Horticultural Plant Breeding: Past Accomplishments, Future Directions

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Abstract

Genetic improvement of agronomic crops through breeding, which typically are marketed as commodities, are grower directed. Breeding objectives principally involve increasing yield, often based on resistance to biotic and non-biotic stress. For example improvement in hybrid maize yields have relied on increasing yield stability under high populations. In horticultural crops, breeding objectives must be consumer directed because consumers make individual decisions on consumption, and make choices between different cultivars and alternate crop species. Indeed, many horticultural industries are based on a very few cultivars with unique qualities [‘Clementine’ mandarin, ‘Kerman’ pistachio, ‘Williams’ (‘Bartlett’) pear, ‘Dwarf Cavendish’ banana]. Unique quality rather than yield per se must be the overriding breeding objective. Successful examples of quality improvement through breeding include the creation of supersweet maize, based on the incorporation of the *shrunken* gene; sugary podded snap peas; seedless triploid watermelons; and the yellow-fleshed, aromatic, pineapple. These breeding innovations have essentially created new Industries and represent the future direction for horticultural breeding. A way must be found to incorporate consumer satisfaction in the selection process. Marketing attempts to obscure cultivar identification and change horticultural crops into commodities need to be resisted by the industry.

HISTORICAL

Plant breeding in the modern sense can be defined as purposeful genetic improvement. Yet genetic improvement of crop plants has an ancient tradition and in fact the greatest feat of plant breeding dates to Neolithic Revolution when our crop plants were domesticated starting about 10,000 years ago. Progress was achieved by selection of elite clones or lines of useful plants, mass growing of elite clones, followed by selection from naturally occurring seedlings. We recognize this technique as mass recurrent selection.

A key step to progress in this technique, especially for tree crops, was developing methods of vegetative propagation based on offshoots, cuttings, and finally grafting to fix genotypes. The concept of lineage and prepotent parents had long been recognized in animal breeding and is found embedded in literature from Virgil to Shakespeare. The Greeks and Romans were long familiar with special cultivars of fruits and extolled their virtue. Pliny the Elder, 1st century CE, could write of the specific attributes of a number of apple, quince, and medlar clones.

Plant breeding in the modern sense is largely a 19th century discipline (Goldman, 2000; Janick and Goldman, 2003) when experimental studies began to confront the problem of inheritance. Its experimental beginnings date to the 18th century; between 1760 and 1766, when Joseph Gottlieb Koelreuter carried out the first series of systematic experiments in plant hybridization using tobacco. Thomas Andrew Knight demonstrated segregation for seed characters of the garden pea but offered no explanation. Later with the help of his daughter he initiated hybridization within various fruit species and introduced a number of cultivars initiating the practical science of fruit breeding. Charles Darwin was the first to demonstrate and explain a mechanism (natural selection) that could account for the highly branched lineages that nature represents (what we now refer to as evolution) but did not come up with a satisfactory theory of inheritance. Jean Baptiste Van Mons, a Belgian horticulturist practiced long term mass selection in pear from open pollinations and introduced a number of new cultivars. It remained for Gregor Mendel to demonstrate that morphological characters were controlled by factors (later termed genes) that interact to form a phenotype and segregated unaltered from one generation to the next. His famous paper on inheritance in the garden pea published in 1865 included what he called species conversion incorporating backcrossing. Between 1840 and 1880, the seedsman, Louis de Vilmorin carried out practical breeding improvement in vegetables using a method he called genealogical selection (progeny testing) by assessing an individual's capacity to transmit characters based on lineage incorporating statistical analysis.

The genetic revolution that followed the rediscovery of Mendel's paper in 1905 had a revolutionary impact on plant improvement. Although breeders had unconsciously been using many appropriate procedures via crossing and selection in the 19th century, the emerging science of genetics, especially the fusion of Mendelian and quantitative genetics, put plant breeding on a firm theoretical basis in the 20th century. The relationship between genetics and post-Mendelian plant breeding is exemplified by a number of now routine breeding protocols. One is the extraction and recombination of inbreds combined with selection to produce heterozygous but homogeneous populations (hybrid breeding); backcross breeding in which individual genes can be extracted and inserted with precision and predictability into new genetic backgrounds; and disease resistance breeding based on an understanding that genetics can control disease reaction in plants and that host plant resistance can be an object of selection. What we now call "Conventional" plant breeding was based on a system of extensive germplasm exploration, sexual recombination followed by a series of selection strategies involving statistical techniques to separate genetic and environmental affects. The technique proved to be powerful and dynamic because plant breeding was shown to be evolutionary as improved plants from the breeders art became the parents of subsequent generations.

