

History of Fruit Breeding

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ABSTRACT

Fruit breeding, the genetic improvement of fruit crops, has an ancient tradition that traces to the domestication process. Through the millennia genetic improvement has been achieved by grower selection, first from natural seedling populations and then from seedlings that occurred naturally from grower fields with desirable genotypes fixed by vegetative propagation. In the middle of the 19th century hybridization between elite genotypes were made followed by selection in segregating progeny. Conventional fruit breeding is based on continuous selection of superior phenotypes from genetically variable populations using cycles of hybridization and selection and special techniques such as mutation induction, interspecific hybridization, and backcross breeding. Recently biotechnology techniques have been employed including *in vitro* propagation, embryo rescue, protoplast fusion, marker-assisted selection, and transgenesis.

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INTRODUCTION

Fruit breeding refers to the purposeful genetic improvement of fruit crops through various techniques including selection, hybridization, and molecular techniques. The beginnings of fruit breeding trace to the domestication process in pre-history and antiquity, where useful fruit species were chosen and cultivated (Janick 2005). Throughout the millennia genetic improvement of these fruit species have been achieved by grower selection, first from natural seedling populations and then from grower fields from unique genotypes fixed by vegetative propagation. Spontaneous hybridization between wild races and cultivated clones was critical to the early domestication of fruits.

Much of the world fruit industry is still based on grower selection from chance seedlings as well as mutations (sports) and as a result many fruit species are characterized by a narrow germplasm base. These elite seedlings have unique attributes such as outstanding flavor and texture, high fruitfulness and productivity, but also special problems associated with limited adaptation, and pest and disease susceptibility. Deficiencies in many cases, have been ameliorated through cultural practices to prop them up including the use of rootstocks, insect and disease control practices, growth regulators, and special handling and storage technology. While some fruit and nut crops – fig, date, and almond for example – are little changed from antiquity some have been so transformed by continuous selection and genetic recombination that they are far removed from their wild progenitors. Not until the beginning of the 19th century was selection purposely imposed through cycles of hybridizations and selection. Current progress has been achieved

through intensification of the same forces that have occurred naturally with emphasis on increased adaptability through hardiness, reducing chill requirements, and photoperiod insensitivity, plus resistance to biotic stress. Because many of our fruits are essentially little changed from wild types continued progress can be expected. Molecular techniques hold out the promise of increasing the efficiency of selection through molecular markers and the direct transfer of useful genes into adapted genotypes through recombinant DNA (transgene) technology.

DOMESTICATION

The origins of fruit culture occurred in the Fertile Crescent in the late Neolithic and Bronze Age, about 8000 years ago, a period known as the second Neolithic Revolution that involved the change from villages to urban communities. The evolution of urban centers is associated with the development of a settled agriculture. This coincides with the beginning of fruit culture, which involved a long-term commitment to a unique piece of ground. In the case of the date and olive, a fruit orchard can remain productive for over a century. It is fruit culture that bonds humans to a particular piece of land and may be a link associated with the concept of territoriality, the development of city-states, and eventually nationhood.

Zohary and Spiegel-Roy (1975) proposed that fruit culture, in contrast with mere collection, originated 4000 to 3000 BCE. Although some information before this period is based on archeological remains, much of it is by inference and conjecture. Perhaps the earliest pictorial evidence of fruit growing occurs in a 1 m tall alabaster vessel known as

the Uruk vase found in Jemdet Nasr levels at Uruk that date from about 3000 BCE. Uruk (Erech) is on the Euphrates just north of Basra, Iraq. The imagery from vase base to rim, depicts water at the bottom, cultivated plants (barley and sesame) and domestic animals above, followed by attendants bearing baskets of fruit offerings presented to the Goddess Innana, later known as Istar, in a marriage ceremony to a king (Bahrani 2002). Unfortunately the fruits cannot be identified, but they are large and of various shapes. Predynastic drawings in Egypt depict the date palm.

The development of fruit culture in the Fertile Crescent evolved at two loci: the Tigris-Euphrates civilization of Mesopotamia and the Nile valley culture of Egypt. Information on the ancient origins of fruit culture comes from archaeological remains of fruit, and from pictorial and literary evidence. The high culture of Mesopotamia and Egypt produced a rich art in which fruit is a common motif. A trove of paintings and sculpture, and desiccated remains is found in Egyptian tombs and monuments. The Sumerian discovery of writing in the 3rd millennium BCE, and Egyptian writings somewhat later, inaugurated the literary tradition that survives today as a result of the near indestructibility of the baked clay tablets used for cuneiform script, the wide use of stone carving for hieroglyphics, and the preservation of papyrus in desert tombs. Later infusions of species and technology came from Greece, Persia, Turkey, India, and China. By classical times in Greece and Rome fruit culture had achieved a sophisticated level, not exceeded for over a millennium.

