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The Origins of Fruits, Fruit Growing, and Fruit Breeding

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I. INTRODUCTION

Crop plants are our greatest heritage from prehistory (Harlan 1992; Diamond 2002). How, where, and when the domestication of crops plants occurred is slowly becoming revealed although not completely understood (Camp et al. 1957; Smartt and Simmonds 1995; Gepts 2004). In some cases, the genetic distance between wild and domestic plants is so great, maize and crucifers, for example, that their origins are obscure. The origins of the ancient grains (wheat, maize, rice, and sorghum) and pulses (sesame and lentil) domesticated in Neolithic times have been the subject of intense interest and the puzzle is being solved with the new evidence based on molecular biology (Gepts 2003).

In the late Neolithic and Bronze Ages between 6000 and 3000 BCE, the ancient Mediterranean fruits (date, olive, grape, fig, sycomore fig, and pomegranate) were domesticated (Zohary and Spiegel-Roy 1975). Fruits such as citrus, banana, various pome fruits (apple, pear, quince, medlar) and stone fruits (almond, apricot, cherry, peach, and plum) were domesticated in Central and East Asia and reached the West in antiquity. A number of fruits and nuts were domesticated only in the 19th and 20th centuries (blueberry, blackberry, pecan, and kiwifruit). Some well-known fruits, although extensively collected, remain to be domesticated, such as lingonberry, various cacti such as pitaya, Brazilnut, and durian. This review will consider the various technologies inherent in the origins of some well-known fruits, emphasizing factors that led to domestication and the genetic changes that ensued.

A. The Origins of Agriculture

The change from food collection to food production requires the domestication of plants and animals. This involves a series of technologies that involves choice of species, bringing them into management or cultivation, genetic alteration brought about by selection—both conscious and unconscious—and the discovery of specific practices (pollination, training, processing) often unique for each crop. Although precise origins are obscure, the first archeological evidence for a developed agriculture is found in Mesopotamia and shortly after in the Nile and Indus Valleys. Evidence suggests a later development in China, Central America, East and West Africa and, perhaps, New Guinea (Diamond 1997, 2002). There is some dispute as to whether the origins of agriculture were completely independent. Those who favor independent invention of agriculture emphasize the adaptability of humans for independent discovery and provide as evidence the domestication of different grains in various parts of the world—wheat in the Mid-East, sorghum in Africa, rice in Asia, and maize in the Americas (Harlan 1992). However, an argument can be made for diffusion based upon the sequential development of agriculture (Carter 1977). Although the diffusion of agricultural information has been ignored in favor of independent development, recent evidence on the domestication of the dog suggests that diffusion of agricultural information may indeed be involved (Leonard et al. 2002; Savolainen et al. 2002). The ancient Neolithic trade in flint suggests diffusion was important to the transfer of ancient technology. It seems doubtful that the complex technology involved in such techniques as fire making, production of weapons like the bow and arrow, ceramic making, and metal working are truly independent discoveries. Evidence of diffusion in the history of agricultural technology includes irrigation technology from Mesopotamia, silkworm technology from China, and horse technology from Central Asia.

In the Mid-East, the change from scavenging, collecting, and hunting to agriculture that occurred about 10 to 12 thousand years ago is rather sudden. Taking into consideration the long history of mankind, the term Neolithic Revolution has been coined for this "rapid" transformation. The domestication of crops was preceded by animal domestication, with Nomadism the link between animal agriculture and farming. The first crops domesticated in the Middle East include cereals, such as barley, emmer, and spelt, and pulse crops such as sesame and lentil. Cereal and pulse culture require a number of technologies, including land preparation, planting, harvesting, threshing, and seed storage, that form the basis of crop agriculture. Because the seed is produced following genetic recombination, thousands of generations occur in which selection, conscious and unconscious, can bring about large changes. The enormous morphological changes that can occur with selection associated with domestication is wonderfully apparent with the myriad breeds of dog, all shown to be domesticated from the wolf, and the changes in *Brassica oleracea* (broccoli, Brussels sprouts, cabbage, cauliflower), and *Beta vulgaris* (table beet, sugar beet, and chard).

B. Origins of Fruit Culture in the Fertile Crescent

Childe (1958) proposed that a second Neolithic Revolution coinciding with the Bronze Age occurred between 6000 and 3000 BCE involving 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.

Information on the ancient origins of fruit culture comes from archeological 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 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.

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 (Fig. 8.1). Uruk (Erech) is on the Euphrates just north of Basra, Iraq. The imagery depicts water at the bottom of the vase, followed by plants (barley and sesame) and domestic animals, and men bearing baskets of fruit with offerings presented to a female, perhaps the Goddess Innana, later known as Istar (Bahrani 2002). Unfortunately, the fruits cannot be identified, but they tend to be large and of various shapes. Predynastic drawings of fruit trees in Egypt depict the date palm (Fig. 8.2).

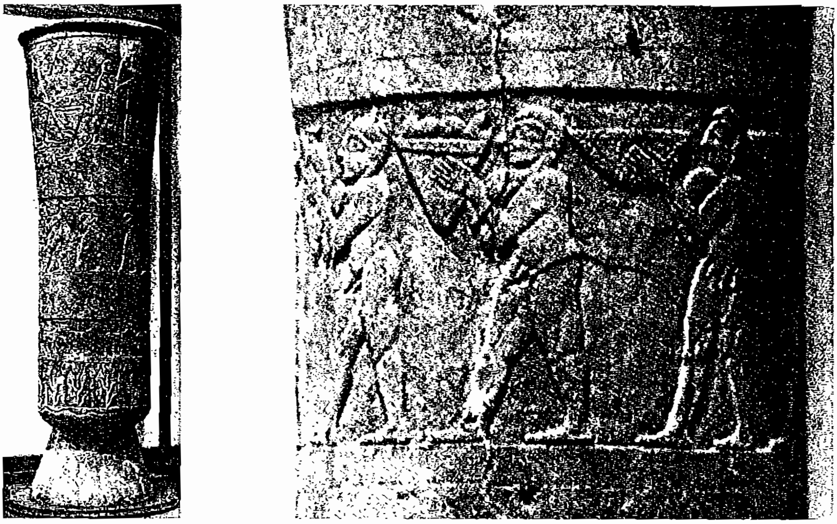


Fig. 8.1. The Uruk vase, late 4th millennium BCE, showing attendants bearing fruit in a wedding ceremony, probably between a priest king and the goddess Innana (Istar). Source: Pollock 1999.

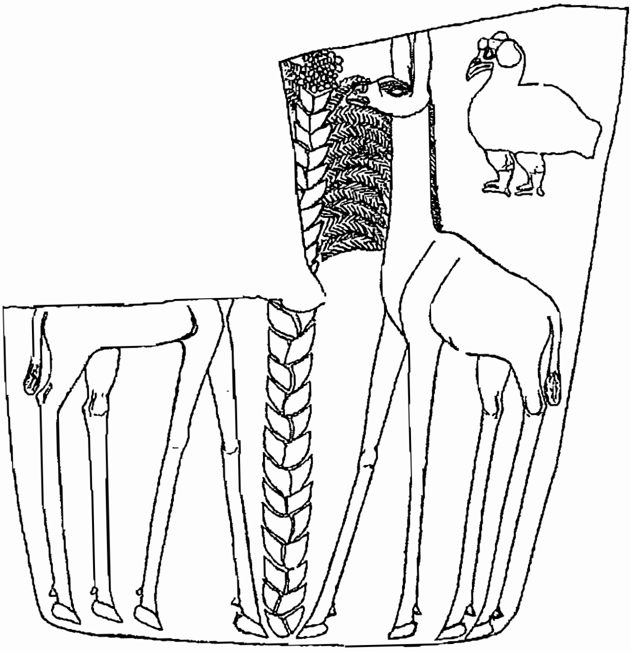


Fig. 8.2. Predynastic representation of date palm flanked by gazelle in Egypt, 4000–3000 BCE. Source: Singer 1958, Fig. 67.

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. Later infusions of species and technology are 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.

II. THE HORTICULTURAL ARTS

Fruit growing involves a more complicated technology than the cultivation of herbaceous annuals such as cereals or pulse crops. Tree crop culture requires a long-term series of horticultural "craft secrets" more or less unique for each species. These include selection of unique clones, vegetative propagation (use of offshoots, cuttings, grafting), continuous irrigation in dry climates, pruning and training, pollination, harvesting, storage, and processing. The cycle of fruit growing is often a year-round activity, and must involve orchard establishment in anticipation of production, which may only ensue after a number of years. Current additions to the technology of fruit growing include the use of dwarfing rootstocks, growth regulators, disease and pest control, long-term storage, protected cultivation, and biotechnology. Here we examine the Neolithic and Bronze Age origins of technologies essential to fruit growing.

A. Species Selection

The first cultivated fruits must have been indigenous species that had obvious human value. This is clearly seen in Egypt where the indigenous date palm was the earliest species cultivated, followed by a succession of introduced fruits such as the sycomore fig and pomegranate (Table 8.1). The earliest fruit culture in Mesopotamia included the date and olive (4000 BCE), grape, fig, and pomegranate (3rd millennium BCE). Later fruits introductions, based on literary sources, include the apple, pear, quince, and medlar (Postgate 1987). The small-fruited *Malus orientalis* and *Pyrus syriaca* are indigenous to the Fertile Crescent, but these were probably not the forerunners of domesticated apple and pear that were introduced from Western Asia probably via Persia. Contacts between East and West date from as early as 1000 BCE as evidenced by silk strands on Egyptian mummies, but intensified with the incursions of Alexander the Great (356–323 BCE). Thus, by the time of the Greek and Roman eras there was an infusion of Central and East Asian fruits, including the citron and a great variety of stone fruits, including almond, apricot, cherry, peach, and plum. In the Age of Exploration in the late 15th and 16th cen-

Table 8.1. Evidence for fruit crops in Egypt. Source: Janick (2002a) adapted from Darby et al. (1976).

Fruit crop	Binomial	Earliest record (dynasty or period)	Type of evidence
Date palm	*Phoenix dactylifera*	Pre-dynastic	Archeological
Doum palm	*Hyphaene thebaica*	Pre-dynastic	Archeological
Sycomore fig	*Ficus sycomorus*	Pre-dynastic	Archeological
Jujube (Christ's thorn)	*Ziziphus spina-Christi*	I (Old Kingdom)	Archeological
Fig	*Ficus carica*	II (Old Kingdom)	Artistic
Grape	*Vitis vinifera*	II (Old Kingdom)	Archeological
Hegelig	*Balanites aegyptiaca*	III (Old Kingdom)	Archeological
Persea (lebakh)	*Mimusops shimperi*	III (Old Kingdom)	Archeological
Argun palm	*Medemia argun*	V (Old Kingdom)	Archeological
Carob	*Ceratonia siliqua*	XII (Middle Kingdom)	Archeological
Pomegranate	*Punica granatum*	XII (Middle Kingdom)	Archeological
Egyptian plum	*Cordia myxa*	XVIII (New Kingdom)	Archeological
Olive	*Olea europea*	XVIII (New Kingdom)	Archeological
Apple	*Malus* ×*domestica*	XVIII (New Kingdom)	Literary
Peach	*Prunus persica*	Graeco-Roman	Archeological
Pear	*Pyrus communis*	Graeco-Roman	Archeological
Cherry	*Prunus avium; P. cerasus*	5 BCE	Literary
Citron	*Citrus medica*	2nd century CE	Literary

turies, a great exchange takes place as fruits of the Americas, including the pineapple, cacao, American species of strawberries, and papaya and the fruit-bearing solanums such as tomato and pepper reach Europe, Asia, and Africa, while East Asian fruits, such as the banana, mango, and persimmon reach the Americas. Some East Asian fruits, such as kiwifruit, are relatively recent introductions, and a great many tropical fruits of both Asia (durian, mangosteen, salaak) and the Americas (passion fruit, sapote) are still not extensively commercialized.

B. Vegetative Propagation

Although most fruit species can be produced from seed (except, of course, seedless clones), this is usually an inappropriate technique. Most fruit species are highly cross-pollinated (peach is an exception) and therefore highly heterozygous. Thus, open-pollinated seedlings will consist of a highly heterogeneous mixture of fruit types, most of which will be inferior to the selected clone. Furthermore, there is a long juvenile period in trees grown from seed. The Hebrew Bible is full of references to degenerate plants that clearly indicate that the ancients were aware of the hazards of seed-propagated fruit crops. Thus, the basis of most fruit cultivation is vegetative propagation of unique phenotypes (elite clones) with subsequent improvement based on sexual recombination of elites. Vegetative propagation is accomplished from offshoots in date, layers in grape, and cuttings in olive and fig and runners in strawberry. Fruit crops that can be easily propagated vegetatively have been considered preadapted for domestication by Zohary and Spiegel-Roy (1975). However, many temperate fruits (apple and pear) do not propagate easily by layers or cuttings and are currently multiplied by graftage.

Grafting is ancient (Vöchting 1892; Mendel 1953) and Childe (1958) has speculated that it was known before 3000 BCE. Although both root and shoot grafting occurs naturally (Fig. 8.3), the technology is not obvious and must be considered one of the horticultural craft secrets. We know this because much of the Roman writings on grafting often confuse which species are graft-compatible. Pliny describes a number of ludicrous combinations, such as apple on plane tree, suggesting that he was not writing from real experience.

Recently, a cuneiform description of budwood importation for grape has been uncovered from Mari, Mesopotamia (Harris et al. 2002) dated to about 1800 BCE, which confirms Childe's (1958) speculation on the antiquity of graftage. The next written evidence of grafting comes from the school of Hippocrates (Pseudo-Hippocrates, about 450 BCE) that discusses the graft union (Meyer 1854), but this reference implies that the technique was very much older. There is speculation that grafting was known in China as early as 1560 BCE (Nagy et al. 1977; Hartmann et al. 1997) but the earliest definitive evidence for grafting occurs in the 1st century BCE of the bottle gourd (*Lagenaria*) in *The Book of Fan Sheng*, while fruit grafting is referred to in *Qi Min Yao Suj*, written by Jia Simiao in the 6th century CE (Guangshu Liu, pers. commun.). Grafting is discussed in detail by Theophrastus, and all the Roman agricultural writers, including Cato, Virgil, Columella, and Pliny, describe it in detail. Grafting is accurately pictured in mosaics in the 3rd century CE (Fig. 8.4). Grafting is not specifically mentioned in the Hebrew Bible but is inferred based on Jewish writings [Mishna in Order Zeraim (seeds), tractate Kilaim written ca. 3rd century CE] interpreting prohibitions against mixing of seeds in Leviticus 19:19. Grafting of olive is found in the Christian Bible (Romans 11:17&24), 1st century):

> *And if some of the branches be broken off, and you, being a wild olive tree, were grafted in among them, and with them became a partaker of the root and fatness of the olive tree do not boast against the branches. . . . But if you boast, remember that you do not support the root, but the root supports you. . . . For if you were cut out of the olive tree which is wild by*

nature, and were grafted contrary to nature into a cultivated olive tree, how much more shall these, which are natural branches, be grafted into their own olive tree.

