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# A History of Grafting

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## I.  INTRODUCTION

Since the origins of agriculture, the progressive domestication of food crops has been intimately related to a series of innovations in plant propagation. In the Fertile Crescent, 10,000 to 12,000 years ago, nomadic peoples subsisted in part by collecting the seeds of auto-gamous (self-pollinating) wild grasses (emmer and einkorn wheat, barley) and pulses (lentils, chickpeas, peas). Unintentional selection for traits useful to humans, such as nonshattering, uniform ripening, and other characteristics known as the domestication syndrome, progressed relatively rapidly. This resulted in some measure of food security, which contributed to social stability and the decline of nomadism. Although fruits, nuts, and other tree-related foods and fibers were an important part of the diet, it was only several thousands

of years later that domestication of woody plants began (Childe 1958; Zohary and Spiegal Roy 1975; Janick 2005). Unlike the grains and pulses domesticated much earlier, most useful woody species are highly heterozygous and do not come true to type from seed, which precluded rapid genetic improvement by seedling selection. What made tree domestication possible was the mastery of cloning via asexual propagation. Initially this involved cloning of genetically superior individuals of species that rooted easily from cuttings or layering or propagated by offshoots. The modification and adoption by early agriculturists of these techniques allowed for the domestication of fig, grape, pomegranate, and olive in the third or fourth millennium (Zohary and Spiegel-Roy 1975); all of which root easily from cuttings, and date palm, which was propagated by division of offshoots. The domestication of woody species that do not root easily from cuttings, such as apples, pears and plums, did not come until the discovery of grafting, at least several thousand years later, about the beginning of the first millennium BCE. Thus, grafting is a pivotal technology in the history of temperate fruits and probably influenced their movement from Central Asia to Europe (Juniper and Maberly 2006). However, when and where detached scion grafting, which made possible the domestication of a new range of fruit trees, was invented is not clear.

## A. Definitions

*Grafting* can be defined as the natural or deliberate fusion of plant parts so that vascular continuity is established between them (Pina and Errea 2005) and the resulting genetically composite organism functions as a single plant. Two adjacent intact plants or different branches of the same plant can become naturally or intentionally grafted together; deliberate grafting involves inserting a previously cut shoot into an opening in another plant growing on its own root system (detached scion grafting). The term *scion* (cyon) refers to the shoot piece or bud cut from a donor plant that will grow into the upper portion of the grafted plant, The terms *stock*, *under stock*, or *rootstock* all refer to the plant that receives and fuses with the scion and functions as the root system of the grafted plant. *Stock* is synonymous with either *rootstock* or *under stock*, but the latter two differ with respect to their configuration within the grafted plant. *Rootstock* implies that only the root system of the composite plant is derived from the original stock, whereas the term *under stock* is used when the lower portion of the grafted plant includes not only the root system but also some portion of the shoot system on which the scion is grafted. In the simplest case, a grafted plant usually consists of a single
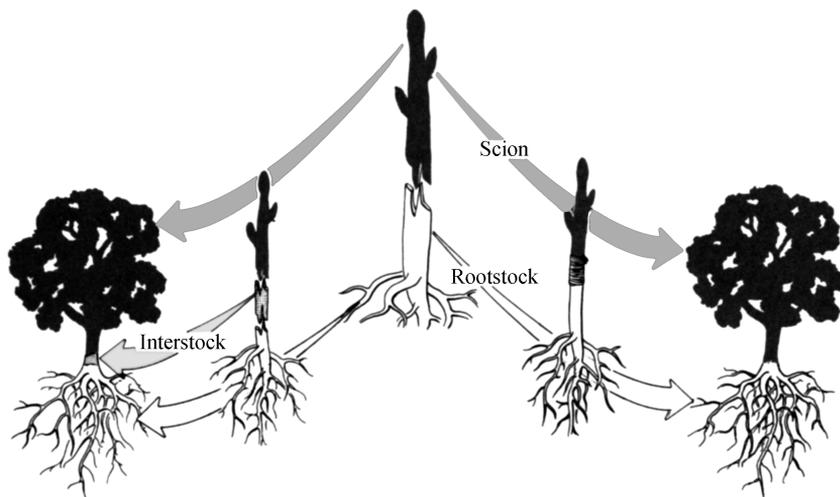
**Fig. 9.1.**   Single-worked and double-worked grafts in fruit trees. (*Source*: Janick 1983).

graft union between a stock and a single scion. However, in a process called double working, a three-part grafted plant is constructed consisting of three genetically distinct parts, (rootstock, interstock, and scion) separated in linear sequence by two graft unions (Fig. 9.1).

From a genetic perspective, grafting involves the creation of a *compound genetic system* by uniting two (or more) distinct genotypes, each of which maintains its own genetic identity throughout the life of the grafted plant. For example, a scion of a red-flowering rose grafted on a white rose stock will continue to produce red roses rather than pink (hybrid) roses. However, controversial claims of graft ''hybridization'' have persisted, and new information on gene silencing cased by the transmission of RNA across the graft union suggests that grafting could have genetic consequences (*see* Section V).

Another important genetic consideration related to grafting concerns the limits of compatibility. That taxomomic affinity is the arbiter of which species can be grafted successfully onto any other has often been misunderstood through the history of grafting (Pease 1933). Broadly speaking, interclonal/intraspecific grafts are nearly always compatible, interspecific/intrageneric grafts are usually compatible, intrageneric/intrafamilial grafts are rarely compatible, and interfamilial grafts are essentially always incompatible. These generalizations are complicated by the observation that the degree of taxonomic affinity necessary for compatibility varies widely across different taxa.