The first fruits crops to be domesticated appear to be the date palm, olive, grape, almond, fig, and pomegranate. Asian temperate pome fruits (apple, pear, quince, medlar) and stone fruits (apricot, cherry, peach, and plum) were fully domesticated by antiquity. Citrus fruits were domesticated early in China but reached the West in waves starting with citron. Tropical Asian fruits (mango and banana) and fruits from the Americas (avocado, papaya, and pineapple) were developed in prehistory. A number of popular fruits were only domesticated in the 18th to 20th centuries including various brambles, vacciniiums, pecan, and kiwifruit, while many fruits, although extensively collected and marketed are in the process of domestication (lingonberry, various cacti, durian). Domestication of fruit crops resulted from selection of elite natural variants with further improvement arising from recombinants produced by natural intercrosses involving selected types. Cultural practices often unique to each crop, such as irrigation, pollination control, grafting, rootstocks, pruning and training, storage, and processing, were developed to extend use, increase productivity, and improve quality.

Fruit domestication and genetic alteration

Fruit crops are characterized by a number of common features. Noteworthy is the obvious appeal of taste which many consider delicious – often a combination of sweetness, acidity and aromatic constituents. The desirable taste of many fruits is a naturally selected trait associated with seed dispersal mediated by mammals. Most fruit crops are highly cross-pollinated, and tree fruits generally have long juvenility and long life. Most importantly, some fruit crops have the ability to propagate vegetatively, by such factors as offshoots, cuttings, or nucellar seed. Subsequent progress in the improvement of fruit crops resulted from continual selection in seedling populations, especially from natural intercrosses among elite clones or with wild or introduced clones, that vastly speeded up the process. This process has been efficacious, and in spite of progress in plant breeding, many grower-selected clones are still being grown.

Domestication of fruits involves a combination of events including species selection, recurrent selection of elite clones, and vegetative propagation combined with horticultural technology such as irrigation in dry climates, pruning and training, pollination in the case of date palm, and storage and processing technology. Genetic changes

associated with domestication of fruits (**Table 1**) include the breakdown of dioecy, loss of self-incompatibility, induction of parthenocarpy and seedlessness, polyploidy and allopolyploidy, loss of toxic substances, ease of vegetative propagation, and loss of spines, thorns, or pubescence. Other changes due to selection include increase in fruit size, increase in sugar content, and increase in storage and shelf life. Factors contributing to genetic improvement include interspecific recombination, polyploidization, and continued selection involving generations of sexual recombinants.

Many fruit crops differ from their wild progenitors by a few characters that have appeared as mutations (**Table 2**). Typically these mutations are not advantageous to the plant in its natural setting as they reduce fitness, but would clearly have been immediately selected by humans. The changes from bitter to sweet seed in almond, and seeded to seedless fruits along with parthenocarpy (banana and plantain, citrus, fig, grape, persimmon, and pineapple) would have negative fitness but very positive selective value. Parthenocarpy has two advantages: it eliminates the need for pollination, and is one path to seedlessness which has proved important in grape, banana, and citrus. In dioecious fruit crops, mutations inducing hermaphroditism (strawberry, grape, and papaya) are associated with domestication. Others mutations associated with domestication include loss of spines (brambles, pineapple, pome fruits, and citrus), loss of fruit pubescence (peach), and changes in growth habit mutations (pome and stone fruits). In many fruit crops, fruit color mutations (sports) have become increasingly important, especially in apple, pear, and grapefruit. Some of these mutations are not heritable because they do not occur in the appropriate meristematic layer.