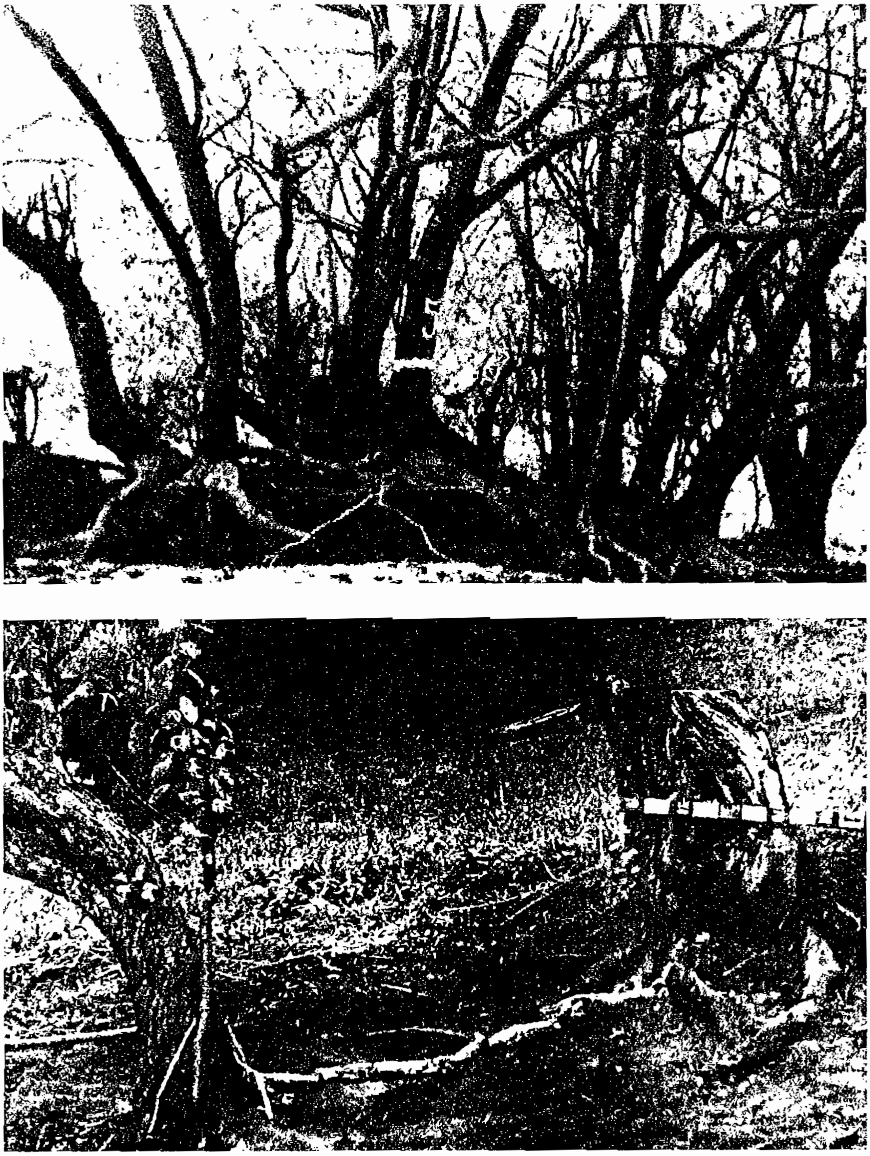


Fig. 8.3. Natural root grafting in wild apple trees. Source: Dzhangaliev 2003.

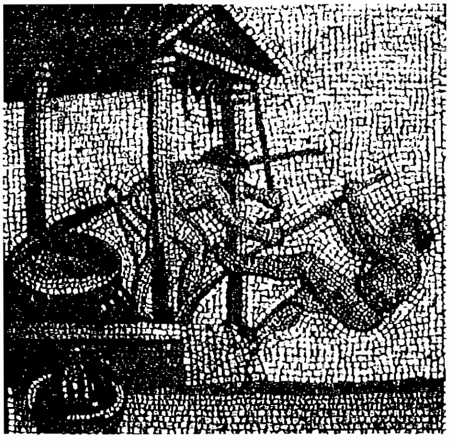


Fig. 8.4. Grafting, fruit harvest, and juice extraction portrayed in Roman mosaic 3rd century CE. Source: St. Roman-en-gal, Vienne, France.

The development of graftage must have influenced the movement of temperate fruits, such as the apple, from Central Asia to Europe. Grafting is then a pivotal technology in the history of temperate fruits. Precisely when and where detached scion grafting, which made possible the domestication of a new range of fruit trees, was invented is not clear. Barrie Juniper (pers. commun.) has suggested that the initiation of grafting was outside the area of Mediterranean horticulture and was probably introduced from the east, perhaps Persia.

Fruit growing has long been associated with clonal propagation of unique wild seedlings with subsequent evolutionary progress derived from intercrosses of superior clones plus intercrosses with wild races (Zohary and Spiegel-Roy 1975), leading to very high seedling diversity. In a number of species, almond for example, the high diversity of wild clones include segregates that are close to domestic types. This would explain why the ecological adaptation of classic Mediterranean fruits has not exceeded the requirements of their wild ancestors. In most cases, present-day fruit cultivars have undergone far fewer sexual cycles than cereal or pulse crops and some may be only a few generations from wild clones. Thus, many of these crops have not diverged from their progenitors, in contrast to cereals in which selection has operated for thousands of generations. This has been confirmed in apples, where present-day cultivars are not distinct from elite selections obtained from wild stands in Alma Alta, Kazakhstan (Harris et al. 2002; Forsline et al. 2003).

C. Pollination and Fruit Set

Practically all fruit species are naturally outcrossing with variability maintained by natural barriers to avoid self-fertilization. These include dioecy (carob, date palm, grape, fig, strawberry, kiwifruit, papaya), self-incompatibility (pome and stone fruits), and dichogamy, the uneven maturation and receptivity of pistils and stamens (avocado, lychee). In some fruits, cross-pollination is based on unique adaptation with insects (fig, sycomore fig) or birds (pineapple).

In dioecious species, accommodation for pollination is necessary. It would be immediately obvious that staminate clones would be non-fruiting. Mass plantings of vegetatively propagated elite pistillate clones would bear few fruit and require either a limited number of staminate plants, proximity to wild pollenizers, or artificial pollination.

This limitation to productivity was solved in various ways, some genetic, some cultural, in different fruit crops. In date palms, early farmers discovered artificial pollination, and this is clearly illustrated in

Assyrian bas reliefs (Fig. 8.5), with the practice codified in the Laws of Hammurabi, ca. 1750 BCE (Roth 2000):

> *§64. If a man give his orchard to a gardener to pollinate (the date palms), as long as the gardener is in possession of the orchard, he shall give to the owner of the orchard two thirds of the yield of the orchard, and he himself shall take one third.*
>
> *§65 If the gardener does not pollinate the (date palms in the) orchard and thus diminishes the yield, the gardener (shall measure and deliver) a yield of the orchard to (the owner of the orchard in accordance with) his neighbor's yield.*

In fig, the presence of the wild monoecious caprifig that harbored the pollinating blastid fig moth (caprification) was understood as essential for fig production by Theophrastus (371–287 BCE), but later selection for parthenocarpy eliminated this practice. In grape, strawberry, and papaya, domestication exploited mutations from dioecism to hermaphroditism and, in some figs and grapes, parthenocarpy reduced the requirement for pollination altogether. In the sycomore fig, introduced to Egypt without the pollinating fig wasp, artificial wounding to ripen parthenocarpic fruit was the solution. In apple and pear, which are self-incompatible and insect pollinated, the problem was solved with the introduction of bees to facilitate cross-pollination along with inter-

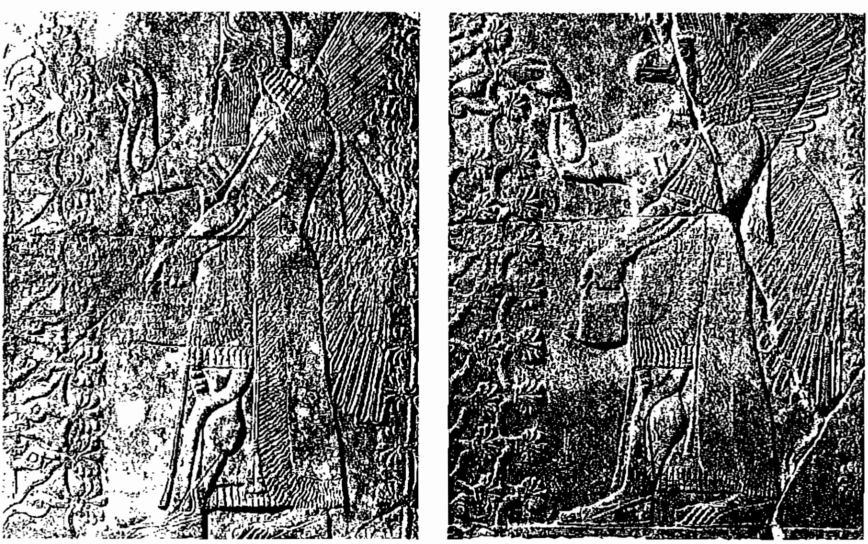


Fig. 8.5. Date palm pollination depicted in Assyrian bas-reliefs. Source: Paley 1976.

planting of pollenizers. In recent times, pollenizers for self-incompatible sweet cherry were eliminated by introducing self-compatible mutations.

D. Irrigation

The civilizations that developed in the arid climates of the Fertile Crescent are dominated by large rivers—the Nile in Egypt and the Tigris and Euphrates in Mesopotamia. In Egypt the regular inundations of the Nile, rising in July until the middle of October, followed by rapid subsidence, permitted a unique horticulture based on basin irrigation (Janick 2002a). The system involved a system of dikes to retain the flood and encourage infiltration into the soil. Earthen banks, parallel to the river together with intersecting banks, created a checkerboard of dike-enclosed areas, between 400 and 1600 ha each. Canals led the water to areas difficult to flood. The flood waters ran through a series of regulated sluices into each basin, flooding the land to a depth of 0.3 to 1.8 m. The water could be held for a month or more; the surplus was drained to a lower level and then returned to canals that emptied into the Nile. The advantage of basin irrigation was that no further irrigation was needed for a winter crop of grain, and the silt, rich in organic matter and phosphates, made fertilization unnecessary.

With fruit tree culture, permanent ponds were an important innovation and the ornamental gardens enclosing ponds testify to their widespread use by the wealthy. In addition, shallow wells, 4 to 35 m in depth, were dug to be replaced later by deeper artesian wells up to 380 m deep. The culture of fruit crops demands constant and controlled irrigation during the spring and summer drought. At first, irrigation was carried out manually with pots dipped in the rivers, carried on the shoulders with yokes, and poured into field channels. By the time of the New Kingdom (1500 to 1100 BCE), the shaduf, a balanced counterpoise, became the irrigating mechanism for gardens. Later, water lifting techniques included Archimedes' screw, the sakieh or chain of pots, and siphons (Fig. 8.6).

In Mesopotamia, cultivation in the Tigris-Euphrates flood plain is and always has been dependent on irrigation, and the management of this technology may have been the impetus for the development of nation-states (Pollock 1999). Irrigation started as small-scale projects but eventually increased in complexity and involved centralized control. The creation of state-controlled irrigation led to a strong central authority requiring conscripted service (corvée) for canal maintenance. The Laws of Hammurrabi richly describe a legal system enforced to maintain the integrity of an irrigated agriculture:

§53 If a man neglects to reinforce the embankment of the irrigation canal of his field and does not reinforce its embankment, and then a breach opens in its embankment and allows the water to carry away the common irrigated area, the man in whose embankment the breach opened shall replace the grain whose loss he caused.

§54 If he cannot replace the grain, they shall sell him and his property, and the residents of the common irrigated area whose grain crops the water carried away shall divide the proceeds.

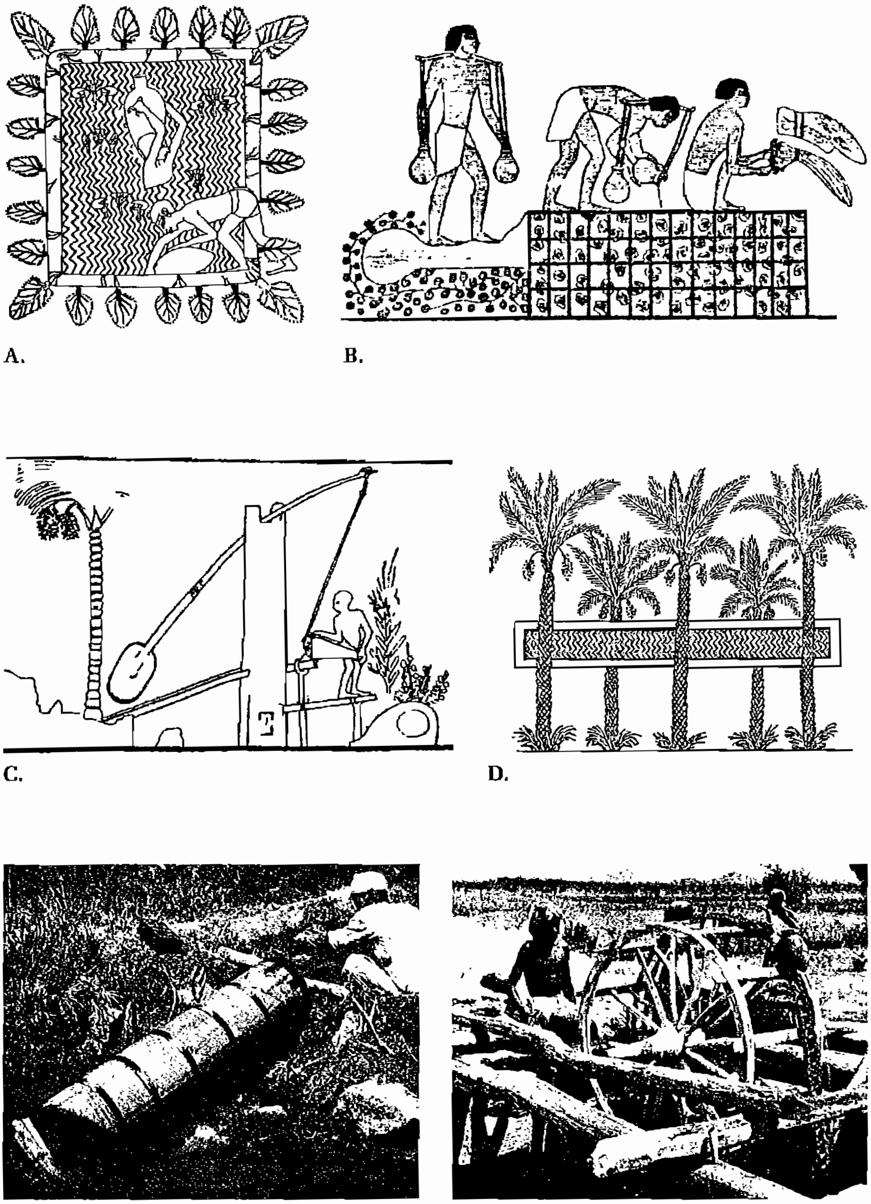
§55 If a man open the branch of the canal of irrigation and negligently allows the water to carry away his neighbor's field, he shall measure and deliver grain in accordance with his neighbor's yield.

§56 If a man opens an irrigation gate and releases waters and thereby he allows the water to carry away whatever work has been done in his neighbor's field, he shall measure and deliver 3,000 sila of grain per 18 iku of field.

Because of the braiding character of the Euphrates, short canals about 1 km in length could be dug from the numerous river channels and managed by local groups (Pollock 1999). The natural flow of the river and overflow resulted in natural levees, and in the process the riverbed was gradually raised until it flowed above the level of the surrounding land. This made it relatively easy to cut irrigation channels through the natural levee and allow the water to flow by gravity to cultivated fields and gardens. The natural levees with their good drainage were prized for fruit tree cultivation, but irrigation required water lifting technology. The natural vegetation of the alluvial plain provided pasturage for sheep and goats; it was once home to game animals such as jackals, lions, gazelles, onagers, and hyenas, as illustrated in the hunting scenes in Babylonian bas reliefs now hunted to extinction. Long-term irrigation, however, led to unintended consequences and today much of the area is a vast salty waste as a result of salinization.