For example, sugar maple (*Acer sacharrum*) cultivars can be grafted on any sugar maple seedling (interclonal/intraspecific), but in the case of red maple (*Acer rubrum*), grafting between different cultivars or seedlings is often incompatible. The interspecific/intrageneric combination of almond (*Prunus amygdalus*)/peach (*P. persica*) is compatible, but almond/apricot *(P. armeniaca)* is not. A comprehensive review by Nelson (1968) assessing the compatibility/incompatibility of many different stock/scion combinations across a wide range of species, genera, and families is useful not only horticulturally but also to our understanding of the physiological nature of compatibility. Andrews and Marquez (1993) recognize four potential factors that may contribute to incompatibility: (1) cellular recognition, (2) wounding response, (3) growth regulators, and (4) incompatibility toxins. In addition to graft incompatability, graft failure also can be caused by anatomical mismatching, poor craftsmanship, environmental conditions, and disease (Hartmann et al. 2002).

## B. Uses of Grafting

Grafting is now a well-developed practice that has many horticultural and biological uses. One of the most ancient of horticultural craft secrets, grafting has had a wide impact on many practices and continues to be a force with implications for current technology. The many uses of grafting are listed next.

**1. Vegetative Propagation.** From the uncertain origins of grafting to the present day, the principal use of grafting has been for vegetative propagation of species that are otherwise difficult to propagate asexually. Through this process of cloning, it is assured that the ramets (vegetative offspring) are genetically identical to the scion donor tree. In the case of scions grafted onto most seedling under stocks (apomictic seedlings are the exception), only the scion-derived top of the grafted plant is clonal.

**2. Avoidance of Juvenility.** Seedlings begin as juvenile plants, which are, by definition, incapable of flowering. In woody plants, this period of juvenility typically lasts several years in fruit trees to several decades in forest species, before the plant undergoes a transition to the mature phase, when it becomes capable of flowering. The next generation of seedlings is juvenile. The long delay in flowering of these juvenile seedlings is economically undesirable. Fruit producers can overcome this delay in flowering by grafting a scion from a mature tree onto any

rootstock (seedling or mature), because a mature scion maintains its flowering state in a graft to a juvenile seedling.

**3. Cultivar Change.** Cultivars of various fruit trees go in and out of style, especially as breeders produce improved ones. Cultivar change can be speeded up by taking advantage of the mature root system. Where the old tree is healthy, new scions can be grafted on scaffold branches of an established tree, a process known as topworking. A related practice is to use grafting to ''build'' a tree with multiple cultivars. When self-incompatibility is a problem, as in cherry and apple, a pollinizer can be grafted to achieve cross pollination within a single tree.

**4. Creation of Unusual Growth Forms.** In the ornamental nursery trade, it is a common practice to graft a scion from dwarf or weeping cultivar onto a tall straight stem of a compatible understock to mimic an arborescent growth habit. Tree roses can be formed by double working using a shrubby garden rose scion, a *Multuflora de la Grifferaie* interstock, to form a straight trunk, and 'Dr. Huey' rootstock. Grafting to create unusual growth forms in a practice called *arborsculpture* involves intertwining and grafting together the stems of two or more plants in order to create domes, chairs, ladders, and other fanciful sculptures (Fig. 9.2).

**5. Repair.** In cases where a root pathogen or bark damage (girdling) adversely affects an established tree, inarching seedlings around the base of the injured tree can effectively save the tree. Bridge grafting also can be used to repair a girdled stem. Brace grafting can be used to strengthen trees by internal grafts between branches.

**6. Size Control.** Certain rootstocks will result in dwarfing or invigoration of the scion cultivar. In apple, a single scion cultivar grafted onto the full range of size-controlling rootstocks can result in trees ranging from 2 to 10 m in height. In other species, certain interspecific scion/stock combinations will result in dwarfing, such as pear on quince and orange (*Citrus sinensis)* on trifoliate orange (*Poncirus trifoliata).*