The development of fruit growing evolved from an interaction of genetic changes and cultivation technology, often unique for each species (Janick 2005). Some idea of how this has occurred can best be inferred from the history of two recent domesticates: cranberry and kiwifruit. What occurred in these crops probably occurred in the past with others, although each crop is unique with its own set of problems and prospects, and each has its own story. Both cranberry and kiwifruit were widely appreciated and entered commerce from wild stands long before domestication. The cranberry had been collected in North America since colonial America, but only became cultivated in the 19th century. Successful cultivation involved developing a series of practices to grow a plant adapted to aquatic conditions. The kiwifruit, a dioecious vine native to China has been appreciated since the 8th century in China and probably much earlier but was never cultivated there. It was introduced to England and North America in the beginning of the 20th century, but New Zealand claims the honor of domestication. While the plant was introduced to England and the United States, the plant languished there, emphasizing the key role of champions. A cultivation system worked out by New Zealand nurserymen and growers involved training and pruning on a trellis, with provision for pollination. The preferred pistillate and staminate clones ('Hayward' and 'Bruno', respectively) were selected from seed introduced into New Zealand from China. After the germplasm was selected, cultivation techniques established, and markets developed, the technology was quickly transferred and kiwifruit became a world fruit crop in less than 25 years.

In both cranberry and kiwifruit, the early elite selections of wild plants were of high quality and could be vegetatively propagated – by cuttings in the case of cranberry and grafting in the case of kiwifruit. Selection, combined with the ability to fix unique combinations by vegetative propagation, was the key breeding technique in these two crops, as in all fruit crops. Breeding work has continued but even after 100 years, the selections made very early still dominate the industry.

In both cranberry and kiwifruit, related species are under consideration as potential new crops. In kiwifruit, the related yellow-fleshed *Actinidia chinensis* has been introduced, and the small-fruited, hardy *A. arguta* (also known

Table 1 Genetic changes associated with domestication and breeding of popular fruits.

Fruit crop	Species (Chromosome no.)	Family	Origin	Flowering in wild species	Changes associated with domestication and breeding
Temperate tree fruits					
Almond	<i>Prunus dulcis</i> $x=8, 2n=16$	Rosaceae	SW Asia	Hermaphroditic, self-incompatible	“Sweet” seed, increased kernel size, self-fertility
Apple	<i>Malus × domestica</i> $x=17, 2n=34, 51$	Rosaceae	Central Asia	Hermaphroditic, self-incompatible	Combination of size aroma, loss of astringency, sweetness, parthenocarpy, triploidy
Apricot	<i>Prunus armeniaca</i> $x=8, 2n=16$	Rosaceae	Central & E. Asia	Hermaphroditic, self-incompatible	Increase fruit size
Cherry–sweet	<i>Prunus avium</i> $x=8, 2n=16$	Rosaceae	Central Europe & W. Asia	Hermaphroditic, self-incompatible	Self-compatibility (recent)
-tart	<i>P. cerasus</i> $x=8, 2n=16, 32$				
Fig	<i>Ficus carica</i> $x=13, 2n=26$	Moraceae	E. Mediterranean basin	Gynodioecious	Parthenocarpy
Loquat	<i>Eriobotrya japonica</i> $x=17, 2n=34, 51$	Rosaceae	China	Hermaphroditic, some incompatibility	Increase seed size, potential for seedless triploids
Olive	<i>Olea europea</i> $x=23, 2n=46$	Oleaceae	Mediterranean basin	Andromonoecious	Increased fruit size, high oil
Peach	<i>Prunus persica</i> $x=8, 2n=16$	Rosaceae	China	Hermaphroditic	Freestone, low chill, fuzzless (nectarine), increased size
Pear	<i>Pyrus communis</i> , <i>P. pyrifolia</i> , <i>P. bretschneiderii</i> , <i>P. ussuriensis</i> $x=17, 2n=34, 51$	Rosaceae	Central and East Asia	Hermaphroditic, self-incompatible	Combination of size, aroma, loss of astringency, sweetness, parthenocarpy, triploidy
Plum	<i>Prunus domestica</i> $x=8, 2n=48$ <i>Prunus salicina</i> $x=8, 2n=16, 32$ <i>Prunus Americana</i> $x=8, 2n=16$	Rosaceae	Europe China North America	Hermaphroditic, Self incompatible	Hexaploid after interspecific hybridization
Subtropical and tropical fruits					
Avocado	<i>Persea americana</i> $x=12, 2n=24$	Lauraceae	Tropical America	Hermaphroditic, synchronous protogynous dicogamy	High oil, smaller seed size
Banana, plantain	<i>Musa sapientum</i>	Musaceae	SE Asia	Monoecious	Seedlessness, parthenocarpy, triploidy
Citrus (orange, mandarin, lemon, lime, pumello, grapefruit)	<i>Citrus</i> spp. $x=9, 2n=18$	Rutaceae	Southeast Asia, China	Hermaphroditic	Nucellar embryony, interspecific hybridization, parthenocarpy
Date palm	<i>Phoenix dactylifera</i> $x=18, 2n=36$	Arecaceae	S. Mediterranean basin	Dioecious	Offshoot production, increased fruit size
Mango	<i>Mangifera indica</i> $x=20, 2n=40$	Anacardiaceae	E. Asia	Hermaphroditic	Nucellar embryony, loss of fibers in fruit
Persimmon	<i>Diospyros kaki</i> $x=15, 2n=90$	Ebenaceae	China	Polygamo- dioecious	Loss of astringency, parthenocarpy
Papaya	<i>Carica papaya</i> $x=9, 2n=18$	Euphorbiaceae	Tropical America	Dioecious	Polygamo-dioecious, reduced fruit size
Pineapple	<i>Ananas comosus</i> $x=25, 2n=50$	Bromeliaceae	Tropical America	Hermaphroditic	Parthenocarpy, seedlessness
Berry and Vine fruits					
Blackberry	<i>Rubus</i> spp. $x=7, 2n=28, 35, 42, 56, 84$	Rosaceae	N. America	Hermaphroditic	Interspecific hybridization, polyploidy, thornlessness
Blueberry	<i>Vaccinium</i> spp.	Ericaceae	N. America	Hermaphroditic	Increased fruit size, interspecific hybridization, polyploidy
Cranberry	<i>Vaccinium macrocarpon</i>	Ericaceae	E. United States	Hermaphroditic	Unchanged
Grape	<i>Vitis vinifera</i> $x=19, 2n=38$	Vitaceae	W. Asia	Dioecious	Hermaphroditic, increased berry size, parthenocarpy
Kiwifruit	<i>Actinidia deliciosa</i> $x=29, 2n=174$ <i>A. sinensis</i> $x=29, 2n=58$	Actinidiaceae	China	Dioecious	Increased fruit size
Lingonberry	<i>Vaccinium vitis-idaea</i>	Ericaceae	Circumboreal	Hermaphroditic	Unchanged
Raspberry	<i>Rubus idaeus</i> , <i>R. occidentalis</i> $x=7, 2n=14$	Rosaceae	Europe, America	Hermaphroditic	Interspecific hybridization, polyploidy
Strawberry	<i>Fragaria × ananassa</i> $x=7, 2n=56$ Other spp. $2n=14, 28$	Rosaceae	Americas	Dioecism	Hermaphroditic, interspecific hybridization

