhound."

As a scion of a wealthy family, Darwin had easy access to other landowners. In 19th-century England, the practice of biological science was carried out by landed gentry who, freed from the daily labors of earning a living, had the time to be naturalists. Even though Darwin looked to landowners as a source of information on artificial selection, the connection between domestic breeding and selection in nature had not been made by any of these contemporaries. A great deal of biological research in England during the 19th century was conducted by clergy. Early in his academic career, Darwin strongly considered life as a clergyman, but rejected it based on his scientific convictions, some of which he perceived to be in conflict with theology. Aside from landowners and clergymen, the hobbyists known as "fanciers" were perhaps most involved in the process of selection. It was this latter group that provided perhaps the key influence for Darwin regarding the power of selection.

During the 1850s, Darwin became a pigeon breeder and began to read the *Poultry Chronicle*. He began to associate with fanciers, particularly in "feather" clubs around London such as the *Philoperisteron* and the *Borough Club*. The latter was filled with working-class men who took to pigeon breeding as an escape from the workaday world. Darwin spent his time in between the two worlds of the gentlemen-naturalists and the blue-collar agriculturists and fanciers. The fact that Darwin was able to go between these two worlds, alternately earthy and stuffy, allowed him access to more information and was instrumental in connecting the process of selection in agriculture with that in nature. Through his connection with fanciers, Darwin acquired the necessary information about the artificial selection process. He had come to see the powerful "selecting hand," and according to Desmond and Moore (1991), it was the "grubby hand" of the fancier.

D. Sexual Selection Is a Suitable Analog for Prediction-based Plant Breeding

Superimposed on the artistry of artificial selection are the vagaries of natural selection, which must act whenever organisms are exposed to what Darwin called "the conditions of life." In this way, selection for a particular plant characteristic is almost necessarily carried out in conjunction with selection for traits such as abundant flowering, pollen production, and seed set in the environment in which selection is being conducted. Using the distinctions of artificial and natural selection, we might say that evolution in nature involves only natural selection, while evolution under domestication involves both natural and artificial selection. However, Darwin came to believe that the process of natural selection also contained an element similar to artificial selection, and he called this part of the process *sexual selection*. Despite only devoting several pages to this topic in the *Origin of Species*, Darwin devotes several chapters to sexual selection in *The Descent of Man* (Darwin, 1874), originally published 12 years later (and in revised form in 1874). Darwin wrote:

> Just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cockpit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature, and have led to the improvement of the natural breed or species. A slight degree of variability leading to

> some advantage, however slight, in reiterated deadly contests would suffice for the work of sexual selection; and it is certain that secondary sexual characters are eminently variable. Just as man can give beauty, according to his standard of taste, to his male poultry, or more strictly can modify the beauty originally acquired by the parent species, can give to the Sebright bantam a new and elegant plumage, an erect and peculiar carriage—so it appears that female birds in a state of nature, have by a long selection of the more attractive males, added to their beauty or other attractive qualities.

Taking this a step further with humans, Darwin commented:

> Man scans with scrupulous care the character and pedigree of his horses, cattle and dogs before he matches them; but when he comes to his own marriage he rarely, or never, takes any such care. He is impelled by nearly the same motives as the lower animals, when they are left to their own free choice, though he is in so far superior to them that he highly values mental charms and virtues. On the other hand he is strongly attracted by mere wealth or rank. Yet he might by selection do something not only for the bodily constitution and frame of his offspring, but for their intellectual and moral qualities.

After the advent of the progeny test and the introduction of predictive methods to plant breeding, the process of breeding exhibited some of the key elements of sexual selection, rather than the more general natural selection, although mate choice was obviously performed by breeders and not organisms under selection. Plant breeders clearly employed the progeny test as a way of valuing individuals as parents and controlling reproduction, much the same way that sexual selection does in nature. It may be instructive to think of pre-scientific plant breeding as analogous with natural selection, while scientific plant breeding is analogous with sexual selection. In this way, pre-scientific plant breeding made use of methods, such as mass selection, which do not focus on mate choice with respect to cross performance. On the other hand, scientific plant breeding clearly involves mate choice and models designed to maximize benefits from cross performance.

III. MODERN SCIENTIFIC PLANT BREEDING

A. Predictability and Development of the Inbred-Hybrid Method

The inbred-hybrid method has been very successful in increasing productivity of many important crop species (Crabb 1947; Duvick 1977; Duvick 1992). The area devoted to hybrids has increased significantly in the past 30 to 50 years for many crop species (Duvick 1999). During the early period of inbred-hybrid maize breeding (1920–1940), inbred lines in hybrid combination began to outperform open pollinated cultivars, although inbred performance per se was poor. At that time, hybrids were produced on hybrid female parents, using the double cross system developed by Jones (1918).