**7. Biotic and Abiotic Stress Resistance.** Just as rootstocks have been selected for controlling the size of the scion, rootstocks also have been selected for resistance to various diseases, pests, and abiotic stresses. Rootstocks have been identified or selected for resistances to viral diseases (tristeza in citrus), bacterial diseases (fire blight on apple),
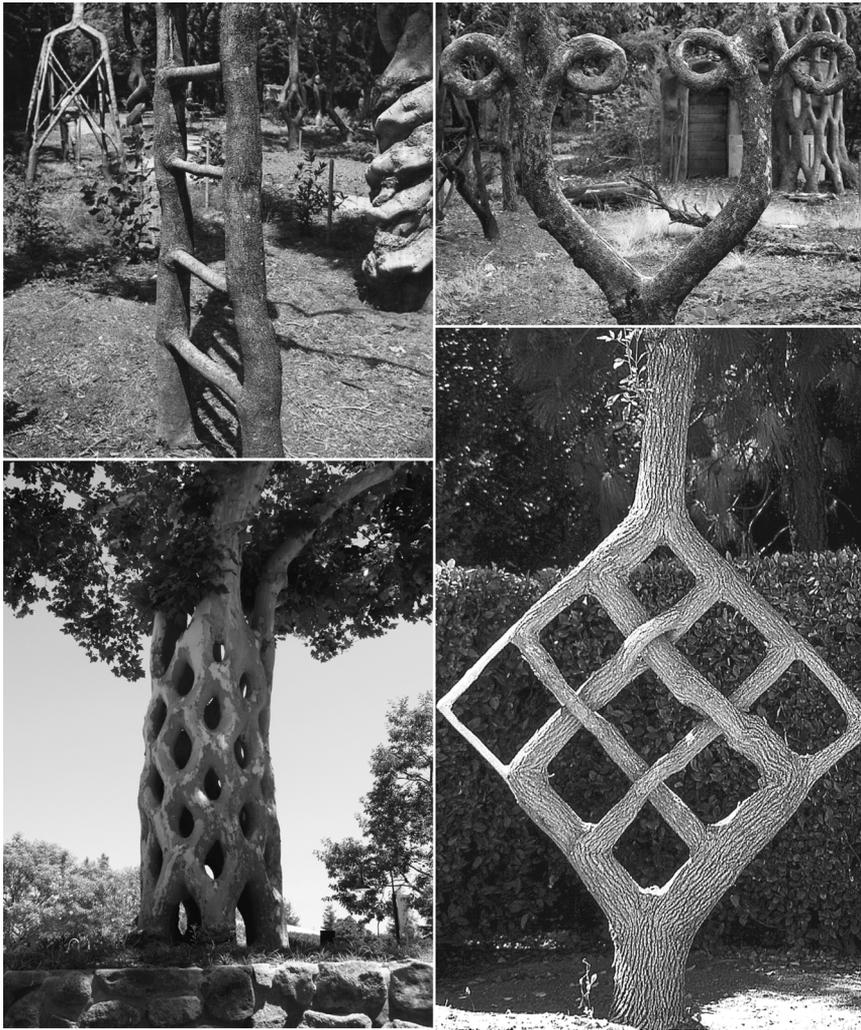
**Fig. 9.2.**    Arborsculpture of Alex Erlandson's *Tree Circus* made in the 1940s. (Photos top and bottom left and bottom right courtesy of R. Reames. Photo top right courtesy of Jon Covello.)

fungal diseases (collar rot caused by *Phytophthora* on apple), nematodes (*Meloidogyne* on peach and walnut), and insect pests (*Phylloxera* on grape). In the last case, grafting *Vinifera* grapes onto native American rootstocks species and hybrids saved the European wine industry in the 19th century (see Section III.I.1). Deliberate selection of rootstock resistance to *Eriosoma lanigerum*, the wooly

apple aphid, allowed apple production in Australia and New Zealand where this pest was abundant (see Section IV). Recent studies also indicate that so-called orchard replant disease syndromes, in which fruit trees fail to establish successfully when planted into old orchard sites, can be mitigated by selection of resistant or tolerant rootstocks (Leinfelder and Merwin 2006). Unlike size control, rootstock resistances to these diseases and pests are not transmitted to the scion cultivar, but instead improve the health and survival of the rootsystem before and/or after grafting. There are also rootstocks selected for tolerance to excessively wet or droughty soils, alkaline or acidic soils, and other potentially stressful abiotic stresses.

**8. Transfer of Infectious Agents.** Virus indexing is the converse of employing virus-resistant rootstocks to prevent viral diseases. Many horticulturally useful plants may harbor devitalizing but otherwise asymptomatic viruses, while other related species readily exhibit symptoms to the same virus. Virus indexing to identify asymtomatic viruses involves grafting a piece of the suspect (asymptomatic) plant onto the susceptible (symptomatic) stock. Since all viruses are graft transmissible, the stock will exhibit symptoms if the virus is present in the scion. Although virus indexing is a reliable diagnostic tool, it is used less frequently since the advent of the more sensitive and more specific enzyme-linked immunosorbant assay (ELISA) or an assay based on the polymerase chain reaction (PCR).

Grafting is used to transfer a phytoplasma (cell wall-less bacterium) to modify the growth habit of poinsettia, which induces a desirable branching (compact) growth habit. In all modern poinsettia cultivars, branching is induced by grafting an ''infecting'' scion onto a new cultivar. Similarly, the presence of latent viruses in certain apple rootstocks may actually improve the performance of scions grafted onto those rootstocks, compared to virus-free clones. For example, apple trees on virus-free EMLA.9 rootstocks are usually more vigorous and less precocious and productive than the same scions grafted onto other M.9 clones, such as M9.337, in which latent viruses have not been eliminated (Autio et al. 2001).

**9. Physiological Studies.** Grafting has been widely used in physiological and genetic studies to determine the transfer of mobile elements in plants. This includes translocation of alkaloids and secondary metabolites (Wilson 1952); transfer of the flowering stimulus (florigen) (Zeevaart 2006); transfer of a potato tuberization stimulus (tuberin) (Ewing and Struik 1992); transfer of growth substances such

as cytokinin from roots to shoots (Foo et al. 2007); and the transfer of RNAs (Tournier et al. 2006) (*see* Section V).