Table 2 Genetic changes associated with domestication in fruit crops.

Breakdown of dioecy:	fig, grape, papaya, strawberry (unchanged, date palm, kiwifruit)
Loss of self-incompatibility:	cherry
Parthenocarpy and seedlessness:	apple, pear, banana, plantain, citrus, fig, grape, persimmon, pineapple
Allopolyploidy:	banana, plantain, blackberry, raspberry, blueberry, citrus, tart cherry, European plum, strawberry
Polyploidy	
Triploidy	banana and plantain, apple, pear
Tetraploidy	tart cherry, raspberry, blackberry, blueberry, kiwifruit (<i>Actinidia sinensis</i>)
Hexaploidy	European plums, kiwifruit (<i>A. deliciosa</i>)
Octaploidy	strawberry
Loss of toxic substances	
“Sweet” seed:	almond
Nonastrigency:	apple, pear, persimmon, pomegranate
Ease of vegetative propagation	
Offshoots:	date palm
Rooting:	apple (rootstock)
Nucellar embryony:	citrus, mango
Loss of spines, thorns, or pubescence:	apple, brambles, citrus, peach, pear, pineapple

as tara fig) is under consideration as a new domesticate and now widely planted in northern home gardens. In the vacciniums, two related crops – blueberry (especially lowbush types in Maine) and lingonberry in Sweden—were also widely appreciated and harvested from the wild, but with remarkably different outcomes. Blueberry had more promise as a commercial fruit than did cranberry or lingonberry because the fruit could be consumed fresh as well as processed and there was greater diversity in a number of species. While the domesticates of cranberry and kiwifruit are little changed from their wild forms, the blueberry has undergone remarkable transformation due to interspecific hybridization and ploidy manipulation. The culture of blueberry was dependent on the understanding that the vacciniums are an acid-loving species and required the ammonium form of nitrogen. Intensive selection and breeding with various species of different ploidy levels transformed this crop into a relatively large industry of wide adaptation. Lingonberry, on the other hand, a large Scandinavia export crop from forest-collection, never became domesticated, probably because there was no shortage of collectable fruit. This crop is still based on merely managed wild plantings.