Because inbred performance was limiting hybrid seed production, identification of superior parental combinations for use as parents of hybrids was necessary. Furthermore, a plethora of inbred lines were available for testing. If a breeder became interested in testing many inbred lines in hybrid combination, the number of possible crosses became limiting. Inbred × open pollinated cultivar topcrosses were suggested as a mechanism for prediction of hybrid yield potential. The top cross method would allow for only n crosses of n inbreds, whereas $n(n–1)/2$ crosses were required for all possible single cross combinations. For this reason, Jenkins and Brunson (1932) introduced a method for evaluating inbred lines in a more efficient manner. In this method, topcrosses were compared to the average performance of the same inbreds in single cross combinations. They found a good correlation between general combining ability from the top cross performance and average combining ability from the single cross performance (Allard 1960). This suggested that the top cross method was a good way to evaluate inbred lines. Jenkins (1935) later expanded upon these ideas by suggesting (1) prediction of double cross performance was possible by evaluating yield of parental single crosses, and (2) early testing of inbred lines for general combining ability. The double cross prediction method streamlined the testing phase of breeding double cross hybrids and was a precursor to more sophisticated predictive models for cross performance in use today (see below). Early testing allowed for measurement of cross performance in the S_0 through S_2 generations, compared to previous methods that made use of inbred lines from the S_2 or beyond, thereby identifying high-yielding genotypes sooner in hybrid development (Jenkins 1935; Sprague 1946).

Even though an abundance of inbred parents made testing every combination a challenge, it was precisely this profusion of inbred lines that Fisher (1965) suggested was behind the success of the inbred-hybrid method. In Appendix C of the second edition of his landmark work *The Theory of Inbreeding*, Fisher (1965) outlined the practical value of inbreeding to plant and animal improvement. Fisher argued that when many homozygous lines are present, seed will be available to test promising crosses over environments with great precision using modern experimental designs. It is easy to see why Fisher, as a biometrician, held this view. Fisher, using the phrase "boon of reliability" to describe this process, also stated that any particular advantage or characteristic of the hybrid remains a permanent quality of the hybrid; thus additional work can have a cumulative effect. In this view, a large quantity of inbred lines serve to increase gain from selection because these lines represent the entire germplasm pool in the form of readily testable and repeatable parent stock. Fisher's thoughts were highly prophetic. Plant breeders began using computers to analyze and summarize yield trial data in the 1970s. By the 1980s, computerized analysis of large databases of inbred-hybrid performance was commonplace in commercial plant breeding programs.

B. Genetic Variances and Combining Ability

From the 1940s onward, geneticists and breeders became interested in explaining the primary types of gene action governing traits of agronomic importance such as yield. Pioneering work by academicians such as G. Sprague, R. Comstock, C. Robinson, C. Cockerham, and others resulted in the development of mating schemes designed to estimate genetic variance components (Hallauer and Miranda 1988, p. 52–89; Stuber 1994). The relative importance of dominance and overdominance in explaining heterosis in maize was widely debated (discussed in Smith et al. 1999). By the 1950s, the importance of non-additive genetic variance in explaining hybrid yield became known. As discussed previously, identification and exploitation of this variance was due directly to methods that started with the progeny test. Because of its reliance on the performance of first-generation crossed progeny, the inbred-hybrid method was a logical starting point from which to identify dominance deviations. Quantitative models developed during this period made use of various cross combinations of parents that possessed known genetic variances and covariances (Falconer 1981, p. 247–253; Hallauer and Miranda 1988, p. 52–89). Estimation of genetic variance due to dominance deviations was an important step toward quantifying the impact of breeding methods that relied on evaluation of the first cross-pollinated generation.

The importance of general and specific combining ability for development of superior inbred lines of maize was identified beginning in the 1930s and continuing through the 1950s (Smith et al. 1999). During this period, the notion of "combining ability" became commonplace in practical breeding programs as well. While early pedigree-based and progeny-test based programs would have identified loose "combining ability groups" decades before, the 1940s saw implementation of methods designed to measure the degree of combining ability. With this in mind, the idea of general combining ability was expanded to include a much larger population of environments as breeding targets. To do so, the commercial seed industry began to make use of wide area testing for identification of superior hybrid combinations in the 1960s (Bradley et al. 1988; Troyer 1996b; Smith et al. 1999).