Despite this extensive list of useful functions, grafting has not been without its critics. L. H. Bailey, the esteemed proponent of scientific horticulture and advocate for grafting, wrote in *The Nursery Book* (1914): ''The opinion is commonly expressed by horticultural writers that graftage is somehow vitally pernicious and that its effect on the plant must be injurious ... akin to magic and entirely opposed to the laws of nature.'' Jonathan Chapman (1779–1845), the legendary Johnny Apple-seed who roamed the frontiers of the upper midwestern United States planting apple nurseries by seed, is reported to have felt that cutting into a tree was cruel, despite the fact that grafting of apples was widely practiced at that time (Tully 2007). More recently, some proponents of organic agriculture proposing a new ethic for plant culture have questioned both tissue culture and grafting (Lammerts Van Bueren. 2007).

To this day, despite considerable advances in the science and technology of plant propagation, grafting still plays an important role in the production of horticultural crops, including fruits, ornamentals, and vegetables (Lee and Oda 2003). Even though the origins of grafting are obscure, the significance of its discovery to crop domestication and agriculture throughout recorded history is quite clear. The ancient and modern history of grafting and its impact on horticulture then, now, and in the future are the focus of this review. The carpentry, anatomy, and art of grafting (*see* Garner 1988) are discussed only peripherally.

## II. NATURAL GRAFTING

Although grafting usually is considered a horticultural practice that involves the deliberate manipulation of stock and scion to form a graft union, both shoot and root grafting occur naturally (Fig. 9.3). It is possible that deliberate approach grafting by early agriculturists came about from an attempt to mimic the natural fusion of two plants or different parts of the same plant that occurs in natural grafting. Juniper and Maberly (2006) have speculated that grafting may have come about by observing natural grafts that occurred in shelters made from arching live poles arranged in a circle and tied together at the top. When poles of an easy-to-root species (e.g. *Salix* spp., *Ficus* spp.) are driven into moist ground, they will root, and if they are tied tightly together, they may also ''naturally'' (nondeliberately) graft to each other.

The same essential requirements that exist for successful detached scion grafting—compatibility, cambial alignment/contact, pressure,

**Fig. 9.3.** Natural grafting. (A) Root grafting of yellow birch. (Photo by K. Mudge) (B) Root grafting of apple. (Photo by Janick 2005) (C) Natural root autografting of strangler fig on sable palm. (Photo by K. Mudge) (D) Shoot grafting of oak. (Photo by R. Uva).

and avoidance of desiccation—apply to natural grafting. The concept of discrete stock and scion is ambiguous in natural grafting when both sides remain attached to a common root system, in the case of self- or auto grafting, or when each remains attached to its own independent root system, in the case of natural grafting between two plants. Natural stem grafting is far less likely to occur than natural root grafting, even though the former would be more obvious and easily detected. Roots cross or otherwise come into contact with each other as they elongate. Embedded within a soil matrix, they are held firmly together as they increase in diameter, resulting in increased pressure between the two. Only when a branch of one tree becomes

wedged in the fork of another is the prolonged contact under pressure likely to persist long enough for graft union formation to occur. Exceptions to the generalization that aboveground natural grafting is infrequent are vines such as *Hedera helix* (English ivy) and the aerial roots of strangler figs, which fuse readily in part because they become tightly appressed against the substrate (tree trunk or wall) on which they are growing (Fig. 9.3D).

Natural shoot grafting has been reported in *Alnus oregano* (Rigg and Harrar 1931; cited in La Rue 1934), *Hedera helix* (Millner 1932, cited in La Rue 1934), red pine, the East African shrub *Maeura triphylla*, black cherry, star magnolia, live oak, and white oak, sugar maple, and sycamore (K. Mudge unpubl.).

Natural root grafting has been widely reported and extensively studied because it is common and affects forest ecology. Graham and Bornman (1966) cited 150 species forming natural root grafts, although Larue (1934) indicated that natural root grafting was scarce in *Larix laricina*, *Populus tremuloides*, *Fraxinus nigra*, and *Prunus serotina.* Natural root grafting has also been observed in strangler fig, white pine, *Populus spp.*, sugar maple, beech, and yellow birch (K. Mudge, unpubl.).

The vast majority of reports of natural root grafting involve two individuals of the same species (intraspecific), but several reports of natural grafting between different species (interspecific) include several species of oak, maple, and pine (Graham and Bornman 1966). Interfamilial combinations have been reported between *Betula alleghaniensis* and *Ulmus Americana* (Larue 1934); and *B. alleghaniensis* and *Acer saccharinum* (Graham and Bornman 1966). However, reports of interfamilial grafts must be regarded with skepticism, since there are no verifiable reports of compatible interfamilial grafts. Based on dissection of apparent graft unions between cedar and hemlock, Eis (1972) found that invariably both were separated by layers of bark and hence were not true graft unions.

Natural root grafting can influence forest ecology in a number of ways: (1) effects on tree distribution and dominance within a stand; (2) effects on a surviving tree after an intergrafted tree adjacent to it is cut down or otherwise dies; (3) mechanical stabilization against wind throw; and (4) disease transmission across graft unions. It can be observed in a natural or managed forest stand that trees of a given species tend to be clumped rather than evenly distributed (Graham and Bornman 1966), which suggests that tree-to-tree interactions are to some extent complementary rather than strictly competitive. Eis (1972) concluded that natural root grafting is a means by which cooperativity occurs, to the extent that a dominant tree could provide resources

(carbohydrate, water, minerals) to its subordinate neighbors, allowing them to persist under low light or drought stress. He speculated that the root systems and lower boles of suppressed trees within a clump may obtain most of their carbohydrate from the dominant tree to which they are root grafted.