FRUIT BREEDING

Fruit breeding as an organized activity is a 19th century innovation. Current progress was achieved through intensification of the same forces that have occurred during domestication with increasing emphasis on increased adaptability through hardiness, lowered chill requirement, photoperiod insensitivity, resistance to biotic stress, plant architectural modifications, and selection of color mutations. Molecular techniques hold out the promise of increasing the efficiency of selection through molecular markers and insertion of individual genes through transgene technology.

Early beginnings of fruit breeding technology can be demonstrated in strawberry and pear. The modern strawberry is derived from hybrids between two octoploid ($2n=56$) native American species, both usually dioecious: *F. virginiana* indigenous to the East coast of the North America but reaching Europe in the 17th century, and *F. chiloensis*, native from Alaska to Chile. Hybrids between these two species were produced naturally in Brest, France early in the 18th century when a pistillate clone of the large-fruited *F. chiloensis*, introduced by Amédee François Frézier, a French army officer (and spy) whose family name curiously derives from the French word (fraise) for strawberry, was inter-planted with staminate plants of *F. virginiana*. The new hybrids (now known as *Fragaria ×ananassa* or pineapple strawberry, after their shape and aromatic flavor, initiated the modern strawberry industry. Selection through the years has resulted in tremendous changes as the plant evolved from a predominantly dioecious species with male and female plants into a hermaphroditic species, in

which flowers contained both stamens and pistils. The development of the day neutral character from interspecific crosses has resulted in continuous fruit production and has transformed the industry. Modern breeding has greatly increased fruit size and firmness.

Systematic breeding of European pear was first carried out by Jean Baptiste Van Mons (1765–1842), a Belgian physician, pharmacist, and physicist and an early apostle of selection in plants. He collected clones of pear and sequentially planted (open pollinated) seed of the best material making new selections for eight generations. An early fruit book, *The American Fruit Culturist* (1863) by John J. Thomas (1810–1895) states that the mean time from seed planting to fruiting in the first cycle was 12 to 15 years, 10 to 12 in the second cycle, 8 to 10 by the third, 6 to 8 by the fourth, and 5 by the fifth. By the 8th generation several fruit trees fruited *at the age of four years* (emphasis by the author, presumably based on correspondence of Von Mons). This may be the first example of data on long-term selection in plants. Recent breeding efforts have concentrated on fireblight resistance.

Thomas Andrew Knight (1759–1838) was the first to improve fruits by selection from genetic recombination derived from inter-pollinations of clones. An early proponent of the development of plant improvement through cross breeding and selection he literally initiated the field of fruit breeding. He released a number of improved fruit cultivars (apple and pear, cherry strawberry, redcurrant and strawberry, and cherry, nectarine, and plum). His studies on the effects of pollen in the garden pea on seed characters pre-saged the work of Gregor Mendel carried out 40 years later. He describes dominance and segregation, although he failed to make the brilliant leap of Mendel in relating phenotypic characters to the factors we now know as genes. Gregor Mendel, the father of genetics, was also involved in designing apple and pear breeding programs.

In the United States, fruit breeding became a part of research at the state and federal experiment stations and many breeding programs were initiated throughout the United States.

Practically each state had fruit breeding programs at one time. Fruit breeding also became an activity of the private sector. An American nurseryman, Luther Burbank (1849–1926), was the first to consider fruit breeding as a commercial endeavor, and although he distrusted Mendelism, he was a staunch believer in the evolutionary theories of Darwin. Burbank was also influential in obtaining passage of the Townsend-Purnell Plant Patent Act signed in 1930 which initiated the protection of fruit cultivars. At present private breeders are an important part of breeding efforts in *Prunus* (especially peach and plum), strawberry, and raspberry.

Although organized programs of fruit breeding by universities, state and federal experiment stations have been a major activity since early in the 20th century, the results

have been variable and vary from ineffectual to extraordinarily successful. The peach is an example where breeding efforts have had great impact. For example breeding peaches with low chill requirements as well as increased hardiness has greatly expanded the areas where this crop can be successfully produced. The development of firm fleshed peaches became the basis for a large processing industry in California.