E. Pruning and Training

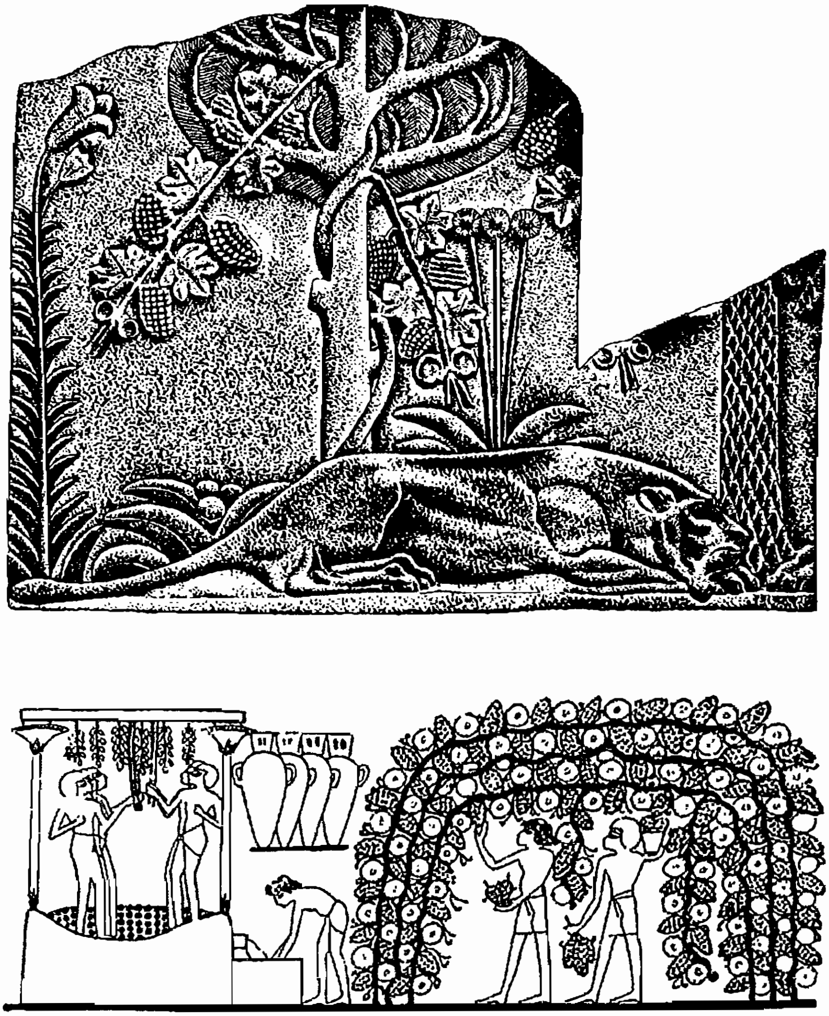
The art of fruit growing is associated with physical techniques to control the shape, size, and direction of plant growth. These include the orientation of the plant in space (training) and judicious removal of plant parts (pruning). In date palm culture the removal of senescing leaves, necessary for both pollination and harvest, is probably the basis of the pruning technique. The dead leaves had a wide variety of uses for shade and basketry. In the case of the grape, vine pruning is essential to control both flowering and yield and to increase fruit quality. Early Babylonian bas reliefs show grapes growing on trees, and the use of arbors



A. B. C. D. E. F.

Fig. 8.6. Development of irrigation technology. A. drawing water from pots, ca 1450 BCE, B. irrigation and harvesting in a vegetable garden using yoke, C. irrigation of a date palm orchard by a shaduf, D. date palm with water-storage pond, E. Archimedes screw, F. sakieh, a chain of pots. Source: Singer et al. 1954 (A–D), British Museum (E), FAO (F.)

and pergolas for grape is well illustrated in late Egyptian paintings (Fig. 8.7). In the Mideast, an ancient training method involved severe pruning whereby the plant was pruned in the fall and mounded with soil over the winter to avoid cold injury.



A.

B.

Fig. 8.7. Training of grape. A. Vine climbing a cypress tree in an Assyrian garden. B. Grapes collected from a round arbor from a tomb at Thebes, Egypt, ca 1500 BCE. Source: Singer et al. 1954.

F. Processing and Storage

Most of our important domesticated fruits are delicious in the mature state and indeed this is one of the chief virtues of fruit crops. However, this is not the case with all fruits. The olive, in particular, is bitter and inedible, even in the mature state, and some wild species are toxic. Clearly, the key technology must have been derived from the ameliorating practice of soaking the fruits to make them less bitter. Many primitive societies such as Amerinds with cassava and Australian aborigines with *Pandanas* (Crib and Crib 1976], independently came to their detoxification techniques (Johns and Kubo 1988). Extraction of oil by pressing the fruit transformed olives into the most widely grown fruit crop in the ancient world. The oil was widely used in cooking and illumination; the flame produced from olive oil has a very high luminosity. Fruit crops grown for their fruit or seed oil also include oilpalm and avocado (used for soap in Brazil).

Most fruits have a short life after harvest so that processing is required to have a year-round supply. The perishability of many fruits is one of the limiting factors of commercialization. In the case of the date, the high sugar content of the dried fruit permits extended storage, and dried grapes (raisins) have long been prized for their concentrated sweetness and long storage. Sun drying of many types of *Prunus*, especially highly sugared plums (prunes) and apricots was facilitated by slicing fruits. The conservation of fruits as jams and preserves was based on the addition of sucrose, a substance unknown until the technology of sugarcane production and processing was developed in the Middle Ages. Some wild fruits, such as lingonberry in Nordic countries have long been collected and stored as preserves. The preservation of fruits by heat (canning) was a 19th century technology developed by Nicolas Appert (1750–1841) as a response to the British blockade of France during the Napoleonic wars. Quick freezing and later freeze drying are 20th century technologies.

In more temperate climates, fruit life could be extended by common storage in caves or basements. Caves in Cappadocia (Turkey) maintain a temperature of 12.8°C and are still used to store lemons. The modern transformation of this technique led to refrigerated storage and low oxygen storage (controlled-atmosphere) storage.

The transformation of fruit juice to an alcoholic product (wine), along with bread making, is a Neolithic discovery. Beer making probably predated wine making. This leap into Bronze-age biotechnology was facilitated by the ubiquitous presence of yeast spores. Although wine can be made from various fruits, the choice species is grape, probably because of its combination of sugars, acids, and tannins. At present, the greatest use of grapes is for wine manufacture. In the East, salting and fermentation technologies were developed as a means of whole fruit storage. A few tropical fruits (e.g., plantain and breadfruit) are staple starch crops and require cooking.

III. ORIGIN, DOMESTICATION, AND EARLY CULTURE OF FRUIT CROPS

The origin and changes associated with domestication of fruits in this review are summarized in Table 8.2.

A. Mediterranean Fruits

1. Date Palm. The date palm (*Phoenix dactilifera*, Arecaceae) is a dioecious palm, thought to be indigenous from Northern Africa through the Arabian peninsula to northern India (Goor and Nurock 1968; Zohary and Spiegel-Roy 1975; Smartt and Simmonds 1995). In antiquity, the date palm was esteemed from India through North Africa for its sweet fruit consumed fresh or dried, for its valuable wood and leaves, and for its long life. As a result of its many virtues, the date was transformed into a sacred tree, symbolically referred to in Babylonian and Assyrian iconography. It may have been the first cultivated fruit and was well-established in the Middle East during the Bronze Age. The precise origin of the cultivated date is open to conjecture. Vavilov considered the origin of the date to be the mountains of northeastern Africa in Ethiopia and Eritrea but there is evidence that the first cultivation occurred in the Lower Mesopotamian Basin. Archeological evidence places date stones in the Ubaidian horizon (about 4000 BCE) in Eridu, lower Mesopotamia. A predynastic representation of a palm tree (perhaps a date) with gazelles has been dated 4000 to 3000 BCE (Fig. 8.2).

The date palm is adapted to long, extremely hot summers with little rain and low humidity from pollination to harvest but requires a source of underground moisture. All cultivated dates set fruit only in dry desert conditions, in contrast to a number of wild species which do not produce suckers and may be adapted to rainy conditions. Since the plant is a monocot and lacks a deep root system, irrigation is essential. An Arab proverb describes the date palm as "its feet in running water and its head in the fire of the sky."

The cultivated date palm is easily propagated from seed and, unlike its wild relative, can be vegetatively propagated from offshoots (suckers)

Table 8.2. Origin and changes associated with domestication of various fruit crops.

Fruit crop	Species (Chromosome no.)	Family	Origin	Reproduction of wild species	Changes associated with domestication
Mediterranean Fruits					
Date palm	*Phoenix dactilifera* $x=18$, $2n=36$	Arecaceae	S. Mediterranean basin	Dioecious	Offshoot production, increased fruit size
Fig—common	*Ficus carica* $x=13$, $2n=26$	Moraceae	E. Mediterranean basin	Gynodioecious	Parthenocarpy
Fig—sycomore	*Ficus sycomorus*	Moraceae	East	Monoecious	Parthenocarpy
Grape	*Vitis vinifera* $x=19$, $2n=38$	Vitaceae	W. Asia	Dioecious	Hermaphroditic, increased berry size, parthenocarpy
Olive	*Olea europea* $x=23$, $2n=46$	Oleaceae	Mediterranean basin	Andromonecious	Increased fruit size, high oil
Pomegranate	*Punica granatum*	Punicaceae	W. Asia	Hermaphroditic	Increased fruit size, sweetness
Asian & European Fruits					
Pome Fruits					
Apple	*Malus* × *domestica* $x=17$, $2n=34, 51$	Rosaceae	Central Asia	Hermaphroditic, self-incompatible	Combination of size aroma, loss of astringency, sweetness, parthenocarpy, triploidy
Pear—European	*Pyrus communis* $x=17$, $2n=34, 51$	Rosaceae	Central Asia	Hermaphroditic, self-incompatible	Combination of size, aroma, loss of astringency, sweetness, parthenocarpy, triploidy
Pyrus—Asian	*Pyrus pyrifolia* *P. bretscheiderii* *P. ussuriensies* $x=17$, $2n=34, 51$	Rosaceae	E. Asia	Hermaphroditic, self-incompatible	Combination of size, aroma, loss of astringency, sweetness, parthenicarpy, triploidy

(*continued*)

Table 8.2. *(Continued)*

Stone Fruits					
Almond	*Prunus dulcis* $x=8$, $2n=16$	Rosaceae	S.W. Asia	Hermaphroditic, self-incompatible	"Sweet" seed, increased kernel size, self-fertility
Apricot	*Prunus armeniaca* $x=8$, $2n=16$	Rosaceae	Central & E. Asia	Hermaphroditic, self-incompatible	Increase fruit size
Cherry—sweet	*Prunus avium* $x=8$, $2n=16$	Rosaceae	Central Europe & W. Asia	Hermaphroditic, self-incompatible	Self-compatibility (recent)
Cherry—tart	*Prunus cerasus* $x=8$, $2n=16$, 32	Rosaceae	W. Asia	Hermaphroditic, self-incompatible	Tetraploidy after interspecific hybridization
Plum—European	*Prunus domestica* $x=8$, $2n=48$	Rosaceae	Europe	Hermaphroditic, self-incompatible	Hexaploid after interspecific hybridization
Plum—Asia	*Prunus salicina* $x=8$, $2n=16$, 32	Rosaceae	China	Hermaphroditic	Increased fruit size
Plum—American	*Prunus Americana* $x=8$, $2n=16$	Rosaceae	North America	Hermaphroditic	Increased fruit size
Peach	*Prunus persica* $x=8$, $2n=16$	Rosaceae	China	Hermaphroditic	Freestone, low chill, fuzzless (nectarine), increased size
Vine Fruit					
Kiwifruit	*Actinidia delicious* $x=29$, $2n=174$ *A. sinensis* $x=29$, $2n=58$	Actinidiaceae	China	Dioecious	Unchanged
Subtropical & Tropical Fruits					
Citrus (orange, mandarin, lemon, lime, pumello, grapefruit)	*Citrus spp.* $x=9$, $2n=18$	Rutaceae	Southeast Asia, China	Hermaphroditic	Nucellar embryony, interspecific hybridization, parthenocarpy
Mango	*Mangifera indica* $x=20$, $2n=40$	Anacardiaceae	E. Asia	Hermaphroditic	Nucellar embryony, loss of fibers in fruit

Persimmon Asian	*Diospyros kaki* $x=15$, $2n=90$	Ebenaceae	China	Polygamo-dioecious	Loss of astringency, parthenocarpy
American Fruits					
Berry Fruits					
Strawberry	*Fragaria* × *ananassa* $x=7$, $2n=56$ Other spp. $2n=14, 28$	Rosaceae	Americas	Dioecism	Hermaphroditic, interspecific hybridization
Raspberry	*Rubus idaeus* (red) *R. occidentalis* $x=7$, $2n=14$	Rosaceae	Europe, America	Hermaphroditic	Interspecific hybridization, polyploidy
Blackberry	*Rubus* spp. $x=7$, $2n=28$, 35,42,56,84	Rosaceae	N. America	Hermaphroditic	Interspecific hybridization, polyploidy, thornlessness
Blueberry	*Vaccinium* spp.	Ericaceae	N. America	Hermaphroditic	Increased fruit size, interspecific hybridization, polyploidy
Cranberry	*Vaccinium macroacarpon*	Ericaceae	E. United States	Hermaphroditic	Unchanged
Lingonberry	*Vaccinium vitis-idaea*	Ericaceae	Circumboreal	Hermaphroditic	Unchanged
Subtropical & Tropical Fruits					
Avocado	*Persea americana* $x=12$, $2n=24$	Lauraceae	Tropical America	Hermaphroditic, synchronous protogynous dicogamy	High oil, smaller seed size
Papaya	*Carica papaya* $x=9$, $2n=18$	Euphorbiacea	Tropical America	Dioecious	Polygamo-dioecious, reduced fruit size
Pineapple	*Ananas comosus* $x=25$. $2n=50$	Bromeliaceae	Tropical America	Hermaphroditic	Parthenocarpy, seedlessness

at the base of the plant (Fig. 8.8). Clearly the production of offshoots is one of the principal characteristics of domesticates. At present, all cultivars can be propagated in this manner and one to several suckers may be removed each year. Offshoots can be planted without roots, but mounding of soil around the base of the mother tree facilitates their rooting. Irrigation is essential to insure survival of offshoots and high productivity.

Since the date is dioecious, production of fruit by pistillate clones requires the presence of a source of pollen. In present-day commercial plantations, one male tree to 100 females is sufficient if pollination is performed by hand. In some cases twigs or branches of the male inflorescence from 10 to 15 cm long and bearing 30 to 50 flowers are tied on the female cluster, but this process must be repeated because of variation in time of maturation of pistillate flowers. Pollen has also been distributed by airplanes or helicopters.

Fig. 8.8. The cultivated date palm is vegetatively propagated from offshoots (suckers) at the base of the plant.

In antiquity, mass plantings of desirable pistillate clones of date palm would have reduced fruitfulness had nonproductive staminate clones not been introduced. The relation between artificial pollination and fruit set was known to early Sumerians and is mentioned in the cuneiform texts of Ur just south of Baghdad in Iraq, ca. 2300 BCE. By the time of Hammurabi the problem of the division of the crop between the landlord and the tenant gardener, who acted as a sharecropper, was defined and penalties for lack of pollination were assessed (*see* IIC). The practice soon took on religious significance, as illustrated by bas reliefs showing pollination of sacred trees by kings and gods (eagle-headed genii) (Fig. 8.5). The sexual nature of the pollination process was probably known as the date palm became a symbol of fertility. Theophrastus, writing in the 3rd century BCE, clearly mentions the parallels and refers to the pollen bearing plant as male and the fruit-bearing plant as female.

Wild date palms often produce small and nonpalatable fruits, while the domesticates are associated with larger size and considerable amounts of sweet pulp. Increased size and quality of the fruit is associated with selection carried out under domestication. Continued clonal propagation of large-fruited dates through offshoots would have increased propagation ability along with fruit size. Genetic improvement ensued from selections of elite wild genotypes, followed by natural intercrosses within elites as well as with wild clones. Since the plant is dioecious, selection must have been confined to pistillate clones. However, selection of male clones may have been facilitated by the presence of metaxenia, the direct effect of pollen on morphology and ripening of the date palm fruit. Thus, selection for fruit characters may have been a method of gamete selection.

At the present time, there are over 3000 cultivars, of which 60 are widely grown. Some cultivars have been known for a thousand years. Cultivars have been divided into soft and semi-dry, based on moisture content and an increasing proportion of sucrose, rather than glucose and fructose. Selection has altered fruit quality, storage, suckering, salt tolerance, and spininess.

2. Olive. Olive (*Olea europea*, Oleaceae) is a slow-growing, long-lived, evergreen tree uniquely adapted to the climate of the Mediterranean basin and considered a defining feature of this climate (Smartt and Simmonds 1995). Indigenous types are still widely found with archeological evidence as far back as 12,000 years ago (Blázquez 1996). The cultivated olive originated about 6000 years ago in Asia Minor, but was generally unknown to the Babylonians and Assyrians, whose source of oil was sesame and walnut. The olive was long known in Syria and the

Holy Land and was introduced to Egypt from Syria between 3000 and 1800 BCE (Goor and Nurock 1968). By 2500 BCE, the ancient city of Elba in northern Syria had fields containing between 500 and 1000 olive trees, producing and exporting various types of olive oil. According to Hittite texts olives were cultivated in Anatolia and imported to Egypt from the time of Ramses II (1197–1165 BCE), where there is mention of the use of olive oil for illumination and as a skin emollient for cracks and sunburn. The olive moved from Egypt to Carthage in North Africa, reaching Italy in the 7th to 6th century BCE.

Olive, along with grape, is the most mentioned fruit in the Hebrew bible. Its importance has permeated the Western world and the olive tree and oil are symbols of beauty, freshness, fertility, wealth, fame, and peace. Greek myths associated with the olive involve Hercules and Athena. The importance of oil is reflected in its widespread use for religious purposes such as consecration ceremonies (anointing) in Judaism and Christianity; the word messiah (Christ) literally means "the anointed one." Olives were introduced to South America in the 16th century and introduced to Mexico, California, and Australia in the 20th century.