The common occurrence of living stumps also supports the cooperative model. Unlike most angiosperm tree species, stumps of most conifers, including white pine, do not regenerate from epicormic or adventitious shoots (P. Smallidge pers. commun.), and hence their persistence cannot be attributed to photosynthates from newly regenerated shoots. Bornman (1966) observed that stumps sometimes persist and continue to grow, for years or even as long as decades, when they are root grafted to adjacent trees but not when they occur singly, suggesting that carbohydrates translocated via root grafts from the standing tree to the stump are responsible for the persistence of the latter.

In this sense, living stumps can be considered hemiparasites on the trees to which they are grafted (Bornman 1966). It should be noted that mycorrhizal interconnections may account to some extent for persistence of living stumps, but these are unlikely to play more than a minor role.

It has been suggested that another beneficial effect of intergrafting of the root systems of a pair or a cluster of trees is the resulting stabilization of individual trees against wind throw (Loehle and Jones 1990). Basnet et al. (1993) found that intergrafted trees of tabonuco (*Dacryodes excelsa*) underwent significantly less hurricane damage than isolated trees. Loehle and Jones (1990) considered the adaptive significance of root grafting in trees from an evolutionary perspective. They concluded that the assimilates gained by a suppressed tree through grafting to a dominant tree could keep the former alive longer so that it could reproduce or until it was released by a change in the surrounding canopy.

Clumping of trees within a forest stand and the persistence of living stumps are positive ecological consequences of natural root grafting. Grafting between adjacent trees can have substantial negative consequences, however, related primarily to the spread of diseases. Two of the best-known and probably most consequential examples are transmission of dutch elm disease (DED) and of oak wilt disease. The causal organism for DED is the fungus *Ophiostoma ulmi* (Brasier 1991). Above-ground transmission is via the elm bark beetle, *Hylurgopinus rufipes*, but root grafts are another major means of transmission (Epstein 1978). Control of root graft transmission requires trenching on a regular basis between trees, with or without fumigation in the trenches. Epstein (1978) considered failure to deal with root graft transmission to be the major reason that many DED control

attempts in the midwestern United States have failed. Oak wilt, caused by *Ceratocystis fagacearum*, is another serious fungal disease transmitted by root grafts. Epstein (1978) reviewed a number of other root graft–transmitted fungal pathogens (*Trametes pini*, *Armillaria mellea*, *Polyporus schweinitzii*, *Endothia gyrosa*, *Fomes annosus*, and *Phytophthora lateralis*). A bacterial disease called citrus variegated chlorosis is transmitted between citrus rootstocks via natural root grafts (He et al. 2000). The viroid ASVBd, causal agent of avocado sunblotch disease (Dodds et al. 2001), and xyloporosis, a viral disease of citrus (Epstein 1978), are transmitted via natural root grafts.

This discussion of natural grafting would be incomplete without consideration of the symbiotic association between mistletoes (parasitic plants in the order Santalales) and a wide range of woody plant species. Parasitic mistletoes are not usually included in the literature on natural grafting, but the intimate associations between stock and scion and between mistletoe and host suggests that they share some common features anatomically and physiologically. In fact, in the mistletoe literature, the union between the parasitic plant and its host tree is sometimes referred to as a ''graft'' union (Thoday 1956). This is particularly interesting considering that the taxonomic range of compatibility between mistletoe and host is much greater than the taxonomic limits for plant to plant grafting. In mistletoes, interfamilial associations with host trees are common, whereas interfamilial graft combinations do not occur in woody plants (Mendel 1953). It would appear that much could be learned about the nature of graft compatibility by studying mistletoe/host plant associations. Nonetheless, there is at least one critical difference between the mistletoe ''grafts'' and nonparasitic plant-to-plant grafts. In both there is apoplastic continuity across the union (Cotzee and Fineran 1989), but nonparasitic plant-to-plant grafts are also interconnected symplastically via plasmadesmata (Tidemann 1989). Plasmadesmata have not been convincingly demonstrated at the interface between mistletoe and its plant host (Cotzee and Fineran 1989). Other systems that may shed some light on the nature of graft compatibility include pollen/stigma interaction and human tissue compatibility.

## III.  HISTORICAL EVIDENCE

### A.  Mesopotamia

The evidence that grafting was used in ancient Mesopotamia is murky at best. Harlan (1995) speculates that grafting developed in Eurasia

before classical times but offers no specific evidence. Circumstantial evidence for grafting is suggested by Harris et al. (2002) and Juniper and Maberly (2006) based on the text of a Sumerian cuneiform fragment dated approximately 1800 BCE. The text, translated and interpreted by Lion (1992), refers to the transport of grapevine shoots to be replanted at Mari (present-day Iraq). However, Lion's commentary does not mention grafting per se, and there is no reason to surmise that the vine shoots were intended as scions, because grape shoots root readily from hardwood cuttings, and cutting propagation was the standard method of grape propagation throughout the Middle East. The suggestion of Juniper and Maberly that gradual salinization of agricultural soils may have motivated farmers to graft edible but salt-intolerant grapes onto salt-tolerant wild grape rootstocks is a fascinating conjecture and if true would represent the first known use of grafting to take advantage of specific rootstock effects.