C. Wide Area Testing

Wide area testing developed both as a response to the importance of general combining ability and, perhaps more important, the need for predictive solutions to plant breeding problems. Predictability was important to the commercial seed industry, whose yearly inventories of products necessarily varied according to environments, grower preferences, and changes in agricultural practices. Troyer (1996b) outlined the change in perspective of a maize breeder in the transition from local adaptation to wide adaptation. Wide area testing identified hybrid combinations that were most broadly adapted to large geographic regions, in some cases covering very large geographical regions. Crossing, testing, marketing, seed production, and other related enterprises of fewer, more widely adapted hybrids improved the efficiency of maize breeding operations. Testing procedures, because they are so crucial to the identification of superior hybrid combinations, command a majority of resources in breeding programs. Because of this, wide area testing became a powerful way to identify superior combinations. Fewer products meant streamlined seed production systems, better inventory control, and the potential to increase expenditures on research (Smith et al. 1999).

In maize, a superior hybrid may exhibit a 5–10% yield advantage over competing hybrids in test plots (Smith et al. 1999). But because yield and other quantitative characters have large measurement errors associated with them, the standard deviation on a testing location basis can be equivalent to one to two times the differences among hybrids in a strip test plot at a testing location (Smith et al. 1999). In addition, large genotype × environment interactions are commonplace for quantitative characters in crop plants. These interactions are poorly understood and very poorly characterized by breeders. Because environments in a particular year are not a random sample of all possible environments, measuring performance in one or a few years may result in bias. Whereas academicians often studied quantitative characters in a few environments, extracting as much data as possible from these locations, commercial breeders began to turn their attention toward a much larger population of environments for testing. Resource allocation in breeding programs shifted from many to one replication at a location, from few to many testing locations, and from emphasis on error control at the local level to emphasis on estimating genotype × environment interactions (Bradley et al. 1988).

Breeders should have difficulty predicting the performance of a hybrid in an environment that is not part of the target population of environments under study. Modern scientific plant breeding efforts have therefore been directed at testing in such a large sample of environments that the superior hybrids identified are more likely to perform well in any future distribution of environments (Smith et al. 1999). In the advanced stage of a commercial maize breeding program, a potential hybrid cultivar may be tested in as many as 1,500 locations, each of which may have only one replicate. And commercially successful hybrids, whose inbreds are chosen for cyclic breeding, are grown in tens of thousands of locations over a period of many years

As inbred per se performance has improved, heterosis has decreased as a percentage of the midparent value (Duvick 1999). Despite this decrease, which began in the 1960s, both inbred and hybrid performance have been increasing steadily. Although the amount of genetic improvement with the inbred-hybrid method has been large, large increases in research funding have been required to continue identifying superior hybrids (Smith et al. 1999). The increased size of many breeding programs has also necessitated the development of more efficient breeding methods.

D. Inbreeding and Inbred-Hybrid Databases

Once maize breeders introduced a method for reliably predicting progeny performance, they began to assemble germplasm pools and parent lines into breeding patterns. This practice followed in many other crops, although it was perhaps best developed in a systematic fashion in maize breeding. The best breeding or crossing patterns resulted in progeny with superior performance. As these patterns solidified, breeders continued to re-select within parental pools and lines, refining and purifying parental stocks for desired traits. As parental stocks became more uniform, predictive methods increased in their power because lower levels of heterogeneity and heterozygosity in parental populations translated into more uniform progeny populations.

The cyclic nature of the inbreeding process purged deleterious recessive alleles and resulted in improvements of inbred *per se* performance (Richey 1945). In addition, highly inbred parents became uniform entities from which to perform controlled crosses. Unlike highly heterozygous and heterogenous open-pollinated cultivars, highly inbred parents are genetically more uniform and the performance of their crossed progeny can be measured in a more precise fashion. Statistical advances, particularly in the realm of experimental design, allowed for improved estimation of progeny performance across multiple locations and years. The highly purified inbred lines developed in the inbred-hybrid method can be viewed as an arsenal of parent lines to be dispatched to exploit particular environmental niches. In fact, the deployment of parental lines from such an arsenal capitalized on predictive models of combining ability and cross performance developed by plant breeders over many decades.