In Mediterranean climates, the olive is often grown without irrigation, although yields are low. Moderate pruning is performed to shape trees and to remove unfruitful wood. Harvest is usually carried out by hand, with the time depending on the use (Fig. 8.9)

Olives may be vegetatively propagated by cuttings, from buried truncheons (large branches in which incisions are made every 8 to 10 cm), or

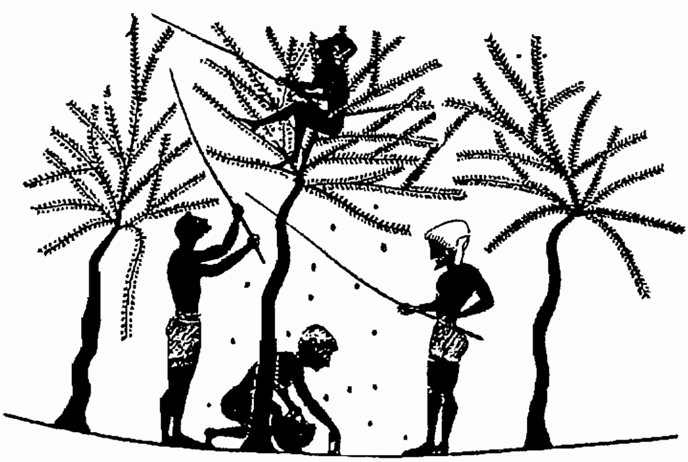


Fig. 8.9. Harvesting olives in ancient Greece from a black figure amphora, 520 BCE. Source: Singer et al. 1954.

from knobs (ovuli) that occur at the base of the trunk. Theophrastus made the astute observation that basal cuttings root better than terminal ones. Early propagation from seed from unique clones probably increased crop diversity, while the introduction of clonal propagation made it possible to fix unique genotypes. Olives have been propagated from grafting since antiquity (*see* Vegetative Propagation). Many present-day cultivars are considered to be thousands of years old.

There are two processing steps involved in olive utilization. The first is transformation of the bitter fruit to an edible form and the second is oil separation. Somehow, Neolithic humans learned to consume a small, bitter fruit, almost inedible and somewhat poisonous as a result of the phenolic glucoside eleuropein found in various concentrations in all olives. This was accomplished by soaking, a technique still used. Further steps in detoxification included pounding, addition of lye (sodium or potassium hydroxide), or lactic acid fermentation induced by sodium chloride (Colmagro et al. 2001). There is ample evidence that so called "primitive" societies learned to leach a number of foods to reduce their content of bitter substances. Australian aborigines used a combination of soaking and roasting with many native fruits and seeds (Crib and Crib 1974).

Later in the Bronze Age, olive processing technology was invented to separate the oil. Olive became the first great industrial crop, grown more for its oil—as a medicinal, for cooking, and for illumination (the light is very bright)—than for direct consumption. The religious practice of anointing probably derived from the medicinal use of olive oil. The ancient golden Menorah with seven arms (*Exodus* 24, 31–40) is an oil lamp. The earliest process of oil extraction was by crushing the fruit in water and spooning the floating oil. Later improvements were the use of oil presses of various types. Typically water was added and the oil removed by decantation. At present 90% of the world olive crop is pressed for oil that is used for culinary purposes; the remainder is used as table olives, a fermented product. Recently, olive consumption has increased with the recognition of the beneficial properties of oleic acid and the increase in consumption of various types of table olives as a gourmet product.

Cultivated olives are characterized by large fruit, large proportion of flesh, and high oil content. At present, olives are grouped as oil types, with fruits containing from 20 to 28% oil used for olive oil production, while types with less oil are for table use, whole or pitted, and for pickling.

3. Grape. Wild grapes of the Old World (*Vitis sylvestris*, Vitaceae) are indigenous to the south Caspian belt, Turkey, and the Balkans, and were widely distributed in the northern Mediterranean area including the Black and Caspian Seas (Zohary and Spiegel-Roy 1975; Smartt and Simmonds 1995; Reisch and Pratt 1996). Wild grapes are dioecious, perennial, forest vines and thrive in cooler and more humid conditions than do olives. Harvest of wild grapes long preceded domestication, as evidenced by carbonized seed in numerous prehistoric sites in Europe. Presence of the wine grape in the Near East is dated as early as the 8th millennia BCE but eastward expansion was limited by lack of winter hardiness and poor adaptation to high summer rainfall. Toward 5000 BCE, and perhaps earlier, the domestic grape, *V. vinifera*, migrated from Anatolia to Syria and thence to the Holy Land. Signs of Bronze Age domestication are found in Mesopotamia, the Holy Land, Syria, Egypt, and the Aegean. By the 2nd millennium BCE there is evidence of vessels for wine storage as well as of raisins. A number of grape species are found in the New World and these types were domesticated after the European encounter with America (Reisch and Pratt 1996). One American species, *V. labrusca*, known as the fox grape, was rapidly domesticated, while others were hybridized with *V. vinifera* to develop *Phylloxera*-resistant rootstocks. Muscadines (*V. rotundifolia*), native to the southern United States, were preserved by Native Americans by drying (Olien 2001) but were not cultivated and can be considered a recent domesticate.

Grapes are easily propagated vegetatively, permitting extensive plantings of unique clones. When vines are in contact with the soil, rooting often occurs at the nodes (layering). Hardwood cuttings also root easily. At present most grapes are propagated by grafting in order to take advantage of rootstocks resistant to soil-borne diseases and insects.

The great genetic change in domestication was the switch from dioecism to hermaphroditism, a mutation in the dominant allele of the male-conferring gene that suppresses development of the gynecium. Other changes associated with domestication include an increase in berry size and sugar content, and selection of various skin colors (white, green, bronze, pink, red, and black). Recently selection of seedlessness has become a key factor for table grapes; seedlessness occurs from both early embryo abortion (stenospermocarpy) or from parthenocarpy (Ledbetter and Ramming 1989). The seedless grape 'Sultanina', known as 'Thompson Seedless' in the United States, is an ancient Turkish cultivar and still one of the most widely grown for table grapes or wine.

The cultivation of grape involves extensive vine training and pruning and in no other fruit crop are these practices more important. The Hebrew Bible is rich in allusions to these practices. The replacement of tree support with arbors or trellises is amply shown in Egyptian iconography (Fig. 8.7). Protection of grapes from birds and thieves is a common feature of the early cultivation of wine, and the construction of walls and towers is associated with vineyards in ancient Israel (Walsh 2000). Various techniques were developed for overwintering, including covering sprawling vines with soil.

Grapes were preserved in two ways. The simplest was sun drying, and the dried fruit (raisins) were prized for their concentrated sweetness, and long-term storage (Fig. 8.10). The transformation of grape juice to wine occurs almost naturally but requires anaerobic conditions. The fermentation of juice into wine was probably based on beer technology, an older practice. The culture of grapes (viticulture) and the technology of wine making (enology) are common themes in biblical writings, and became infused in Judaism (Walsh 2000) and Christianity, although drunkenness was frowned upon. Wine was the beverage of choice in ancient Greece and Rome. Wine is prohibited in Islam but grapes and raisins are highly prized. At present wine is the major use of grapes, far surpassing table grapes and raisins.

4. Fig. The common fig (*Ficus carica*, Moraceae) is a gynodioecious species consisting of monoecious wild types (caprifig) and pistillate domesticates (Condit 1947). Figs, borne on small trees, are considered one of the classic fruits of the Mediterranean basin. Signs of fig cultivation are found at various Neolithic and late Neolithic sites (Zohary and Spiegel-Roy 1975), and from Bronze Age sites in the 4th millennium BCE. Domestication was generally contemporary with olive and grape in the Eastern Mediterranean basin; it was mentioned by King Urukagina ca 2900 BCE and became known to the Assyrians as early as 2000 BCE. Egyptian records indicate fig cultivation in Canaan in the 3rd and 2nd millennia BCE (Goor and Nurock 1968) and there are many paintings of fig from antiquity (Fig. 8.11, 8.12). The fig is easily propagated by seed, as well as by cuttings or layers. Propagation by grafting and budding was described by Cato in the 3rd century BCE.

The fig is marvelously adapted to insect pollination (Condit 1947; Storey 1975). The fruit is a syconium, a fleshy branch transformed into a hollow receptacle bearing minute flowers on its inner surface and

Fig. 8.10. Storing raisins, from a tomb at Beni Hasan ca. 1900 BCE. Source: Singer et al. 1954.

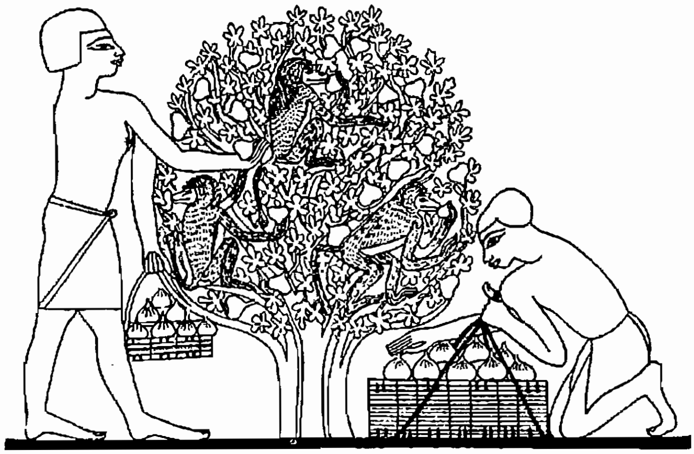


Fig. 8.11. Harvesting figs, from a tomb at Beni Hasan, Egypt, ca. 1900 BCE. Source: Singer et al. 1954.

open to the outside by a small orifice (ostiole). The monoecious caprifig, or goat fig, the name indicating its lack of worth, contains both staminate and short-styled pistillate flowers within the syconium and serves for the multiplication of the parasitic fig wasp (*Blastophaga psenes*). Pollination is carried out by this tiny (about 1 mm) wasp, an association described by Theophrastus. The insects overwinter in the larval stage in the pistillate flower, pupate in early spring, and emerge as adults within the synconium. The wingless male impregnates the female inside the ovary and then perishes. The winged female exits the synco-

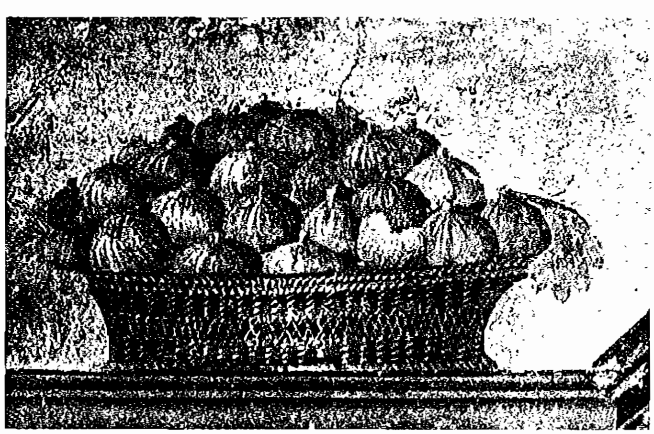


Fig. 8.12. Wall painting of a basket of figs. Villa at Torre Annunziata. Source: Jashemski 1979.

nium through the ostiole, where she is covered with pollen from staminate flowers clustering around the orifice. The winged female then migrates to other small figs, deposits an egg in each of a number of pistils and then dies. However, when the female enters the common fig that contains only long-styled pistils that are not adapted to oviposition, the insect perishes, but not before pollination has been accomplished.

There are as many as three crops of figs in each season. The first crop, called *profichi*, are formed on wood of the previous year's growth. They may contain the wasp or, if uninhabited, are called blanks. The inhabited profichi are usually dark green, firm and plump, while the blanks are yellowish green, ribbed and inclined to be spongy. The next crop, called *mammoni*, are produced in the axils of the current season's growth and are often pollinated by wasps from the profichi crop. The last crop is called *mamme* and remains on the tree during the winter season.

Parthenocarpy, the ability of the fruits to grow and mature without fertilization, is of two types, vegetative or stimulatory (Condit 1947; Storey 1975). In vegetative parthenocarpy fruit development occurs without any stimulation (oviposition or pollination). In stimulative parthenocarpy, insect stimulation or fertilization is required. In most caprifigs, the syconium fails to set unless pistillate flowers are stimulated by oviposition with larval development of the wasp. Some caprifigs are partly parthenocarpic, producing seedless figs more or less freely; some are completely parthenocarpic. The domesticated Smyrna-type figs are completely non-parthenocarpic, and thus require pollination; this is often accomplished by introduction of the wasp-bearing caprifig, hence the term caprification. Some cultivated figs are partially parthenocarpic in that the early crop (called *brebas*) is parthenocarpic but the second crop is non-parthenocarpic. Common type figs such as 'Mission', 'Dottato', and 'Brunswick' are completely parthenocarpic in both crops.

Domestication is associated with increase in size of the fruit (syconium), and sugar content, as well as parthenocarpy (Storey 1975). Other characters of figs include various colors (white, amber, red, and purple) in the skin and flesh, increased sugar content, and resistance to splitting when mature. There are many known cultivars; Condit (1955) has described over 600, many of which may be synonyms. 'Condit's Adriatic', now called 'Conadria', was the first release from a breeding program, and is characterized by high fresh and processing quality and resistance to splitting.

Figs are consumed fresh or dried and are often processed as a paste for pastries or canned. The fruit can be fermented and distilled into alcohol.

5. Sycomore Fig. The sycomore fig (*Ficus sycomorus*, Moraceae) originated in the savannas of eastern Central Africa where they grow spontaneously and reproduce by seed. The tree is easily propagated by cuttings. It was introduced to Egypt in predynastic times, before the 3rd millennium, and became an important cultivated plant in the Early and Middle Kingdoms. Although the fruit was not considered exceptional, the tree was highly prized and held sacred, especially to Hathor, goddess of love, and representations of fruit and tree are found on bas-reliefs and commemorated in song. Fruit and leafy branches were placed in funeral offerings. The wood is decay resistant and esteemed for household utensils, construction, boxes, and coffins. The tree was introduced to the Levant, present-day Israel, Lebanon, and Syria as well as Cyprus. It was well known in Biblical times and became a food for the poor.

Flowers are pollinated by the chalcidoid wasp, *Ceratosolen arabicus*, but the plant was introduced to Egypt without the wasp. Although fruits developed parthenocarpically, they did not enlarge or ripen successfully unless wounded. This fact is found in a famous quote from the Hebrew Bible (Amos 7, 14): *I was no prophet, neither was I a prophet's son but I was a herdman and a "piercer"* (mistranslated as "gatherer" in the King James translation) *of sycomore fruit.* The phrase refers to the practice of ripening the fruit by scraping it (Fig. 8.13). Wounding of the fruit results

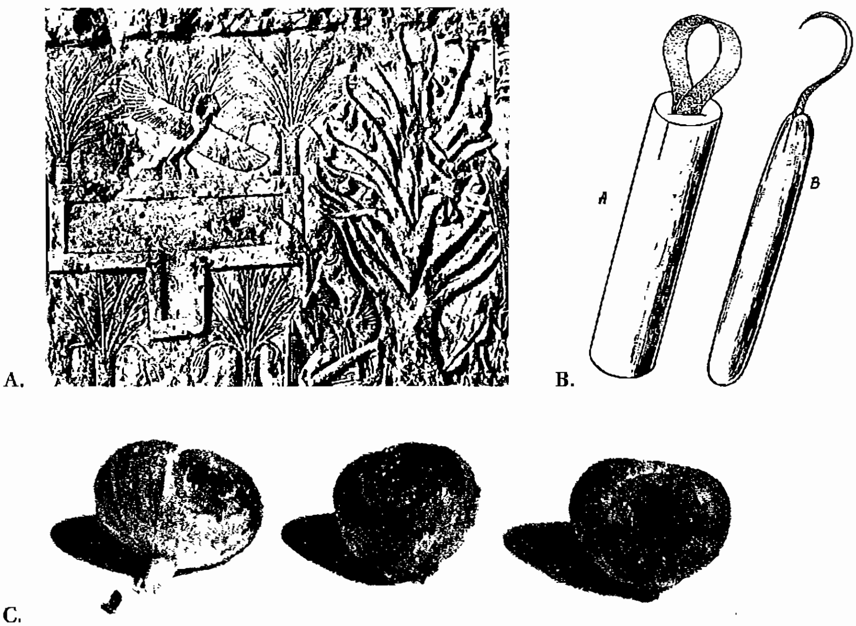


Fig. 8.13. Induced ripening in sycomore fig. Source: Galil 1968. A. Bas-relief showing a sycomore tree with gashed fruit; B. knives used for gashing; C. gashed sycomore fruit.