Dramatic advances in biology in the second half of the 20th century introduced a third revolution involving biotechnology, a catch-all term that includes both cell and DNA manipulation. The conventional baseline was 1953, the date of the brilliant Watson and Crick paper on the structure of DNA. One pathway in biotechnology developed from a series of investigations into gene function and structure and another from the culture and physiology of cells using microbial techniques. Molecular biology introduced two new techniques that were to have a profound effect on plant breeding. One was the establishment of molecular markers which made possible genotypic selection and the other was the transfer of genes between non-related organisms via recombinant DNA (transgene technology). By the end of the 1990s herbicide and insect resistance had been transferred into cotton, maize, and soybeans. These advances were quickly adopted, and engendered great expectations for agriculture but the technique has come up against a rising chorus of opposition based on little more than fear of the unknown. The future course of this technology, at least for the short run, cannot be predicted with certainty.

Plant breeding in the 20th century has accomplished a number of powerful achievements in agriculture. Perhaps the most important have been the increase in yield and adaptability of our major crop plants. At least half of the tremendous increases in yields of our major crops (as much as 6 to 7 fold) in the 20th century are attributed to genetic improvement. The development of photoperiod insensitive, short stemmed, fertilizer responsive rice and wheat—the Green Revolution of the late 1960s—is the high point of 20th century plant breeding.

HORTICULTURAL CROP BREEDING

The goal of this paper is to address the future of *horticultural* plant breeding. In this respect it may be enlightening to distinguish between horticultural and agronomic crops (Table 1) because the case can be made that there is a fundamental difference between these crops that may affect the future course of genetic improvement. The difference between horticultural and agronomic crops is primarily one of usage. Horticultural crops are those that serve to fit the special food and esthetic needs of humans. They are crops that not only make life possible but make life worth living.

In horticultural crops, quality is supreme. While it is true that *de gustibus non est disputandum*, there is no arguing about taste, the fact of the matter is that many horticultural crop cultivars with unique qualities are so unique, admired, and appreciated that they become the basis for entire industries. Examples include the 'Bartlett' ('Williams') pear which dominates fresh fruit production and is almost the only cultivar used for processing, 'Hayward' kiwifruit, 'Kerman' pistachio, 'Smooth Cayenne' pineapple (for processing), 'Clementine' mandarin, and 'Dwarf Cavendish' banana.

Differences between horticultural and agronomic crops are reflected in genetic improvement objectives. Agronomic crops become commodities in which the product is interchangeable. Breeding objectives are based on increasing yield, often determined by resistance to biotic and non-biotic stress. For example improvement in hybrid maize yields are based on increasing yield stability under high populations. In horticultural crops, breeding objectives must be consumer directed because consumers make individual decisions about consumption and make choices between different cultivars and alternate crop species. There are many examples of large breeding efforts that have had little grower acceptance because they have not been able to compete in the marketplace based on quality. For example, consumers have no interest in disease resistance of food crops but buy on the basis of their eyes, and continued purchase based on their palate. Thus, unique quality rather than yield per se must be the overriding breeding objective. It also must be stressed that grower-directed traits can often be solved by non-genetic means, while consumer-directed traits, especially quality, are often not amenable to alternate solutions.

A further profound influence on plant breeding, is the effect of individual breeder's imagination in proposing startling new innovations. To emphasize this point, four examples of outstanding horticultural breeding advances that have taken place in the last half century are presented below. These remarkable achievements are based on the inspiration and research of individuals. These successes emphasize the impact of imagination and skill combined with the plant breeder's art and science on the future direction of horticulture.

Super Sweet Maize

The introduction of super sweet corn is based on an innovation by a single breeder, John R. Laughnan (1919–1994), maize breeder and geneticist of the University of Illinois (Tracy, 1977; Steffensen, 2000). He suggested that the *shrunken 2 (sh2)* allele would have application to the sweet corn industry, and single handedly, with a minimum of support, transformed the fresh and later processed sweet corn industry. Laughnan's work originated as a genetic study in which he found that *sh2*/*sh2* kernels were unusually sweet with a pleasant malty flavor. The effects of the *sh2* allele was to increase the sugar content two to four fold and increase shelf life. It was reported to the industry but, incredibly, was not followed up by others. Fortunately Laughnan began a breeding program on his own with personal resources and created "supersweet" counterparts of 'Golden Cross' and 'Iochief' hybrids (later known as 'Illini Chief'). In fewer than eight years after his original suggestion he developed a commercially acceptable hybrid that was to transform the sweet corn industry. Further breeding by Emil Wolf of the University of Florida contributed to the success of supersweet maize. Interestingly Laughnan never received personal financial compensation; his acknowledgement by the industry was in the form of a plaque.