Data from a multitude of crosses collected over many years and locations also resulted in the establishment of large inbred-hybrid performance databases, similar to the suggestion made by Fisher in 1965 (see Section III A). Such databases revealed important performance patterns and parental cross groupings, termed combining ability groups, allowing for enhanced levels of prediction of plant performance. A combining ability group refers to inbreds that react similarly in crosses. During the 20th century, high-performing F_1 hybrids resulting from these controlled crosses became the cultivars of choice in many crops. Although much has been written regarding the proprietary control and resulting profit motive afforded commercial seed companies by the inbred-hybrid method, the establishment of performance databases of inbred parents crossed in a wide variety of combinations was equally powerful in advancing the scientific and practical value of the inbred-hybrid method. The past several years have seen the development of sophisticated prediction algorithms such as the Best Linear Unbiased Prediction (BLUP) method based on high-powered computing and large databases of inbred-hybrid performance (Bernardo 1998). The BLUP method makes use of estimates of genetic covariance among relatives from the pedigree information and statistical models that separate genetic from non-genetic effects. Such methods are extensions of the progeny test in that they are designed to take advantage of the predictive aspects of cross performance and use them to advantage in designing breeding programs. The BLUP method has been used to gain better estimates of the genetic potential of parents in both cross and self-pollinated species. Increasingly, breeders have become interested in predicting single cross performance prior to choosing breeding parents, making test crosses, and evaluating hybrids, thereby greatly increasing efficiency.

Today this situation is true not only with cross-pollinated crops, but many self-pollinated crops have been incorporated into the inbred-hybrid system. As pollination control mechanisms were mastered, inbred crops such as tomato (*Lycopersicon esculentum*) and rice (*Oryza sativum*) have been developed into hybrid crops using the inbred-hybrid system. This transition reflects a desire to apply predictive methods to the selection process in crop breeding.

E. Molecular Genetics

Arguably the most successful application of predictive methods to plant breeding has arrived as biotechnological methods have been applied to crop improvement. Predictability in plant breeding derives from the fact that many traits of agricultural interest are under genetic control. Molecular genetics has heightened the level of predictability as the genes behind selected simple traits have been characterized, cloned, and inserted into a variety of crop species. Transformation technologies have made it possible to introduce single gene traits in a single generation across species, genera, and even kingdom boundaries. Despite challenges associated with transgene expression (Bruening 1998), transformation has made it possible to reliably introduce synthetic constructs carrying genes of agricultural interest into elite lines or populations in rapid fashion. Coupled with newer versions of standard plant breeding techniques such as marker-assisted backcrossing, recovery of the recurrent parent genome in segregating populations can be accomplished in only several backcross generations. Recently, marker-assisted selection (MAS) approaches have been extended to consider quantitative traits (Knapp 1998). Transformation and MAS approaches, which combine advances in molecular biology with traditional crop improvement strategies, have helped to change both the pace and the face of modern plant breeding. Importantly, both of these approaches make use of predictive methods for accomplishing plant breeding goals.

As wide area testing approaches continue to advance, the cost of identifying superior hybrid combinations will undoubtedly increase. As transgenic, or genetically modified (GM), versions of standard lines or populations become commonplace in the seed market, greater efficiency will be realized by modifying elite germplasm with single gene traits via transformation. Predictability gained from the genomic revolution will move plant breeding further in the direction of a scientific enterprise. Detailed knowledge of individual transgenes in a variety of backgrounds will significantly increase the chance of deriving superior genotypes, thereby increasing predictive strategies in plant breeding.

Recently, Somerville and Somerville (1999) proposed the use of gene chips and microarrays to assess gene function in the expression of heterosis. Gene chips and microarrays allow for all the genes of an organism to be placed on a matrix and used as hybridization targets for all the genes in a mRNA sample (Somerville and Somerville 1999). These authors suggest that the ability to characterize differences in gene expression between inbred parents and hybrids, and among hybrid genotypes, may pave the way toward more concrete explanations of the phenomenon of heterosis. Furthermore, if particular gene expression patterns can be correlated with performance of hybrids in specific environments, it may be possible to design more predictive strategies for hybrid cultivar development using DNA microarrays as a tool (Somerville and Somerville 1999).

IV. CONCLUSIONS

For millennia, plant improvement was essentially an art with both practical and esthetic goals. Predictability was key to the transformation of plant breeding from an art to both art and science in 19th-century Europe. Development of the progeny test, statistical methods of data analysis, and identification and exploitation of new sources of genetic variation moved plant breeding inexorably toward predictive systems. The traditional natural selection paradigm for plant breeding may be more accurately described using a sexual selection model, which allows for predictability by controlling mate choice. Modern scientific plant breeding in many crops is characterized by the inbred-hybrid method, a system built upon databases with predictive value. Emphasis on wide adaptation and greater efficiency in product development in the commercial sector dictates greater reliance on predictive models for breeding success. Future trends in plant breeding suggest increased use of statistical tools and large databases for predicting inbred and hybrid performance. Molecular approaches to crop improvement have already made significant inroads into hybrid breeding programs via marker assisted selection and transgene introduction. DNA microarrays may enable characterization of gene expression patterns contributing to heterosis, thereby increasing predictability in inbred-hybrid breeding programs. Construction of predictive models by plant breeders is an important step toward understanding fundamental biological principles surrounding the complexities of combining ability and heterosis.

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