in ripening through the release of ethylene. This remarkable technological discovery was known to Theophrastus, who writes: *The sycamore cannot ripen unless it is scraped but the Egyptians scrape it with iron claws, the fruit thus scraped ripens in 4 days.*

6. Pomegranate. Pomegranate (*Punica granatum*, Punicaceae), native to the southern Caspian belt (Iran) and northeast Turkey, is a Bronze Age fruit that has been cultivated for 5000 years (Goor and Nurock 1968; Zohary and Spiegel-Roy 1975). Its presence in Syria, the Holy Land, Egypt, and Mesopotamia indicates domestication. The Latin name *Punica* refers to Carthage and the fruit was once known as the apple of Carthage. Remains are found in Nimrud, Arad, and Jericho. The pomegranate was introduced into Egypt from Syria about 1600 BCE before the 19th Dynasty during the inflow of Semitic people (Hyksos). The fruit is commonly illustrated in Egyptian art (Fig. 8.14) from the New Kingdom and widely found in Jewish and Greek art. The pomegranate is easily

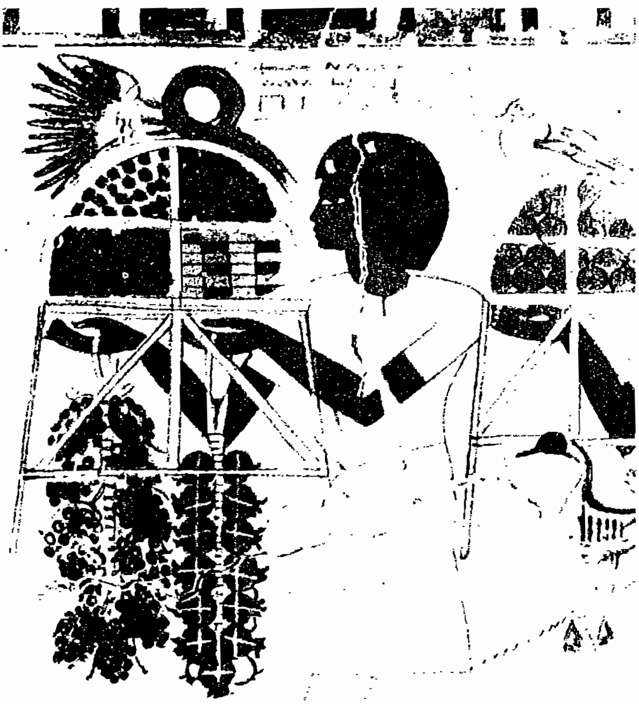


Fig. 8.14. Offering bearing pomegranates, grapes and flowers, New Kingdom, Egypt. Source: Darby et al. 1977.

propagated by hardwood and softwood cuttings. Domestication is associated with increased fruit size, and sweetness, and a shift to clonal propagation. Some types have degenerate embryos and are called seedless.

In Egypt, juice from the pomegranate was consumed and converted to wine. The rind was prescribed as a medicinal and the flowers were crushed to make a red dye for leather. Based on extensive iconography, the pomegranate seems little changed from antiquity. Peel color varies from bright red to leathery brown.

B. Central Asian Fruits

1. Pome Fruits. Pome fruits of the Rosaceae include apple, pear, quince, and medlar, of which the apple is the most important tree fruit of the temperate world. The trees require an annual period of chilling to break dormancy for proper growth, and the seeds require a period of cold stratification before they will germinate, and must be separated from the placental tissue of the fruit to germinate.

Apple. The apple is cross-pollinated and most cultivars are self-incompatible. Most cuttings of apple and pear trees do not root from cuttings so that vegetative propagation is difficult without grafting. There are 24 primary species of *Malus*, distributed in Europe, Central Asia, and Eastern Asia and three in North America (Way et al. 1990). Most of the wild apples are small and bitter. However, the large, sweet-smelling domestic apple (*Malus* × *domestica*) clearly originated in Central Asia, specifically Almaty, Kazakstan (Dzhangaliev 2003) and was introduced to the West via Persia in antiquity. Recent explorations in Kazakhstan (Forsline et al. 2003) support Vavilov's suggestion that *Malus sieversii* = *M. pumila* is the major progenitor of the cultivated apple, and this has been confirmed by recent work with molecular markers (Harris et al. 2002). The explorations in Kazakhstan also indicate that elite wild material contains all the characters of modern apples (Fig. 8.15) including size, quality, and various colors from red to yellow to green. Barrie Juniper (pers. commun.), has made the intriguing observation that the selection mechanism for large size may not have been human but rather the result of millions of years of selection for large size by bears endemic to the area who consume large numbers of apples; their droppings provide a unique germination medium. All of the other species of apple appear to be distributed by birds, providing no selection mechanism for large size.

Fruits of wild relatives of the domesticated apple occur in the Mideast and Europe and were frequently collected by Neolithic and Bronze Age

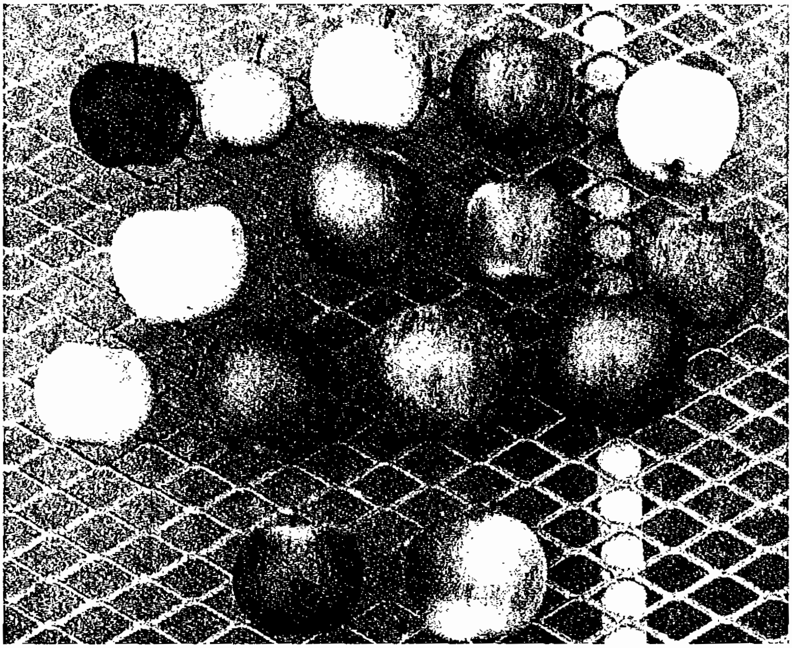


Fig. 8.15. Cultivated seedlings of elite wild apples from Kazakhastan. The two fruits on the bottom are 'Empire' and 'Gala'. Source: Forsline et al. 2003.

farmers. However, it is difficult to know precisely when the larger, sweeter apples of central Asia reached the West because reference to apple (hazur) in the early Sumerian literature may in fact refer to the indigenous, bitter, small-fruited species, *Malus orientalis*. The earliest archeological evidence (early Dynasty III, about 2200–2100 BCE) of dried apples are rings of small fruits (11 to 18 mm in diameter), possibly threaded on a string, on saucers in Queen Pu-abi's grave at Ur near present-day Basra, Iraq (Postgate 1987; Renfrew 1987). Apples lose their bitterness when dried (Barrie Juniper, pers. commun.), and if wild *M. orientalis* were harvested it might have been consumed in this manner. A Sumerian cuneiform literary manuscript, entitled *Disputation between the Hoe and the Plow* (Vanstiphout 2000), dated about 1900 BCE, refers to gardens of apples. In Anatolia (Turkey), the Hittites, who rose to dominance in the 2nd millennium BCE, referred to 40 apple trees on one estate. Later biblical references to sweet-smelling apples such as in the Song of Songs, written probably no earlier than 1000 BCE, suggest introduction before the 1st millennium BCE. In any case, by the 1st millennium BCE apples were a part of western agriculture. Homer (8th or 9th century BCE] refers to apples in the gardens of King Alcinöus, the king of the Phaeacians, a legendary country. Apples, however, were unknown in Egypt until Greco-Roman times.

How did the apple reach the west from Central Asia? Because apples and pear do not propagate easily from cuttings, the most likely explanation is the introduction of seed carried in saddle bags by caravans along the trade routes, passing through the fabled cites of Bukara and Samarkand to Persia, perhaps facilitated by seed germination in horse droppings, but propagation from root suckers is another possibility (Fig. 8.16). Another explanation is that grafting technology, dated as early as 3800 years ago (Harris et al. 2002), may have been involved with Persia as an intermediary stop. Persia is clearly the source of many fruits from Central Asia and China.

Whatever the precise mechanism, the apple clearly passed through Persia and Greece, and, by the time of the Romans, apple technology including grafting, pruning, storage, and selection of unique adapted clones was perfected. Even the use of specific rootstocks seems to have been discovered (a low growing type is described by Theophrastus) and it is no coincidence that these easily-rooted dwarfing clones are called Paradise, the Persian word for garden.

The apple cultivated by the Romans was transported throughout the empire and became naturalized throughout Europe, resulting in thousands of unique types. Possibly some intercrosses with the small, astrin-

Fig. 8.16. Propagation of wild apples from root suckers. Source: Dzhangaliev 2003.

gent *Malus sylvestris*, native to northern Europe, gave rise to cider apples that are still cultivated. Interestingly, a secondary center of diversification was established in the United States in the 18th and 19th centuries as seed from European cider mills was imported, resulting in a new cycle of selection by fruit growers (*see* IV C). As a result, most of the new cultivars of apple now grown worldwide derive from American and Canadian selections.

The technology of apple production led to improved methods of storage in cool areas, first underground storage, later cooling with ice and, finally, refrigeration in modern times. Special methods to control diseases and insect pests, which have always been a problem, were sought but were largely unsuccessful until the 19th century when the fungicidal properties of lime sulfur was discovered and used to control such diseases as apple scab, and lead arsenate was used to control codling moth, a practice that is now illegal. The original apple processing consisted of drying; later juice was extracted and converted to a fermented product called cider, then distilled into a liquor (calvados or apple jack). Apples are now consumed fresh, or cooked, whole or as a sauce, and are especially popular in pastries.

Genetic changes in apple include the selection of triploids derived from unreduced gametes, parthenocarpy, mutations involving growth habit, particularly spurry and short internode types, and various forms of pest and disease resistance. Fruit changes include shape, and various quality factors such as flesh firmness, sweetness, acidity, flavor, and shelf and storage life (Janick et. al. 1996). Triploidy seems to confer an advantage to cultivated apples, for about 10–20% of cultivars are triploid yet nonreduction occurs in only about one in a thousand seed. The ability of layered shoots to root is advantageous in rootstocks, which are propagated by mounding soil around the bases of shoots (stooling). 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 2002b).

Pear. The pear has a story similar to that of the apple except that the domestication of the pear followed two separate paths. *Pyrus communis*, native to Central Asia, gave rise to the European pears characterized by intense flavors, flesh softening after the climacteric, and a wide range in sizes and shapes. The European pear is described by Homer as one of the fruits in the garden of Alcinöus, and the Roman agricultural writers Cato, Varro, and especially Pliny describe many types (Hedrick 1921).

In eastern Asia, the crisp, sweet-fleshed fruit of *Pyrus pyrifolia*, *P. bretschneiderii*, and *P. ussuriensis* are round, aromatic, and crisp-fleshed, and now known either as Asian pears or under the Japanese name *nashi* (Watkins 1995; Bell et al. 1996). The pear has been known in China for 4000 years [Wang 1990].

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 systematically collected clones of pear, planted (open pollinated) seed of the best material and made selections for eight generations. In an early fruit book, *The American Fruit Culture* (1863), John J. Thomas (1810–1895) stated 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. Sexual hybridization to produce new pear cultivars (as well as apple, cherry, strawberry, red currant, plum, and nectarine) was first attempted by Thomas Andrew Knight (1759–1838).

2. Stone Fruits. The genus *Prunus*, Rosaceae, is the source of almond, apricot, cherry (sweet and tart), peach (and nectarine), and plum. With the exception of the almond, which is cultivated for its seed, all are soft-fleshed temperate fruits known for their delectable flavors. *Prunus* originated in Central Asia, with secondary centers in Eastern Asia, Europe, and North America (Watkins 1995). The introduction of apricot, cherry, and plum into the Mediterranean basin was associated with the incursion of Alexander the Great (356–323 BCE), who conquered Persia and then continued east through Turkistan, Afghanistan, Pakistan, and northwestern India up to the Indus river. Greek settlements and commercial posts were founded between the Mediterranean and India along the western section of the trade routes, which later were dubbed the Silk Road, and through it passed central Asian as well as east Asian fruits, The Roman names for the stone fruits suggest their presumed origin [peach (*persica*) from Persia, apricot (*armeniaca*) from Armenia, cherry (*cerasus*) from Kerasun on the Black Sea], but it is clear that these locations were clearly way stations from Central and East Asia. The peach originated in China and will be discussed in Section III C 1.

Almond. Almonds (*Prunus dulcis*, Rosaceae, syn. *P. amygdalus*] grow wild throughout southwest and central Asia, from Turkey and Syria into the Caucasus and into the deserts of Tian-Shan and the Hindu Kush mountains (Zohary and Spiegel-Roy 1975). Based on biblical literature, the introduction of the almond may have occurred as early 2000 BCE, and some almond remains have been found in the 18th Dynasty in Egypt (1550 BCE). It does not seem to have been widely cultivated in Egypt until Roman times. It was brought into Greece about 200 to 300 BCE and gradually reached the entire Mediterranean basin.

There are two principal types: sweet and bitter. The bitter kernels are due to high levels of the glucoside amygdalin which hydrolizes to benzaldehyde and cyanide when exposed to the enzyme emulsin (Kester and Gradziel 1996). This trait discourages seed predation by birds and rodents and limits its use for human consumption. (The predominantly benzaldehyde flavor of almond extract is derived from bitter almonds). The nonbitter or sweet almond flavor is controlled by a single dominant gene that occurs relatively frequently in wild populations. Domestication involved selection for sweetness and increased kernel size. Two thousand years of continuous culture in the Mediterranean basin concentrated almond into specific regions where well-defined land races evolved, and where almond culture became a low input dryland crop in semiarid areas. Almond types are further separated into hard and soft shell, with the soft-shell types predominating in California and Australia and the hard-shell types being grown primarily in Mediterranean countries. In Arabic countries, the immature fruit is often consumed after slight cooking.

The almond has hermaphroditic flowers; self-pollination is avoided by gametic incompatibility but many new cultivars are self-fertile. The tree is easily grown from seed, and seed propagation has been widespread from the beginning of almond cultivation and still exists in Iran, Turkey, Afghanistan, Greece, Crete, and the Balearic Islands. Vegetative propagation is now principally by bud grafting. The introduction of almond cultivation into irrigation production systems has created a high-yielding commodity crop in large areas of California, which is now the major world almond production area.

Apricot. The history of apricot (*Prunus armeniaca*) goes back 5000 years in China with the first attribution to the Emperor Yu (2205–2198 BCE), with other references in 658 BCE; and superior orchards were described in 406–250 BCE (Faust et al. 1998). Grafting of apricots began about 600 CE with defined cultivars developed after this time. There are at least 11 cities in China that contain xing (apricot) as part of their name. The closely related *P. mume*, Japanese apricot, noted for its early bloom, is especially revered in China for its gnarled branches, profuse early flowering, and fragrance. Painting of this species is a specialized art form.

In Central Asia, the apricot appears to have become naturalized in Sogdiana (associated with fabled trading city of Samarkand) as well as

Armenia, but the lack of wild apricots suggests that Armenia is merely the route through which apricots entered Europe. Alexander the Great brought the apricot to Greece and Epirus (Albania), from whence it reached Italy. Mention by Dioscorides and Columella and Pliny but not by Theophrastus, Cato and Varro, indicates an arrival into Rome by the 1st century CE. Armenia was attacked by Roman legions through Syria in 69–63 BCE, and this may explain its introduction to Rome.

Throughout its history, apricot has been noted for delicious flavor, delicate velvety fruit surface, and early flowering and fruiting. The name apricot is a corruption of the Arabic and Greek *al-praecox*, which means the early fruit. The old spelling "apricock" is retained in English until the 17th century. The fruits are mainly consumed fresh but are also cooked and often stuffed. The high sugar content makes them suitable for drying. In China they were also preserved by salting and smoking. Other uses include fruit leathers, nectars, and liquors. Current breeding efforts are directed toward increasing fruit size, adaptability, hardiness, and processing quality (Layne et al. 1996).