Snap Pea

The development of sugary podded peas (known as snap peas) is a Cinderella story (Myers et al., 2001). A thick podded mutation from 'Dark Skin Perfection'; a garden pea, was crossed with a snow pea by Dr. Calvin Lamborn who joined the Gallatin Valley

Seed Company in 1968. Derivations of a sweet, thick podded segregate was named 'Sugar Snap.' Because the pods are sweet both the immature thickened pod and seeds are consumed. It differs from the edible podded snow peas where the pods are thin and only very young pods and seeds are eaten. Snap peas (sometimes called butter peas) were known in the late 19^{th} century and described by Hedrick (1928) but disappeared from the seed trade. The commercialization of 'Sugar Snap' pea was further refined by breeding (mainly for shorter vine type, elimination of strings in the pod suture, and disease resistance); over 33 cultivars were reported in 2001. In 1984 the first stringless cultivars were released and commercial processing of snap peas became a reality. Because of problems with pod moisture, processing is centered in arid regions. Stringless snap pea, now a tremendously successful product, is traceable to a single breeder and the persistence and promotional activities of the Gallatin Valley Seed Company.

Seedless Watermelon

The seedless watermelon is a novel horticultural creation of the great Japanese cytogeneticist Dr. Hitoshi Kihara (1894–1986) based on research in polyploidization via colchicines, hybrid breeding, and the physiology of parthenocarpy (Eigsti, 1989). Seedless watermelons are obtained by planting triploid seed produced from crosses of induced tetraploids and diploids. The triploid seed produced seedless melons when provided with diploid pollenizers. The English version of Kihara's paper was published over 50 years ago (Kihara, 1951) but an earlier paper in Japanese with English summary was published in 1947. The small icebox sized triploid melons are characterized by relative seedlessness, combined with rich flavor. The production of seedless melons for the US trade was promoted by Dr. O.J. Eigsti through the American Seedless Watermelon Corporation which developed a number of adapted triploid hybrids. Although the triploid watermelons had long been popular in Asia, it took about 40 years for seedless melons to become a prominent part of the industry in the United States. At the present time, seedless melon has reached 60% of production and is increasing due to high consumer acceptance and its suitability for fresh sliced fruit (Maynard, 2001).

"Gold" Pineapple

'Smooth Cayenne', the principal world processing pineapple is not well adapted to fresh fruit sales because quality is often poor due to high acidity, poor internal color, uneven ripening and low sugar in winter production. However, the world fresh fruit market has recently exploded with the availability of a new hybrid produced by David D.R. Williams and Calvin H. Oda, plant breeders who worked at the Pineapple Research Institute on the island of Maui in Hawaii. Two selections, one named CO-2 (the initials of Calvin Oda) and the other MD-2 (named after the wife of a senior Del Monte executive in Hawaii) derived from two exceptional parents PRI#58-443 and PRI#5858-1184 were characterized by yellow, low acid flesh, very sweet flavor, and resistance to browning and internal rot (Janick, 2003; Grieg, 2004). MD-2 under the name Del Monte Gold Extra Sweet is now marketed under a number of names. Rarely, if ever, has an industry been so transformed by the introduction of a single new cultivar. A billion dollar industry has been creased as a result of high quality, appearance, and consumer acceptance worldwide.

THE FUTURE

The breeding innovations described above have essentially created new industries. They underscore the concept that unique quality rather than yields per se must be the overriding breeding objective for horticultural crops. These attributes, characterized by quantum advances in quality and consumer friendly traits, make these new cultivars instantly desirable to consumers, and point the way for future directions in horticultural breeding. Innovations of individual breeders combined with further breeding efforts to increase usefulness and adaptation are the key to horticultural progress. It is clear that a way must be found to incorporate consumer satisfaction in the selection process.

Marketing attempts to obscure cultivar identification and change horticultural crops into commodities need to be resisted by the industry.

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Table

Table 1. Horticultural vs agronomic crops.

Characteristic	Horticultural crops	Agronomic crops
Ultimate consumers	Human	Typically animals
Appearance	Important	Non-critical
Taste	Critical/subjective	Non-critical
Final product	Often consumed fresh in living state	Consumed processed or dried
Market type	Choice (non-commodity)	Commodity
Calories	Low density	High density
Vitamins and minerals	High	Low
Price per unit	High	Low
Total value per crop	Relatively low	High
Variability of cvs	High	Low
Breeding objectives	Quality, appearance	High yield, yield stability