## B. Biblical and Talmudic Sources

The Hebrew Bible, one of the most important of ancient documents, is composed of numerous books written over 1,000 year period (ca. 1400–400 BCE), including law, prophecy, poetry and parables, many of which relate to plants and agriculture. Grafting is not specifically mentioned, but many references appear to suggest that it was practiced. The several biblical texts that allude to grafting concern the grapevine as a parable and refer to reversion from cultivated to wild types: ''And I planted you 'Sorek', all true seed, and how did you revert into a wild, alien vine'' (Jeremiah 2:21). This could be construed as an undesired mutation that appeared in the grapevine; more likely it can be understood as an outgrowth of the stock on which the grape was grafted. A similar text is from Isaiah 5: 1–2: ''My beloved had a vineyard in a very fruitful hill. He digget it and cleared it of stones, and planted it with choice vines; he built a watchtowere in the midst of it, and hewed out a wine vat in it; and he looked for it to yield grapes, but it yielded wild grapes.''

The book of Leviticus 19:19, dated to about 1400 BCE, states: ''Thou shalt not sow thy field with two kinds of seed.'' This is the basic admonition against mixing seeds of different kinds or sowing them in close proximity, which was discussed in detail in the Talmudic tractate Kilayim of the Mishna (commentaries on biblical law composed in the third century CE.) Although the Mishna explicitly states (Kilayim 1:7) ''It is unlawful to graft tree on tree, vegetable on vegetable, tree on vegetable or vegetable on tree'' [if they belong to a different species], it is questionable whether grafting was originally included in the prohibition

of mixing mentioned in Leviticus. The art of grafting may have not yet been practiced in ancient biblical times.

Greek and Roman sources (see Section II.C,D) indicate that grafting was well known and widely practiced the Mediterranean region by the fifth century BCE and during the Talmudic–Hellenistic times, when the Mishna was composed. In the Mishna, grafting and layering of grapevines appear as a common practice (Tractate Orla' 1:5) and planting, layering, and grafting are often described together as regular methods of fruit tree propagation (Tractate Sheviith' 2:6; Sota 8:2).

One paragraph of the Mishna (Kilayim 1:4) lists several fruit tree stock/scion combinations, mostly from the Rosaceae: ''And in trees: grafting pear with krustomal [a kind of pear], or quince with *Crataegus* is permissible. However, grafting of apple with wild pear, peach with almond or *Ziziphus vulgaris* with *Ziziphus spina-Cristi*, in spite of their similarity, is forbidden'' [translated from Feliks (1967)]. In several Talmudic parables, marriage is compared to grafting; thus we find that marriage of a scholar into a noble family is to be praised, comparable to a graft between high-quality grape cultivars; whereas marriage of a scholar into a family of illiterates is as unacceptable as a graft between quality grapes and wild grapes (Talmud Bavli Pesachim 49a). However, according to Talmudic sources (Yerushalmi Kilayim 1:7), the verse ''Your sons like olive seedlings surrounding your table'' (Psalms 128:3) is interpreted ''Just like olive trees, which are never grafted, so your offspring will be flawless.''

This may indicate that even where permissible, grafting was understood as some kind of breeding. This idea is actually stated clearly by the Talmudic scholar Shmuel (third century CE) who finds a hint to the prohibition of interspecific grafting in Leviticus 19:19: ''Thou shalt not sow thy field with two kinds of seed, nor breed two kinds of animals.'' Thus, just as it was forbidden to breed two kinds of animals, it was forbidden to graft two plant species (Talmud Bavli Kidushin 39a). A kinship between grafting and sexual intercourse is borne out also by the reasoning of the prohibition of mixing provided by Maimonides (*see* Section III.F). The notion that breeding can lead to the appearance of a new species is also mentioned in Talmudic sources (Yerushalmi Kilayim 1:4), just as in the contemporary Roman sources, as is discussed in detail by Feliks (1967).

The grafting of etrog (citron, *Citrus medica*) onto lemon (*C. limon*) or other citrus stock is still a matter of contention among orthodox Jews. Citron is an important component in the feast of Tabernacles (Succoth) and is still highly prized as a gift for orthodox Jews during this joyous holiday (from which the feast of Thanksgiving derives). From its

introduction to Palestine by the second century BCE, citron was the only citrus fruit in that region until lemon arrived in the seventh century CE. At some point after its introduction, lemon was being used as a rootstock for citron. Based on Jewish law, interspecific grafting (or ''hybridization'') was not permitted. In the 16th century, that law was specifically applied to citron grafted onto lemon, resulting in attempts to locate ''pure'' citron trees that have never been grafted or sexually hybridized. In a recent study involving citron populations from Yemen, Morocco, Israel, and Italy, using randomly amplified polymorphic DNA (RAPD) and sequence characterized amplified regions (SCAR) molecular analyses conclude that there has been no genetic introgression by lemon or other citrus species (Nicolosi et al. 2005).

Grafting is specifically mentioned in the New Testament (Christian Bible). In Romans 11:24, it is used as an analogy for how Gentiles can become one with Israel: ''For if you were cut off from what is by nature a wild olive tree, and grafted, contrary to nature, into a cultivated olive tree, how much more will these natural branches be grafted back into their own olive tree?''

A similar and clearly derivative passage on grafting is found in the Book of Mormon (Jacob 5:17–18), which implies a belief that the fruit of the scion could be drastically improved by the root stock:

> And it came to pass that the Lord of the vineyard looked and beheld the (''tame,'' not wild) tree in which the wild olive branches had been grafted; and it had sprung forth and begun to bear fruit. And he beheld that it was good; and the fruit thereof was like unto the natural (''tame'') fruit. And he said unto the servant: Behold, the branches of the wild tree have taken hold of the moisture of the root thereof, that the root thereof hath brought forth much strength; and because of the much strength of the root thereof the wild branches have brought forth tame fruit.