Cherry. Cherry consists of three main groups: the sweet cherry (*Prunus avium*, $2n$=16); the tart (sour) cherry (*P. cerasus*, $2n$=32); and the ground cherry (*P. fruiticosa*, $2n$=32). Tart cherries are hybrids between sweet cherry and ground cherry via non-reduced gametes. Natural hybrids between non-reduced gametes of sweet with tart cherries are called duke cherries ($2n$=32). The origins of the three species overlap and include Central Europe and areas surrounding the Black Sea, with the sweet cherry as far east as central Russia (Fig. 8.17). There is archeological evidence of sweet cherry about 5000 to 4000 BCE in Switzerland, France, Italy, Hungary, Germany, and England. The first description of sweet cherry is by Theophrastus (ca 300 BCE), who named it *kerasos*, after the town Kerasun in ancient Pontus on the Black Sea, but the town may have been named after the fruit. By Roman times, cherries were a common fruit and are described by Pliny and Virgil, but generally as wild trees (Faust and Surányi 1997).

Sweet cherries are usually consumed fresh, but are also used in cold soups, dried, or converted to maraschino cherries, which are often covered with chocolate. Tart cherries are canned or frozen, usually as a filling for pastries and pies, and made into jams and jellies. Dried tart cherries known as chaisins are gaining in popularity. The flowering cherry, *P.* × *yedoensis*, is particularly revered in Japan; the flowering cherry trees of Washington D.C. are a 1912 gift from Japan after earlier shipments were destroyed by insect infestations.

The appearance of the cherry seems little changed from Roman times. There is diversity in fruit color (from yellow to red to black), flesh color,

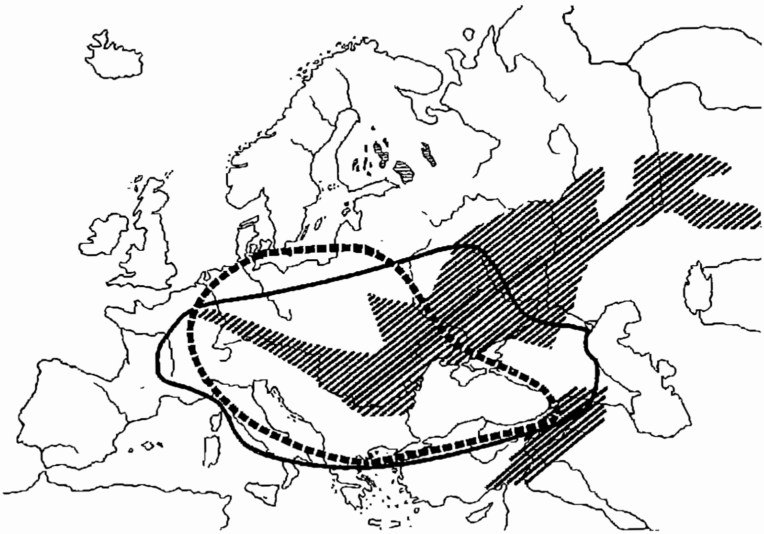


Fig. 8.17. Distribution of sweet cherry (striped area), sour cherry (solid line), and ground cherry (broken line). Source: Faust and Surányi 1997.

and season of ripening. The presence of pollen incompatibility groups makes it essential that this character be understood in laying out plantings. Recent advances have been made by breeding for self-compatibility originally induced by irradiation (Brown et al. 1996).

Plum. The plums have the greatest diversity among *Prunus* species and have been domesticated on three continents (Okie and Weinberger 1996; Faust and Surányi 1999). They are the link between the major subgenera (Watkins 1995). Archeological finds of plums in Europe date to Neolithic times (Faust and Surányi 1999). While there are many species with edible fruit, the principal ones are *P. domestica* (European plum, 2*n*=48, hexaploid, native to Europe); *P. domestica* ssp. *P. insititia* (damson plum, 2*n*=48, hexaploid, native to Europe); *P. salicina* (2*n*=16, diploid, native to China); and *P. americana* (American plum, 2*n*=16, diploid, native to North America). The European plum may be an amphidiploid derived from *P. cerasifera*, 2*n*=16, and *P. spinosa*, 2*n*=32 (Crane and Lawrence 1956). The present plum industry is based on *P. domestica* and *P. salicina*. Neither of these species has wild progenitors and both entered into human use highly developed. The garden plum and the Japanese plum emerged as important fruit crops about 300 BCE.

Horticulturally, there are many different types of plums with many different names, shapes, colors, and attributes (e.g., sloe, bullace, damson, green gage, mirabelle). Various plums are converted to juice, liquors, brandy (slivovitz), cognac, and cordials, and widely used for baking and confection. Plum trees are especially revered in China for their gnarled branches, profuse early flowering, and fragrance, and the painting of plum trees is a specialized art form. The dried sweet European plums are known as prunes or prune plums. The dried black fruit can be stored almost indefinitely, and is sold partially rehydrated for use as filling for pastries, and for juice. Because of its role in digestive regularity, mention of the word prune has become a source of hilarity in the United States, so much so that the California trade association has changed its name from prune to dried plum. Interspecific hybridization of plums with other *Prunus* with the same chromosome number are producing a number of new fruits such as plumcot (plum × apricot).

C. Chinese and Southeast Asian Fruits

1. Peach. China is the origin of the peach (*Prunus persica*, Rosaceae), domesticated before 3300–2500 BCE (Faust and Timon 1995). Peach culture dates to 2000 BCE and there are now thousands of cultivars in China (Wang 1985). The peach is mentioned in Chinese literature as early as 1000 BCE and became entwined in Chinese mythology and folklore. A number of forms were selected in different parts of China. In the north, the peach tree is characterized by high chilling requirements, long internodes, single flower buds, upright branching, large flat leaves, and largely cling- or semi-clingstone fruit. In the south, a warm area with mild winters, trees are characterized by more lateral branching and require less chilling; this is the area of peen-tao (a flat fruit now marketed as the donut peach) and the 'Honey' type peach, an elongated-pointed (beaked) fruit with a deep suture near the base. In the high mountain area small-fruited peaches are found, including those with smooth seed (*P. mira*).

The peach tree is largely self-pollinated (70 to 85%) so that propagation by seed often provides less variability than in cross-pollinated species. According to Pliny the peach was grown in Greece by 332 BCE. They were probably introduced into Persia from China by seed in the 2nd or 1st century BCE; its name in the West, *persica*, a misnomer, is based on the incorrect assumption that it originated in Persia. A painting from Herculaneum, near Naples, Italy, destroyed by the eruption of Mount Vesuvius in 79 CE, shows large green free-stone peaches with yellowish flesh (Fig. 8.18); large peaches persisted in Italy as depicted in Renaissance paintings by Campi (1580) and Caravaggio (1590s).

The peach was introduced by the Spanish to America soon after the conquests of Cortez and became naturalized in Mexico and the southeastern United States and a number of selections were subsequently made. Until recently, naturalized wild peaches called "Tennessee nat-

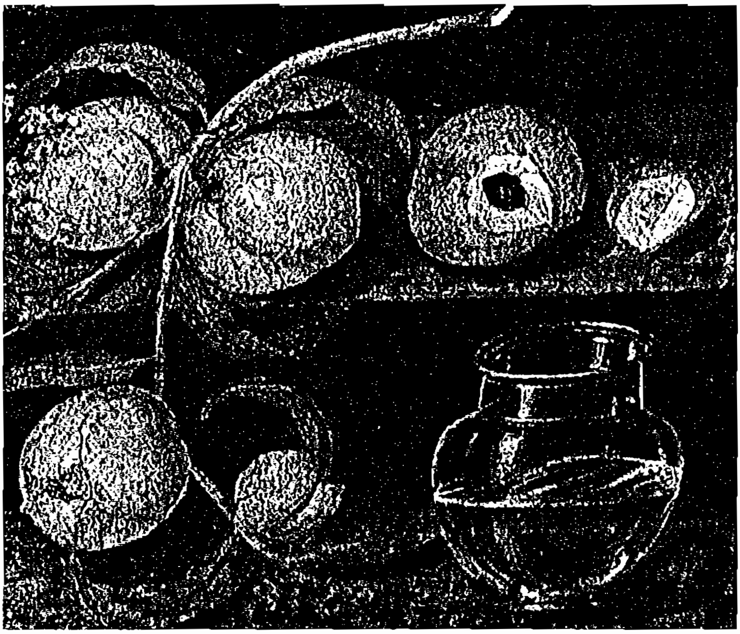


Fig. 8.18. Roman painting of peach from Pompeii, before 79 CE. Source: Jashemski 1979.

urals" were widely used as rootstocks. In addition, soft and white-fleshed English selections were introduced. The peach is unadapted to England and was grown as a novelty or a conservatory plant. In 1850, an introduction from China via England called 'Chinese Cling' ('Shanghai'), adapted from the southern group of Chinese cultivars, was to completely change the peach industry. This introduction proved to be well adapted to warm, moist summer conditions. Open-pollinated progeny ('Chinese Cling' was pollen sterile) included 'Belle of Georgia' and 'Elberta'. 'Elberta' is large and highly flavored, and firm enough to withstand shipping, in contrast with the naturalized North American seedlings. Descendants of this material now forms the basis of the modern United States and European peach industry (Scorza and Okie 1990).

Extensive breeding activity has occurred in the United States, with California breeders concentrating on rubbery-fleshed cultivars for processing and both east and west coast breeders emphasizing a succession of freestone cultivars for fresh market (Scorza and Sherman 1996). As a result, various types have been selected that include a complete range of maturity, round to flat fruit shape, yellow to red fruit color, freestone and clingstone, white, yellow and red flesh, and pubescent and nonpubescent. The "fuzzless" peach, known as nectarine, which resembles a cross between a plum and a peach, is the result of a mutation that occurs commonly in peach, probably a deletion, because back-mutation from nectarine to peach is unknown.

Extensive efforts for extending the adaptability of peach have been carried out by breeding for low chilling requirement and cold hardiness. One of the problems with peach adaptation to cold climates is that freeze avoidance is due to deep supercooling which limits cold hardiness (Layne 1992). In peach, temperatures between –20° and –25°C kill flowers, and temperatures below –30° damage the wood. Breeding for low chilling requirement has extended the range to subtropical areas. Soil-borne problems have become increasingly important and nematode-resistant rootstocks have been selected. Recently, size-controlling rootstocks have been sought. There are a number of mutations for different growth types from dwarf to weeping that may be useful (Fideghelli 2003).

2. Citrus. Rutaceae consists of six genera of which three, *Citrus*, *Poncirus* (trifoliate orange), and *Fortunella* (kumquat), have commercial value. The genus *Citrus* includes a diverse group of evergreen Old World fruits originating in southeast Asia (eastern India, Burma, and southern China) and is now grown throughout the tropics and subtropics worldwide (Soost and Roose 1996). The principal horticultural groups include citron (*C. medica*), lemon (*C. limon*), lime (*C. aurantifolia*), pummelo (*C. grandis*), sour orange (*C. aurantium*), sweet orange (*C. sinensis*), mandarin (*C. reticulata*), and grapefruit (*C. paradisi*). These "species" designations are a convenient if inaccurate way to consider this group. Domestication of all but grapefruit occurred before 1000 BCE.

The taxonomy of citrus is controversial and reflects philosophical differences in defining relationships in an ancient group of cultivated plants, complicated by outcrossing, apomixis, and selection (Roose et al. 1995). Thus, Toshio Tanaka proposed 162 species; Walter T. Swingle recognized 16 species, while R. W. Scora, based on biochemical analysis has concluded three primary species: *C. medica* (citron), *C. reticulata* (mandarin), and *C. grandis* (pummelo). Molecular evidence supports the hybrid origin of many so-called species.

The Japanese botanist, Tyozaburo Tanaka, has proposed a line of demarcation (now known as the Tanaka Line) from the northeast border of India to the island of Hainan that separates the development of *Citrus* species and close relatives. The lemon, lime, citron, and pummelo, sweet and sour orange occur south of this line while most mandarins as well as *Poncirus* and *Fortunella* occur north of this line. Most citrus is cross-pollinated (pummelo is cleistogamous) and many are characterized by apomixes (associated with nucellar polyembrony), permitting cloning to be carried out by seed propagation.

Sexual hybridization between cultivated species has led to many new types of citrus, as indicated by their names. These include tangelos (tangerine × grapefruit), tangor (tangerine × orange), orangelo (orange × grapefruit), citradia (*Poncirus* × sour orange), and citrangequat (citrange × kumquat). Interspecific hybridization is the mechanism for the origin of the grapefruit (forbidden fruit) that first appeared in Barbados in the 18th century. It is derived from a natural cross of the non-apomictic pummelo (called a Shaddock in Barbados) with the apomictic sweet orange (Gmitter 1995). The grapefruit inherited the apomictic character from the sweet orange and can be proliferated by seed propagation. All grapefruit seem to be a single clone; subsequent changes, such as seedlessness and pink flesh and fruit, have occurred via selection of somatic mutations.

The first citrus to reach the West was the citron, whose name, *C. medica*, suggests Media (Persia now Iran) as the source. According to De Candolle, citron is found in the Himalayas in India and was reported in Iran in 300 BCE. It may have reached the West before this date and Goor and Nurock (1968) suggest it was referred to in Nippur in South Babylon as early as 4000 BCE, but this is not confirmed by Postgate (1987). It is not mentioned in Egyptian writings until the 2nd century CE.

Biblical references to the "fruit of the goodly tree" considered the *etrog* (the Hebrew name of the citron in Leviticus (23:40) would date it to about 1200 BCE. It soon became a sacred tree to Jews and the citron (with the style attached) is still offered as gifts at Succoth (the Feast of Tabernacles). The citron became associated with winter by the Romans, and citrons are found in mosaics celebrating the seasons (D. Parrish, pers. commun.). The baroque painter Bimbi (1648–1729) included various citrons in his paintings of fruit cultivars (Consiglio Naazionale delle Ricerche 1982).

The sweet and sour orange reached Europe in the 11th century via the Arabs. The Arabic name *haranj*, Persian *harang*, and Spanish *Naranja* is the source of the name for the color we know as orange. The lemon and pumello were introduced to Europe in the 12th century and the lime in the 13th. The greatest wave of citrus into Europe was in the 15th century from merchants arriving from southeast Asia overland. A second wave occurred in the 16th century by Portuguese sailors who introduced citrus of higher commercial quality. The development of protected culture (orangeries) in the European Renaissance to overwinter citrus trees initiated a vogue for the nobility and the wealthy, who enjoyed the fragrant flower and beautiful fruit, to produce citrus in containers. Mandarins, which originated in Vietnam and China, were important fruits in China and Japan in the 12th century but did not reach Europe until 1805 (Roose et al. 1995).

Although propagation from polyembronic (nucellar) citrus seed is true-to-type, the long juvenile period, as well as juvenile characters such as thorniness and thick albedo, make propagation by grafting desirable. Various citrus have been used as rootstocks. However, because seedlings are virus-free, nucellar clones have been used to eliminate viruses from citrus. Recently meristem grafting, combined with thermotherapy, has been used to produce virus-free clones.

Selection in citrus is associated with changes in size, shape, color of flesh and peel, acidity, ease of peeling (mostly from mandarins), and seedlessness. Seedlessness may be induced by x-rays. In the United States, the popularity of orange juice has created a tremendous industry for concentrate, and so-called "fresh" chilled juice. Much of citrus processing has moved to Brazil where the climate around Sao Paulo is very suitable for citrus. Easy-peel citrus is desirable for consumer use and represents the future of the fresh fruit industry.

3. Banana and Plantain. Bananas and plantains (*Musa* species, Musaceae) are indigenous to southeast Asia and the Pacific (Simmonds 1995). These are large, herbaceous, perennial plants with a pseudostem consisting of tightly whirled leaf sheaths through which the inflorescence emerges. Bananas are the name for fresh fruit types, while plantains refer to cooking types. They are propagated vegetatively by corms (the true stem) through offshoots. The early evolution and migration of the banana is unknown but is ancient. Banana is referred to by Theophrastus and certainly originated thousands of years earlier. Bananas reached west Africa before European contact, and a few clones from there reached the New World in the late 15th century. They were widespread in the tropics by the end of the 16th century.

The wild bananas are seedy and diploid. The cultivated bananas and plantains exhibit a combination of parthenocarpy, sterility, and polyploidy, principally triploidy. Parthenocarpy results from complementary dominant genes found in wild species of *M. acuminata*. Parthenocarpic triploids arose from unreduced gametes ($2n+n$) and are seedless. These types must have been immediately selected and multiplied by offshoots. Hybrids between diploid *M. acuminata* (AA genomes) and *M. bulbisiana* (BB genomes) produced diploid AB hybrids and AAB and ABB triploids, the plantains and cooking bananas. These are assumed to have originated by migration of the edible diploid, male-fertile AA types into area of *M. balbisiana* (BB) followed by nonreduction to produce triploidy. Some tetraploid hybrids (AAAB, AABB, and ABBB) also exist.