Much of the world fruit industries are still based on grower-selected clones. The reason for the lack of progress of fruit breeding programs is two fold. First, vegetative propagation permits the genetic fixation of naturally occurring variation. Because of the vast populations involved in seedling orchards, the quality of the selected clones over hundreds and even thousands of years of selection is very high. Second, the difficulties and expense inherent in fruit breeding have inhibited long term breeding efforts. Progress from breeding a number of fruit crops, however, has shown significant advances in the second half of the 20th century and selections from controlled crosses are increasingly important in many crops. In apple, although chance seedlings such as 'Delicious' and 'Golden Delicious' have long dominated the world market. 'Fuji', a seedling derived from a Japanese breeding program ('Ralls Janet' × 'Delicious') is now the leading world cultivar.

Hybridization and selection

Selection from sexual recombinants is still the dominant force in the domestication process as well as modern fruit breeding. The isolation of elite selections, combined with mass plantings created a situation where mass selection and recurrent selection could operate naturally. This has recently been confirmed in apple, where elite selections from Kazakhstan are very close to cultivated varieties (Harris *et al.* 2002).

Selection from sexual recombination in apple can be clearly followed in North America, now considered a secondary center of origin (Janick 1996). In colonial America, starting in the 1600s, the apple was imported by immigrants, some as scions but most as seeds from Holland, Germany, France, and the British Isles (Beach 1905). Pioneers were encouraged to plant apples and the requirement for settling Ohio (1787–1788) included that the settler must harvest at least 50 apple or pear trees and 20 peach trees (Morgan and Richards 1993). Apples, once introduced, were carried far into the wilderness by Native Americans, traders, and missionaries and became naturalized. In 1806, Jonathan Chapman (the legendary Johnny Appleseed), distributed apple seeds from cider mills in western Pennsylvania and founded a nursery in West Virginia. The apple flourished in the new territories with the greatest use for hard cider, the distilled product called apple jack, and vinegar for preservation of fruits and vegetables. Many of the imported apple clones were unadapted, and the selection of natural seedlings from orchards became the glory of 19th century American pomology. In 1905, 698 apple cultivars were described in Beach's (1905) *Apples of New York*. In the United States the screening of open-pollinated, chance seedlings resulted in thousands of selections, many of which proved to be outstanding cultivars, including 'Golden Delicious', 'Delicious', 'Jonathan', 'McIntosh', 'Rome Beauty', 'York Imperial', 'Stayman Winesap', 'Yellow Newtown', 'Winesap', 'Rhode Island Greening', 'Northern Spy', and 'Gravenstein'. These unique selections selected from thousands of growers became the starting point for hybridization programs in the early history of apple breeding. 'Golden Delicious' had a profound influence on apple growing in Europe in the 20th century and further proved to be a prepotent parent producing many important new cultivars from breeding efforts (Janick *et al.* 1996).

Differences in tolerance to many pests are observed in any large collection of apples. Immunity to apple scab has been transferred from *Malus floribunda* by backcrossing, but the problem of races has also appeared in some areas.

This places the durability of this gene (*Vf*) in question, although it has held up for many years in the United States (Janick 2002).

Conventional plant breeding based on continuous selection of superior phenotypes from genetically variable populations derived from sexual recombination is powerful because it is evolutionary. Progress can be cumulative with improved individuals continually serving as parents for subsequent cycles of breeding. Thus, genetic improvement has made substantial changes in a number of fruit species when the effort has been well supported and long term.

The objectives of fruit breeding varied with location. In northern locations objectives were based on hardiness. Breeding for apple hardiness is an essential character in the northern US and in Scandinavia. In southern locations low chill requirements received attention. Breeding for low chill has greatly increased the range of peach and nectarine in subtropical areas. Throughout the humid parts of the country disease and pest resistance were important objectives. In the western US, the main characters being selected were firmness and amenability to long distance shipping. Selection for fruit quality, based on flavor, color, and shelf life, and texture was the goal of modern fruit breeding programs but this factor often was sacrificed for appearance and shipping quality. Improved fruit texture has been important in apple and peach. Where processing was important to the industry, processing quality became key. Many processing industries soon came to be dependent on unique cultivars with special qualities such as 'Bartlett' pear. The processing industry of pineapple was long based on a single cultivar. 'Cayenne' and its spineless sport ('Smooth Cayenne') that was uniquely adapted to producing canned slices. However, organoleptic quality is increasingly being considered as key if fruits for the fresh market. A sweeter, yellow-fleshed seedling of pineapple resulting from a hybridization in Hawaii, PRI 73-114 (MD-2) is now being marketed as "Del Monte Gold" and has transforming the world fresh fruit industry because of better fresh fruit quality and appearance that 'Smooth Cayenne'.