## C. Ancient Greece and Persia

**1. Greece.** The earliest verifiable written account of grafting is from the Hippocratic treatise, *On the Nature of the Child*, thought to have been written in about 424 BCE by one or more of the followers of Hippocrates, hence referred to ''Pseudo Hippocrates'' (Meyer 1854; Vochting 1892; Lonie 1981; Mendel 1953):

> Some trees however, grow from grafts implanted into other trees: they live independently on these, and the fruit which they bear is different from that of the tree on which they are grafted. This is how: first of all the graft

produces buds, for initially it still contains nutriment from its parent tree, and only subsequently from the tree in which it was engrafted. Then, when it buds, it puts forth slender roots in the tree, and feeds initially on the moisture actually in the tree on which it is engrafted. Then in course of time it extends its roots directly into the earth, thorough the tree on which it was engrafted: thereafter it uses the moisture which it draws up from the ground. (Lonie 1981)

The passage suggests that grafting was a common technique at that time and thus must be centuries older than the fourth century BCE. In this treatise, the embryonic and subsequent development of a child is related to that of a seed. Unlike many later references to grafting over the next two millennia, the author recognizes that a grafted plant produces fruit true to the scion cultivar rather than the stock. At the time, this was considered a paradox, consistent with the belief that each species nourished itself by drawing from the earth a species-specific fluid through its roots. This is the theory of ''specific fluid'' as described by Lonie (1981). The paradox is as follows: ''The rootstock of a grafted plant obtains its nourishment (specific fluid) directly from the soil. The scion would not have direct access to its own specific fluid, but only that of the rootstock, and hence it would be transformed by this rootstock fluid into the rootstock variety.'' To explain this paradox, the author proposed that rather than the scion being merely joined to the stock, it was rooted directly into the stock. The roots of this scion ''cutting'' grew down through the stem of the stock directly into the soil. There it was able to take up and transport its species-specific fluid and hence maintain its species (genetic) identity, giving rise to fruit of the scion cultivar rather than that of the stock (Fig. 9.4). This idea of specific fluids is one that persisted, at least in some circles, until the seventeenth century in England. The same paradox was confronted by Robert Sharrock's (1672) in his book *The History of the Propagation & Improvement of Vegetables by the Concurrence of Art and Nature,* although he suggested another ''metaphysical'' solution to the problem, which will be discussed in Section III.H.

Theophrastus (371–287 BCE), a student of Aristotle and now considered the father of botany, reiterated the view of Pseudo Hippocrates that grafting is ''propagation in another tree'' (the stock as substrate for rooting of the scion) rather than mere juxtaposition. He discussed grafting techniques, such as the importance of avoiding desiccation by cutting the stock and scion precisely so that they fit together tightly and the core is not exposed to drying. This was the reason for wrapping the stock/scion junction with layers of lime bark,
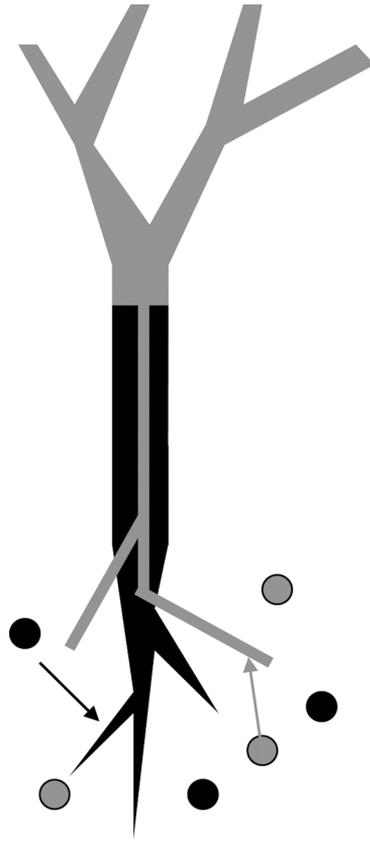
**Fig. 9.4.** The theory of the preservation of graft identity from Pseudo-Hippocrates: scion rooting through the graft union permits the extraction of its specific ''fluid'' from the soil.

plastered mud, and hair. In extreme cases, ''set a pot of water over it and let the water drip.'' No mention is made of what we would call genetic/taxonomic aspect of compatibility but rather the importance of stock and scion having ''like bark'' and time of bud break. Theophrastus comments on dwarf fruit trees, which were likely to have been introduced to Greece by Alexander the Great during his conquest of Asia Minor. Among these was a small, low-growing type of apple. This may have been predecessor to the current dwarfing apple rootstock 'Malling 8' (Tukey 1964).

**2. Persia.** The origins of Persian gardens may date to the fourth millenium BCE based on evidence of pottery. Remnants of the gardens

of Cyrus the Great date to 500 BCE. Persia was at the crossroads of importations of fruits from the East. Juniper and Mabberly (2006) suggest that grafting likely originated in Persia, but they present no direct evidence.