Some AAA triploid types (known as the Cavendish group) include the main bananas of commerce. Selection for somatic mutations has resulted in a number of clones but they are very similar and the banana industry is threatened by the perils of monoclonal culture. Breeding efforts have begun but are beset by the difficulties of working with a seedless crop. Efforts are being made to produce new AAA triploids from AA × AAAA crosses and breeding efforts are underway for the cooking types taking advantage of unreduced gametes (Ortiz 2003).

4. Mango. Important crops of the Anarcardiaceae include the mango (*Mangifera indica*) and pistachio (*Pistacia vera*) native to East Asia, and the cashew (*Anacardium accidentale*) native to tropical Brazil. The mango, the most popular fruit in India, is now the fourth most important fruit crop in the world. In 2001 over 25.1 million tonnes of mango were produced from about 90 countries, with about 77% produced in Asia (Galán Saúco 2003). The mango originated in the Indo-Burma region and grows wild in the forest of northeast India and is an allopolyploid between *M. indica* and *M. sylvatica*. Known for 4 to 6 thousands years, the mango spread through the Indian subcontinent, and reached Malaya in the about the 5th century BCE (Purseglove 1968), East Africa in the 10th century, and the New World in the beginning of the 19th century. It was successfully introduced to Florida in 1861. Mango is consumed fresh, dried, or processed and is widely used in chutneys. To mango enthusiasts, the mango is a fruit that the peach only aspires to become.

Nucellar polyembryony is widespread in the mango, allowing vegetative propagation of some types from seed. Two major groups of mango are recognized, the Indian race (monoembryonic) and the Philippine race (polyembryonic). Diversity in mango is very high for fruit size, skin color, and flesh quality that ranges from fibrous to smooth with flavor from turpentine-like to mild. Many generations of selection have produced cultivars free of seed fibers without the turpentine flavor. A number of attractively colored cultivars selected in Florida (Tommy Atkins, Kent, Keitt, Haden, Van Dyke, Sensation Palmer, and Parvin) mainly derived from Indian clones such as ‘Mulgoba’ predominates in the export market.

5. Persimmon. The genus *Diospyros* (literally “fruit of god”), Ebenaceae (x=15) consists of about 400 species widely distributed in the tropics of Asia, Africa, and the Americas. The temperate species, *D. kaki*, (2n=90) known as kaki or Japanese persimmon, originated in China. It is a beloved fruit in China, Korea, and Japan and has been known from prehistoric times but there is some production in the United States (California), Italy, Israel, Brazil, Australia and New Zealand (Yonemori et al. 2000). The American species *D. virginiana*, (2n=60, 90) known as persimmon, a name of the Algonquin Indians of Virginia, is a backyard fruit with a number of local selections, but there is essentially no industry, and it is debatable if the fruit can be considered domesticated.

Kaki is an attractive fruit with yellow, orange, to deep red skin color, while the intense red color of the autumn leaves makes it an attractive ornamental. The species is considered polygamo-dioecious with three types of sex expression: pistillate, monoecious, and polygamo-monoecious (hermaphroditic, pistillate, and staminate flowers) suggesting selection away from dioecy during the domestication process. There are presently over a 1000 known cultivars with distinct types resulting from mutations involving parthenocarpy and astringency. Parthenocarpy is an important factor controlling productivity because fruit drop in seeded types is a major problem; the higher the parthenocarpy the less the early fruit drop. Parthenocarpy also eliminates the problem of providing pollenizors for pistillate cultivars. Seedless fruits are preferred by the consumer.

The developing fruit are extremely astringent due to soluble tannins in the vacuoles. Non-astringent (NA) cultivars lose astringency naturally during fruit development, whereas astringent cultivars (A) retain astringency until maturity. Astringency can be reduced by ethylene application. There is a further classification of cultivars based on the effect of seed on flesh color: pollination variant (PV) and pollination constant (PC). The flesh of PV types becomes dark around the seed, whereas the flesh color of PC types is uninfluenced by seed. The four types of fruit (PCNA, PVNA and PCA and PVA are categorized in Table 8.3. The goal of modern fruit breeding is to obtain parthenocarpic PCNA offspring. Breeding efforts are now facilitated by molecular markers.

6. Kiwifruit. The kiwifruit (*Actinidia deliciosa*, Actinidiaceae, $2n=174$, $x=29$), a dioecious vine, is an example of an ancient fruit species domesticated in the 20th century (Ferguson and Bollard 1990). It derives from a gathered fruit known as *mihautao* (monkey peach), which had long been appreciated in China (Fig. 8.19) but was collected rather than cultivated (Ferguson 1990). Introduced to the United States and New Zealand early in the 20th century by the plant explorer E. H. (Chinese) Wilson, it was referred to as Chinese gooseberry in the United States. Although it remained a curiosity in the United States, New Zealand growers and nurserymen succeeded in domesticating the crop by selecting suitable male and female clones, as well as developing techniques for cultivation. One seedling selected by A. Hayward Wright and subsequently named 'Hayward', became the mainstay of the world industry. The fruit was exported to the United States where it was promoted by Frieda Caplan, a marketer of new crops. In 1959 the relatively unattractive brown fruit received the new name kiwifruit after the kiwi, an endemic flightless bird often used as a nickname for New Zealanders. Kiwifruit has a pleasant but weak flavor with very high Vitamin C

Table 8.3. Horticultural classification of persimmon cultivars by astringency and flesh color of fruit. Source: Yonemori et al. 2000.

Seed effect	NA (Non-astringent)	A (Astringent)
PC (Pollination constant)	**PCNA** Non-astringent at maturity whether seeded or not. Flesh color unaffected by seed at maturity. Tannins are not coagulated by ethanol treatment at immature stages when fruit is still astringent. (**VIG**[z])	**PCA** Astringent at maturity unless treated. Flesh color unaffected by seed at maturity. Tannins are coagulated by ethanol treatment even at immature stages. (**VDG**[y])
PV (Pollination variant)	**PVNA** Non-astringent at maturity only if seeded. Flesh turns brown at maturity if seeded. Tannins are coagulated by ethanol treatment even at immature stages. (**VDG**)	**PVA** Astringent at maturity unless treated. Brown flesh color only around seed at maturity. Tannins are coagulated by ethanol treatment even at immature stages. (**VDG**)

[z]VIG; Volatile-independent group.
[y]VDG; Volatile-dependent group.

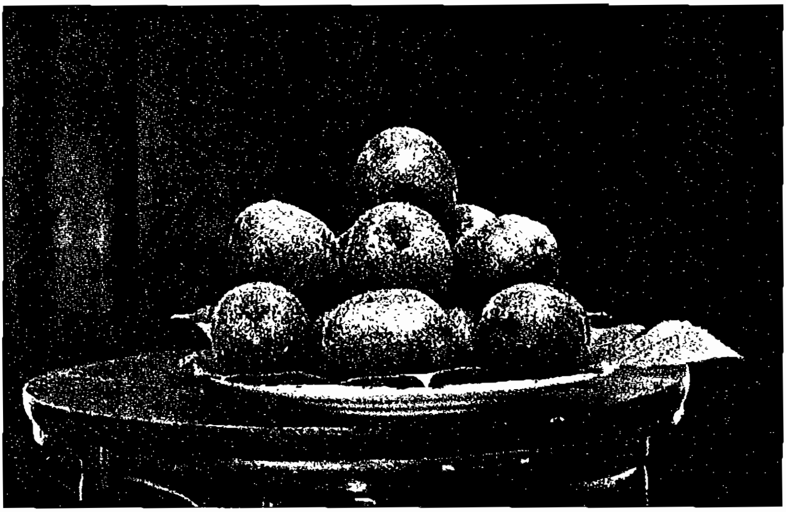


Fig. 8.19. Fruit of mihautao (kiwifruit) taken by W. H. Wilson in western Szechuan, China in 1908. Source: Ferguson and Bollard 1990.

content, but the nutritious quality of the fruit has not been promoted; rather, it was the beautiful and unique appearance of the sliced flesh, which is used as a garnish on bakery products or as a component of mixed fruit, made this fruit popular worldwide. The long storage life of the fruit made it possible for New Zealand to export the fruit year-round. The popularity of the crop made millionaires of many New Zealand growers, but as kiwifruit began to be grown in such countries as the United States, Italy, and Chile, the boom crashed and New Zealand growers had to struggle to survive. Kiwifruit is consumed out of hand in New Zealand, usually scooped with a spoon, but this technique has not caught on, and further expansion is probably linked to development of a simple method for peeling. A yellow-fleshed kiwifruit marketed as Zespri™ Gold (*A. chinesis*, $2n$=58, a tetraploid) was recently introduced, and the New Zealand growers are attempting to control its distribution. It is too early to know if this will succeed. A small-fruited, hardy and fuzzless species (*A. aguta*, $2n$=96, 114), sometimes called tara fig, is now cultivated in gardens, but has not been commercialized.

D. American Fruits

1. Strawberry. Strawberry is the most widely grown of the berry fruits, sometimes called small fruits based on plant size (Darrow 1966). Strawberries are herb-like perennial plants, but the compressed stem may become woody. The plant propagates naturally from runners or from crown divisions. Strawberry has an interesting history. *Fragaria vesca*, Rosaceae known as the wood strawberry, a diploid species ($2n$=16) with bisexual flowers, has small, aromatic fruit and is found in Europe, northern Asia, northern Africa, and North America. It was mentioned by Pliny in the 1st century and in the 14th century white- and red-fruited selections and, later, everbearing types (*F. silvestris*] were cultivated in Europe, both as a fruit crop and as an ornamental, little changed from the wild. It is still being grown in Europe as a gourmet fruit. Later, a tetraploid species, *F. moschata* ($2n$=32) known as the hautbois, was briefly grown in England.

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 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. Through the years selection has resulted in tremendous changes as the plant evolved from a predominantly dioecious species into a hermaphroditic species, in which flowers contain both stamens and pistils. As a result of extensive breeding in the 20th century (Hancock et al. 1996) fruit size has been greatly increased as well as fruit firmness (too firm for some), and resistance to a number of leaf diseases. Flowering and runnering are both affected by photoperiod but adaptation has been increased with the introgression of the day-neutral character from *F. virginiana*. Although strawberry is widely adapted, the strawberry industry is now concentrated in California in the United States, in Spain, and in Italy. Some strawberries are now grown in greenhouses.

2. Brambles (*Rubus*). The genus *Rubus*, Rosaceae (x=7), is very diverse and many species throughout the world are harvested from the wild. The cultivated *Rubus* species, known collectively as brambles, includes red raspberry (*R. idaeus*), black raspberry (*R. occidentalis*) both diploids, $2n$=14, and polyploid blackberries (many species of *Rubus*) and, now, many interspecific hybrids between raspberry and blackberry, such as loganberry, and tayberry ($2n$=42), and boysenberry ($2n$=49) (Jennings 1995; Daubeny 1996). *Rubus* is divided into sections: Idaeobatus and Eubatus. Idaeobatus (raspberries) is often divided into two subspecies, *R. idaeus vulgatus*, the red raspberry of northern Europe and Asia, and *R. idaeus striosus*, the red raspberry of North America. Eubatus (blackberries) is native to the New World. Brambles have delicious flavors but marketing has been a problem because of the soft texture of the fruit.

The first records of the European raspberry date to antiquity and Pliny writes of wild raspberries as coming from Mt. Ida. The European raspberry has been cultivated since medieval times but there is little evidence of distinct types. During the 19th century, crosses between European raspberry (subspecies *vulgatus*) and North American types (subspecies *strigosus*), made in both continents, gave rise to present-day cultivars, and recent breeding efforts have introduced new genes from a number of *Rubus* species. The black raspberry (*R. occidentalis*), indigenous to eastern North America, was first cultivated in the early 19th century, and subsequently purple types were derived from hybrids between black and red raspberry.

The blackberry has a complex origin and includes wild species from diploid ($2n$=14) to dodecaploid ($2n$=84). Trailing blackberries are selections from *R. ursinus*. Many other local species are cultivated, including dewberries (*R. trivialis*) in the southern United States, *R. parvifolius* in

China and Japan, and *R. phoenicolasius* in Japan. Attempts at domestication were first reported in Europe in the late 17th century with *R. laciniatus*. In eastern North America, selection from natural stands of interspecific crosses contributed to domestication. The main problem was excessive thorniness. A spine-free variant of the octoploid 'Austin Mayes' called 'Austin Thornless', served as a dominant source of spinelessness. Later recessive sources of spinelessness were obtained. Selection among various *Rubus* has concentrated on thornlessness, plant habit, fruit quality, fruit size, disease and pest resistance, adaptability to machine harvest, chilling requirements, and postharvest life (Daubeny 1996).

3. Vacciniums. Species of *Vaccinium*, Ericaceae (x=12), include cultivated blueberries and cranberry, both domesticated in the 20th century. The lingonberry is widely gathered but can hardly be considered domesticated despite recent selections of elite types; cultivation consists almost entirely of managing natural stands. A number of *Vaccinium* species such as bilberry (*V. myrtillus*) and bog bilberry (*V. uliginosum*) are potential domesticates (Galletta and Ballington 1996).

Blueberry. There are five major classes of blueberry grown commercially: lowbush, highbush, halfhigh, southern highbush (low chill), and rabbiteye. In lowbush (tetraploid *V. angustifolium*, diploid *V. myrtilloides*, diploid *V. boreale*), improvement has originated from selection of wild clones (Galletta and Ballington 1996). There is still an industry from natural stands of lowbush blueberry in Maine and commercial lowbush production is still more than 95% from unselected wild plants. Highbush blueberries are derived from tetraploid genotypes of *V. corymbosum,* although some have *V. angustifolium* in their pedigree. These types were developed by F. V. Coville, USDA botanist from 1888 to 1937, and subsequent breeders. Halfhigh blueberries are derivatives of lowbush-highbush hybrids, usually *V. angustifolium* × *V. corymbosum*, but breeding in Finland and Poland has emphasized hybridization between *V. corymbosum* and tetraploid genotypes of *V. uliginosum* to improve cold hardiness and tolerance to *Fusicoccum* canker. Southern highbush blueberries are similar to highbush types but have a low-chilling requirement as a result of crosses with *V. darrowi* and other species. Finally, rabbiteye blueberries, highly vigorous plants adapted to the southern United States, belong to the highly polymorphic hexaploid *V. ashei*. Recent progress in breeding has resulted in increased fruit size, productivity, and adaptability to mechanical harvest.

Cranberry. Cranberries are usually divided into two species, the circumboreal *V. oxycoccus*, and the large-fruited *V. macrocarpon*, native to eastern North America. In the 18th and 19th centuries the large-fruited cranberry was gathered from natural bogs, but substantial plantings had been made by 1850 in New Jersey, Massachusetts, and Wisconsin, and the technology of wetland cultivation was developed (Dale et al. 1994). Domestication of *V. macrocarpon*, which is adapted to lowland acidic soils, has been achieved by selection from elite wild plantings and subsequent hybridization (Galletta and Ballington 1996). Most cranberry cultivars originated as single-plant selections of native bog populations, and four of them still accounted for 90% of the total American production area in 1990. Although cranberry was a traditional holiday fruit consumed at Thanksgiving feasts in the United States, expansion of the industry has occurred with innovative processing involving freezing, juice production—particularly mixtures with other juices—and as a dried fruit. Cranberry has also been considered a health food and the juice is recommended for urinary tract health in women.

Lingonberry. Vaccinium vitis-idaea is a circumboreal, woody, dwarf to low-growing, rhizomatous, evergreen shrub. The plant is indigenous to Scandinavia and has been harvested from natural stands since the Bronze Age, based on remnants of lingonberry wine in Danish graves (Hjalmarsson and Ortiz 2001). Icelandic law of the 13th century limited berry picking in other people's land to that consumed on the spot, indicating its importance as human food. Although elite selections have been made, there is essentially no industry aside from the management of wild stands. Lingonberry has a long history of commerce and 20 million kg of fruit were exported from Sweden, typically to Germany in 1902. Lingonberry preserves, once a traditional delicacy in Scandinavia, are now considered a luxury food.