BIOTECHNOLOGY AND FRUIT BREEDING

There are a number of restraints to conventional fruit breeding which are especially limiting in tree fruits with their long juvenile period, large plant size, and which are represented by unique, highly-selected heterozygous genotypes. These restraints include: (1) the reliance on naturally occurring variation which may be unavailable, or more likely found in very primitive and unadapted genotypes; (2) restraints due to the inability of the sexual system to incorporate genes from non-related species and especially the inability of the sexual system to incorporate small changes without recombination resulting in the loss of unique combinations; (3) problems with incompatibility and sterility; (4) the randomness of induced mutation; (5) the difficulty of selection in detecting infrequent or rare recombinants, (6) and the dependence of conventional breeding on time to generate cycles of recombination; and space to grow the necessary populations to recover superior recombinants; and resources to be able to select, identify, and evaluate desirable recombinants.

The biotechnological revolution in the last half of the 20th century is based upon novel genetic strategies derived from microbial and molecular techniques including, in vitro propagation, embryo rescue, protoplast fusion, marker-assisted selection and recombinant DNA (transgene) technology. Advances in molecular genetics may overcome some of the limitations to conventional fruit breeding by increasing selection efficiency using molecular markers and by transgene technology whereby individual genes from various sources may be inserted without disturbing unique genetic combinations. Biotechnology has reinvigorated the art and science of fruit breeding. For example, embryo rescue techniques have been a key factor in the breeding of seedless grapes. However, the great hopes for marker-

assisted selection and transgene technology has yet to reach its potential.

Marker-assisted selection

Advances in genomics, the study of the DNA structure of genomes, has led to complete genetic mapping of many crop plants including fruits species. Efforts are underway to map the genomes of many fruit species with special emphasis on the Rosaceae (Folta and Gardiner 2009). Full genomic sequencing in peach, apple, and strawberry has made it possible to locate useful genes include those affecting quantitative traits. The combination of advances in informatics, sequencing technology, and genomics makes it theoretically possible to select on the basis of the genotype instead of the phenotype. This has potential benefits to fruit breeding where the cost of phenotype selection are very high because of the long time necessary for fruiting and the large amounts of land required for each seedling.

Transgene technology

This innovation theoretically offers many advances for fruit breeding because it allows discrete changes to be made of well-adapted genotypes. For example it would be possible to induce such characters as fireblight resistance into 'Bartlett' pear, uniquely suited for processing, without changing any of the quality characters. Progress has already been achieved in incorporating virus resistance in papaya (Gonsalves *et al.* 2006). However, fears of consumer resistance has been a problem when introduced genes are considered from widely divergent species. However, syteny in Rosaceae (Arús *et al.* 2006) suggest that the transfer of genes within the family will partially calm the fears of consumers. However, at the present time it is clear that the future of fruit breeding lies in the use of these new techniques as a tool to enhance but not replace traditional methods.

Patents and the privatization of fruit breeding

In the 20th century most organized fruit breeding programs were carried out with free release of germplasm. The advantages of this practice were cooperation among fruit breeders and especially the sharing of germplasm. However, because fruit breeding turned out to be an expensive activity most experiment stations slowly receded from this activity as the competition among institutions began to be spurred by the funds generated by granting institutions favoring more basic research. In the United States this led to severe decrease in breeding activity. However, the increase in patent protection indicated that fruit breeding could be made self supporting. This was made evident by the large royalties generated by the strawberry breeding program of the University of California. The rise in patent protection has also invigorated a number of private breeding programs.

The situation was made more complex when the concept of club cultivars was developed (Janick 1994). Under this system, with the protection of patents, unique cultivars could be released to a small selection of growers so that quality could be controlled and supply could be limited. Under this system the profits from plant breeding extended to the revenues generated by the fruit crop each year where heretofore it was generated merely by the sale of plants. Under this system, revenue of superior genotypes could be very much extended to the life of the plant itself.