4. Pineapple. The pineapple (*Ananas comosus*, Bromeliaceae) was domesticated in pre-Columbian tropical South America, probably north of the Amazon River with a possible secondary center in southeast Brazil (Leal 1995; Leal and Cioppens d'Eeckenbrugge 1996). Selection was based on fruit size, seedlessness and parthenocarpy, long, fibrous smooth leaves and ease of vegetative propagation. In fact, the pineapple can be propagated in a number of ways (stumps, offshoots, slips, and the fruit crown). The pineapple plant is very tough and desiccation resistant and wide distribution occurred in the Americas though human migration and exchange. It was present in all adapted areas of the New World at the time of the European encounter with America (Fig. 8.20). The early description by Pigafetta in 1519 is exuberant: "*this fruit resembles a pine cone and is extremely sweet and savoury; in fact it is the most exquisite fruit in existence.*"

Fig. 8.20. The first description of pineapple in 1535 shows a fruit similar to present-day cultivars.

The pineapple has changed little from that era except that genetic variability has been greatly reduced. There are about 6 cultivar groups (Spanish, Cayenne, Queen, Pernambuco, and Maiopure), but only two 'Cayenne' and 'Queen' were commercially important for most of the 20th century despite the fact that the pineapple became associated with a tremendous processing industry. The 'Cayenne' cultivar has been the mainstay of the processing industry because of its robust, large, romboid fruit, which produces many slices, the most valued product. Despite a number of industry-sponsored breeding programs, it has not really been displaced. Continual selection of somatic mutants is important, especially for less spiny types ('Smooth Cayenne'), and for improved fruit shape and quality. 'Cayenne' is not highly valued for fresh fruit, but recently a new cultivar, derived from sexual hybridization at the Pineapple Research Institute, now defunct, has become very popular for fresh fruit and is being marketed as 'Del Monte Gold'.

5. Avocado. *Persea* is one of 50 mainly tropical genera of the Lauraceae, most of them from the New World. The early history of avocado (*P. americana*) is unknown but it seems to have originated from southern Mexico to present-day Panama (Bergh and Lahav 1966). There are remnants of seed from 7000 BCE with evidence of selection after 2000 BCE based on seed size (Bergh 1995). The Spanish conquistadores found the avocado (from the Aztec *ahucalte*) cultivated from northern Mexico to Peru. The avocado are one of the oily fruits, consumed either fresh as part of a salad, or, in Brazil, whipped into a creamy dessert, and also used as a primitive soap.

Three horticultural races or subspecies (ecotypes) based on their presumed area of origin are recognized (Mexican, Guatemalan, and West Indian) but it is now clear that the West Indian race is a lowland type originating in the western coast of Central America. In general, the Mexican and Guatemalan types are considered subtropical and native to highlands, while the West Indian are adapted to tropical lowlands. The largest fruit are found in the Guatemalan types, but oil content is highest in Mexican race.

The avocado has perfect flowers but cross-pollination is promoted by protogynous dichogamy with synchronous complementarity. Type A types are functionally pistillate in the morning and functionally staminate the following afternoon, while B types are pistillate in the afternoon and staminate the following morning. Thus, both A and B types are required for successful pollination.

Most of the current cultivars are based on selection for high oil as well as relatively small seed size, high productivity, and disease resistance. 'Fuerte', the most important present-day cultivar, was selected in 1911, from seedlings by the Rodiles family near Atlixco, Mexico. Breeding efforts are hampered by long juvenility, sometimes as long as 15 years. 'Haas', originating as a chance seedling in California, is increasing in importance.

6. Papaya. *Carica*, Euphorbiacia, a genus with about 40 species is indigenous to tropical America (Purseglove 1968). Papaya (*Carica papaya*), derived from natural hybridization involving *C. peltata*, is a frost-tender, non-woody plant reaching a height of 8 m. It is widely grown as a dooryard plant throughout the tropics for the melon-sized fruit usually consumed for breakfast. The proteolytic enzyme papain has been exploited as a meat tenderizer and has been used for some surgical procedures.

The tree is commonly dioecious, although there are types that are considered polygamo-dioecious with both hermaphroditic and pistillate plants. In these types (e.g., 'Solo', the popular Hawaiian cultivar with fruit averaging about 600 g) fruit shape of the hermaphroditic types is pyriform (the preferred type) while the fruits from pistillate trees are round. The tree has a short juvenile phase but is short lived. Papaya is one of the few fruits that are propagated exclusively by seed.

Fruit size varies from small to very large, up to 9 kg. The fruit, yellow when mature, has flesh color from orange to red. Recently the inbred 'Solo' papaya has increased in popularity for export to the United States and Japan and is now widely grown in Brazil, although large-fruited Mexican types are also exported to the United States. The papaya has serious virus susceptibility and cannot be grown in Florida for this reason. Recently, resistance to the tomato mosaic virus has been introduced by transgene technology.

IV. GENETIC CHANGES AND CULTURAL FACTORS IN DOMESTICATION

The genetic changes associated with domestication in fruit crops is presented in Table 8.4. Despite some well-known exceptions, fruit crops are characterized by a number of common features. Noteworthy is the obvious appeal of taste—often a combination of sweetness and acidity with many considered delicious because of aromatic constituents. The appealing, sweet taste of many fruit is probably a trait associated with natural selection for seed dispersal mediated by mammals. Most fruit crops are highly cross-pollinated, and tree fruits generally have long juvenility and long-life. Some fruit crops have the ability to propagate vegetatively. Subsequent progress in the improvement of fruit cultivars resulted from continual selection of seedling populations, and from intercrosses among elite clones or with wild or introduced clones, that vastly speeded up the process. This process has been very efficient and in spite of progress in plant breeding, replacing grower-selected clones has not been easy (Table 8.5).

A review of the fruit crops discussed above indicates that the origins of fruit growing evolved from an interaction of genetic changes and cultivation technology, often unique for each species. 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

Table 8.4. Genetic changes associated with domestication in fruit crops.

Breakdown of dioecy	
carob, fig, grape, papaya, strawberry (unchanged, date palm, kiwifruit)	
Loss of self-incompatibility	
cherry	
Parthenocarpy & 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**
Tetraploid:	**tart cherry, raspberry, blackberry, blueberry, kiwifruit (*Actinidia sinensis*)**
Hexaploid:	**European plums, kiwifruit (*A. deliciosa*)**
Octaploid:	**strawberry**
Loss of toxic substances	
"Sweet" seed:	**almond**
Nonastringency:	**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	

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. Cranberry cultivation

Table 8.5. Effects of organized fruit breeding on the commercial world industry.

Negligible	Slight	Moderate	Major
Banana & plantain	Cranberry	Almond	Blueberry
Chestnut	Cherry (tart)	Apple	Brambles (raspberry & blackberry)
Date palm	Citrus	Apricot	Cherry (sweet)
Fig	Hazelnut	Avocado	Currants
Grape (wine)	Papaya	Pear Asian	Grape (table)
Lingonberry	Persimmon	Pecan	Strawberry
Olive	Pear European		Peach & nectarine
Pomegranate	Pineapple		Plum

has recently been adopted in Chile. The kiwifruit, a dioecious vine native to China but never cultivated there, has been appreciated since the 8th century in China and probably much earlier. 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 (see IV D). 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 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—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.

A. Mutation as an Agent of Domestication

Many domesticated fruit crops differ from their wild progenitors by a few characters that have appeared as mutations (Table 8.4). 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 that has proved important in grape, banana, and citrus. In dioecious fruit and nut crops, mutations inducing hermaphrodism [carob (Zohary 2002), grape, papaya, and strawberry] are associated with domestication. Other mutations associated with domestication include loss of spininess (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. Many of these mutations are not heritable because they do not occur in the appropriate meristematic layer.

B. Interspecific Hybridization and Polyploidization

Many of our fruit crops have resulted from interspecific hybridization, polyploidy, or both (Table 8.4). This is particularly obvious in *Actinidia*, *Citrus*, *Fragaria*, *Musa*, *Prunus*, *Rubus*, and *Vaccinium*. The evolutionary divergence within these genera into different "species" is often associated with polyploidy. These changes represent the divergence of interbreeding populations that became isolated, known as nominalistic species (Spooner et al. 2003). Domestication within these groups and subsequent transfer by human migration would facilitate intercrosses. This development has been well worked out with bread wheat (*Triticum vulagare*), a hexaploid amphidiploid of the genomic constitution AABBDD. Genomic analysis has identified the three species involved: AA from *Triticum urartu*, or einkorn, BB from *Aegilops speltoides*, and DD from *Aegilops tauschi* or goatgrass. The cross of emmer (AABB) with goatgrass (DD) is presumed to have occurred about 6000 BCE. This process occurred in many fruit crops (cherry, banana and plantains, citrus, brambles) as well as in deliberate chromosome manipulation (blueberry). Recently, "interspecific hybridization" has been used to create new fruits in citrus (tangelos, tangors), *Prunus* (plumcot), and *Rubus* (tayberry).

C. Hybridization and Selection

Zohary and Spiegel-Roy (1975) have concluded that spontaneous hybridization between wild races and cultivated clones was critical to the early domestication of fruits. 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. In the case of apple, Barrie Juniper (pers. commun.) has made the case that selection for large fruit may have been due to selection by bears over millions of years.

Selection from sexual recombination can be clearly followed in North America, now considered a secondary center of origin for the cultivated apple. 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 (Beech 1905). In 1634, Lord Baltimore instructed the first Maryland settlers to carry "*kernalls of pears and apples, especially of Permains and Deesons, for making thereafter of Cider and Perry*" (Calhoun 1995). 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), born in 1744 in Leominster, Massachusetts, distributed apple seeds from cider mills in western Pennsylvania and founded a nursery in West Virginia, distributing seeds along the way. 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 Beech's (1905) *Apples of New York.* Roueché (1975) estimated that 100,000 clones have been selected from literally hundreds of millions of seedlings and evaluated by millions of fruit growers. 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. '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).

Among the characters that are influenced by selection is the ease of propagation. The key to domestication of fruit crops is vegetative propagation of elite types, followed by natural intercrosses between elites and wild species. This can clearly be seen in the date palm, in which domesticates, but not wild species, are naturally propagated by offshoots. It also occurs in the apple; dwarfing rootstocks are clonally propagated by layering (stooling) and this character, at least before the advent of micropropagation by tissue culture, is an essential trait. A number of nut trees, black walnut and pecan in particular, have been difficult to propagate vegetatively and are often still propagated from seeds, resulting in a negative effect on productivity.

Selection for fruit quality, based on flavor, color, and shelf life, is the goal of modern fruit breeding programs. Selection is nowhere more important than in pineapple where the processing industry was long based on a single cultivar, 'Cayenne' and its spineless sport ('Smooth Cayenne') that was uniquely adapted to producing canned slices. A sweeter, yellow fleshed seedling produced from hybridization is now being marketed as 'DelMonte Gold' and is transforming the world fresh fruit industry because of better fresh fruit quality and appearance.

D. Champions

The decisive contribution to domestication made by individuals is unknown in most fruit crops and these great horticulturists are largely unremembered and unsung. However, in a few cases of recent domestication, key persons have been identified. These champions are essential to the domestication process. In the case of the kiwifruit, this includes the great plant hunter E. F. Wilson, who introduced the fruit to Britain; a missionary, Katie Frazier, who imported seed to New Zealand, possibly derived from Wilson; and H. R. (Hayward) Wright, who selected the pistillate clone that bears his name. The technology for orchard development was made in New Zealand from grafted plants, principally by F. J. Walker in the town of Wanganui.

Domestication of blueberry was initiated by a single researcher, Frederick Vernon Coville (1888–1937), USDA botanist, who recognized the potential of this species, and later had a fortunate collaboration with Elizabeth White, a blueberry enthusiast from Whitesbog, New Jersey. Later influential researchers included George Darrow and Arlen Draper, both USDA researchers. In strawberry, Amédee François Frézier introduced

F. chiloensis to France, resulting in the fortuitous hybridization with *F. virginiana*, and the great French botanist, Antoine Nicolas Duchesne, who explained the dioecious nature of *Fragaria*, interpreted *F. ananassa* as an interspecific hybrid, and identified hermaphroditic types. The origin of the grapefruit (once known as forbidden fruit), which was discovered from natural intercrosses between orange and pummelo, called shaddock in Barbados, can be traced to the trader Philip Chaddock, who in the mid-17th century introduced the pummelo to Barbados. Domestication does not just happen but is carried out by acts of real people and they need to be honored.

E. Lost Fruits

Although a number of fruits have Cinderella stories, many lose out. Some fruits, once popular and widely grown, fall into disuse. Perhaps this can be considered reverse domestication. Examples include sycomore fig, medlar, quince, and the Asian apple (*M. asiatica*). A number of fruits languish as regional fruits. Thus, *Ribes* species (gooseberries, red and black currants) have never been popular in North America, the Asian persimmon (kaki) has never been really popular outside of Asia, and grapefruit, popular in the United States, is only slowly being adopted in Europe and Asia.

F. Fruit Breeding

Fruit breeding as an organized activity is a 19th century innovation. Its origins trace to mass selection efforts in strawberry (*see* III D 1) and pear (*see* III B 1).

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 (Knight 1806). 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 presaged 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 apple and pear breeding programs.

In the United States, fruit breeding became a part of research at the state and federal experiment stations and a number of important breeding programs were initiated throughout the United States. Fruit breeding also became an activity of the private sector. 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 evolutional theories of Darwin (Crow 2001). At present, private breeders are an important part of *Prunus* (especially peach and nectarine and plum) and recently strawberry and raspberry.

Although fruit breeding has been a major activity since early in the 20th century, the results have been uneven and vary from ineffectual to extraordinarily successful (Table 8.3). Many of the world fruit industries are still based on grower-selected clones. The reason for the lack of progress 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 programs. 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.

G. Predicting Future Changes

Knowledge of domestication should be used to predict future changes, and to help domesticate new candidates. 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 in banana and plantain (now in jeopardy because of lack of genetic diversity), the creation of new stone fruits, and the creation of new seedless, easy-to-peel citrus. 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 are required, since many selections are somewhat insipid (Mizrahi et al. 2002).

A number of generalizations can be made concerning the origin and future development of fruit crops. The first is that most fruit crops are little removed from wild species, some perhaps by only a few generations, so that continued progress should be possible. The key breeding system has evolved from selection of elite clones followed by fixation by vegetative propagation. The development of fruit culture is based on an interaction between genetic changes and cultural practices. Indeed, in many fruit crops, once desirable clones are discovered, intensive efforts have been made to prop them up by cultural practices. These include artificial pollination, the use of disease-resistant and size controlling rootstocks, extensive methods of disease control, including 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. Despite some intensive breeding programs, extremely successful in *Prunus*, strawberry, and blueberry, many of our fruit cultivars are ancient and based on grower-selected seedlings and somatic mutations (Table 8.2). Advances in molecular genetics may overcome some of the limitations to conventional fruit breeding based on sexual recombination 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. Progress has already been achieved in papaya (virus resistance) and apple (fireblight resistance) but fears of consumer resistance is a problem.

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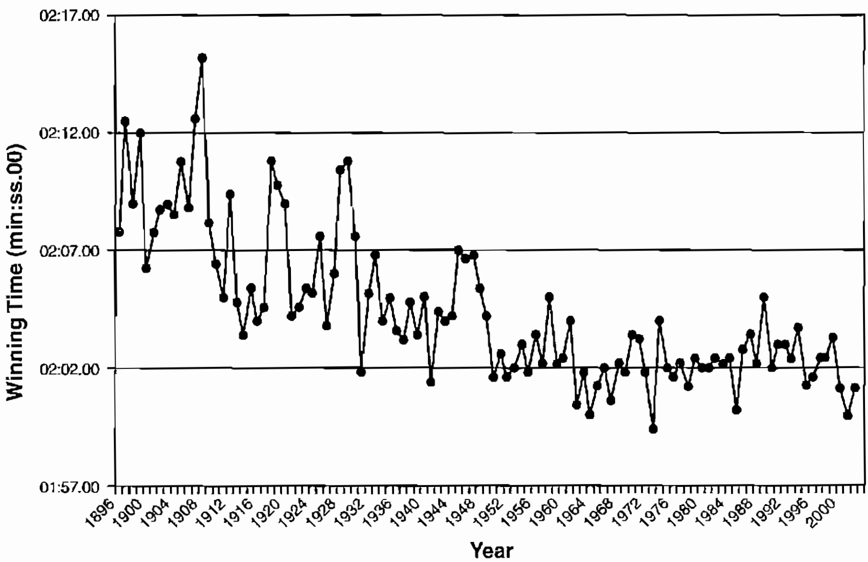

Race times in horses—The Kentucky Derby

data source: http://www.drf.com/home/crown2001/kd/derby_stats.html