THE FUTURE OF FRUIT BREEDING

Fruit breeding has been in a state of flux because the traditional support by government experiment stations received throughout the world has declined as a reaction to the high costs of long term programs that are necessary. However, the globalization of the fruit industry has underscored the economic value of improved germplasm indicating that sup-

port for fruit breeding needs to be increased. Returns from patents offer one solution to impede the decline in funding and to encourage breeding effort. Patents are essentially a direct tax on the industry to improve breeding and also offer an incentives to breeders when they share in patent royalties. In some countries the costs of foreign patents has encouraged investment in local breeding programs.

The objectives of breeding efforts in the future must be twofold. The most important is to increase quality in order to increase consumption. This is important to reverse the decline in per capita fruit consumption in developed countries. The second effort must be to increase the efficiency with special emphasis on productivity, annual bearing, and pest resistance. However, the future of fruit breeding is crop specific. For example the tremendous advances in seedless table grapes have intensified breeding efforts. In contrast, the breeding of wine grapes is impeded by the association of traditional cultivar name with the name of the wine. As a result the wine industry has not encouraged cultivar change except for clonal selection. Practically no advances have been made in the genetic improvement of banana but there are major projects via international efforts (International Network for the Improvement of Banana and Plantain or INIBAP). The lack of diversity in export banana makes breeding essential due to disease pressure (such as sigatoka) but seedless banana is notorious difficult to hybridize.

Similarly, citrus industry has increased in efforts to produce new seedless, easy-peel clones while the threat of diseases such as hanglongbing (citrus greening) is an upcoming problem that may require a genetic solution. The success of breeding in *Prunus* has encouraged a number of private breeding organizations especially vibrant in peach and plums. Recent studies of a partially stoneless plum described by Luther Burbank suggest that the hard stone might be eliminated in *Prunus* (Callahan *et al.* 2009). Similarly the success of breeding efforts to produce late ripening cherries in British Columbia, Canada has indicated the high economic returns made possible by sustained breeding effort. Apple breeding has produced many new cultivars and the success of 'Fuji' and 'Honeycrisp' has underscored the returns from improved quality. There are large efforts in breeding loquat in China including triploid, seedless clones (Lin *et al.* 2007).

In the case of underutilized or new fruit corps, knowledge of domestication should be used to predict future changes. Thus one might anticipate that in kiwifruit, hermaphroditic mutations would eliminate the need for staminate clones as pollinators, and that fruit skin mutations or breeding could lead to non-pubescent clones, with more attractive and more edible fruit surface. The use of interspecific hybridization should lead to improvement *Prunus* and *Rubus*. A number of tropical fruits are candidates for commercialization, provided postharvest technology can be improved. One of the likely candidates for domestication is pitaya (species of *Selenicereus*, *Hylocereus*, and *Cereus*), an extremely attractive fruit of columnar cactus, but breeding efforts to improve quality is required, since many selections have been insipid (Mizrahi *et al.* 2002).

Most fruit crops are not far removed from wild species, some perhaps by only a few generations, so that in most cases continued progress should be possible. Yet, many of our fruit cultivars are ancient and based on grower-selected seedlings and somatic mutations. In conventional breeding systems, elite clones are selected followed by fixation by vegetative propagation, and these provide the raw material for subsequent cycles of hybridization and selection. The development of fruit culture is based on an interaction between improved clones and cultural practices. Deficiencies are compensated by such techniques as artificial pollination, the use of disease-resistant and size controlling rootstocks, extensive methods of disease control, involving complex schedules of pesticide application, the control of fruit size and annual bearing by manual and chemical fruit and flower thinning, the control of fruit abscission with growth regulators, and extensive pruning and training systems. The

dilemma is to determine if breeding emphasis should concentrate on quality for consumers or rather to overcome production problems for growers by genetic solution. Obviously both must be objectives in modern breeding programs. Because fruit breeding depends on genetic diversity the development of germplasm resources must be strengthened by collections *in situ*. In some cases these collections suggest that a number of fruits that have been ignored, such as quince, are candidates for increased breeding efforts.

Finally advances in biotechnology must be attached to breeding efforts. Marker assisted selection could offer significant help in disease and pest resistance breeding but much genetic work must still be pursued to locate these quality traits. Similarly transgene technology could find a place in fruit breeding and the example of virus resistant papaya has demonstrated that success can be achieved. However, the rationale for transgene technology assumes that the present germplasm is optimum. This is a conservative approach somewhat similar to backcross breeding but it is true that many high quality fruits are difficult to replace.

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