## D. Rome

During the Roman era, a number of authors wrote about grafting as a common agricultural practice. Marcus Porcius Cato (234–148 BCE), the earliest of the Latin writers, is his famous work *De agri cultura,* described various methods of grafting that are still used with different fruit crops, including cleft and approach grafting as well as budding. He described another curious technique that combines grafting and layering:

> With an awl bore a hole through the vine which you are grafting, and fit tightly to the pith two vine shoots of whatever variety you wish, cut obliquely. Join pith to pith, and fit them into the perforation, on each side. Have these shoots each two feet long; drop them to the ground and bend them back toward the vine stock, fastening the middle of the vine to the ground with forked sticks and covering with dirt. Smear all these with the kneaded mixture, tie them up and protect them in the way I have described for olives. (Hooper 1935)

Marcus Terrentius Varro (167–27 BCE) addressed the issue of the limits of stock/scion compatibility directly: ''you cannot, for instance, graft a pear on an oak, even though you can on an apple.'' He goes on to describe the curious view of soothsayers that multiple cultivars grafted onto a single understock ''attracts the lightning and turns into as many bolts as there are varieties.'' He indicates that a scion of a tree of better type should be grafted onto a lesser one.

It seems likely that approach grafting was perhaps the earliest method of deliberate grafting, and preceded detached scion grafting. Varro describes approach grafting as a method that had recently been developed, in cases ''where the trees stand close to each other.'' A particularly interesting commentary on the genetic limits of compatibility (or lack thereof) was put forth by Publius Verglius Maro (known as Virgil, 70–19 BCE). Virgil, best known for his epic poem the *Aeneid*, later spent seven years writing a didactic collection of fourth ''books'' on farming called the *Georgics* (a Greek word meaning ''tillage, agriculture, and rural affairs''), which was akin to an almanac for a gentleman farmers. A passage in the Georgics states: ''But the rough arbutus with walnut-fruit is grafted; so have barren planes ere now stout apples borne, with chestnut-flower the beech, the mountain-ash

with pear-bloom whitened o'er, and swine crunched acorns 'neath the boughs of elms.'' This passage makes clear that at least some of Virgil's knowledge of grafting was not firsthand because his understanding of the limits of compatibility was decidedly incorrect. A compellingly poetic verse describing cleft grafting is presented next in the famous translation by John Dryden (1631–1700) (Virgil 1953).

> But various are the ways to change the state
> Of plants, to bud, to graff, to inoculate
> For, where the tender rinds of trees disclose
> Their shooting germs, a swelling knot there grows:
> Just in that space a narrow slit we make,
> Then other buds from bearing tress we take;
> Inserted thus, the wounded rind we close,
> In whose moist womb the admitted infant grows.
> But when the smoother bole from knots is free;
> We make a deep incision in the tree.
> And in the solid wood the slip inclose;
> The battening bastard shoots again and grows;
> And in short space the laden boughs arise;
> With happy fruit advancing to the skies.
> The mother plant admires the leaves unknown
> Of alien trees and apples not her own.

Several decades later, Caus Plinius Secondus, known as Pliny the Elder (23–79 CE), wrote about graft compatibility, demonstrating a lack of understanding similar to that of Virgil, when he described ''inoculation'' (budding) of fig and apple, but goes on to remark that: ''Thus far has Nature been our instructor in these matters.'' He gave precise instructions for grafting grape vines, and advised: ''Engraft moist places from a white grape, dry places from a black'' (Book XVII, Bostock and Riley 1855). However, Pliny gives a logical explanation of wide grafts in a discussion of the first discovery of grafting:

> Nature has also taught us the art of grafting by means of seed. We see a seed swallowed whole by a famished bird; when softened by the natural heat of the crop, it is voided, with the fecundating juices of the dung, upon some soft couch formed by a tree; or else, as is often the case, is carried by the winds to some cleft in the bark of a tree. Hence it is that we see the cherry growing upon the willow, the plant upon the laurel, the laurel upon the cherry, and fruits of various tints and hues all springing from the same tree at once. It is said too, that the jack-daw, from its concealment of the seeds of plants in holes which serve at its store-house, give rise to a similar result. (Book XVII, Bostock and Riley 1855).

**Fig. 9.5.** Detached scion grafting from a third-century mosaic from St. Roman-en-gal, Vienne, France. (*Source*: Janick 2005).

A Roman mosaic found in St. Roman-en-gal, Vienne, France, from the third century CE displaying a series of agricultural events during the calendar depicts detached scion grafting (Fig. 9.5). This image is the oldest definitive image of grafting.

Rutilius Tauros Aemilianus Palladius (fourth century CE) authored a 14-book work *Opus agriculturae* of which the last book, in elegiac verses, is on grafting (Owen 1897). Crops include grape, olive, pear, pomegranate, apple, peach, medlar, citron, plum, carob, fig, mulberry, service tree (*Sorbus*), cherry, almond, pistacio, chestnut, and walnut. Compatibility is reported for olive with wild olive; pear with quince, medlar, wild ash (fallacious), chestnut (fallacious); apple with medlar, service tree (*Sorbus*), plum (fallacious), willow (fallacious), plane-tree (fallacious), peach (fallacious), plum (fallacious), poplar (fallacious), chestnut (fallacious); plum with chestnut (fallacious); carob with other fruits (?); mulberry with fig (fallacious), ash (fallacious), beech (fallacious), chestnut (fallacious), terebinth (wild pistachio) (fallacious); service tree (*Sorbus*) and quince (fallacious); cherry with plum, plane tree (fallacious), poplar (fallacious); almond with plum, chestnut (fallacious); pistachio with almond (fallacious); chestnut with willow

(fallacious); and walnut with arbutus (fallacious). The high number of fallacious (incompatible) combinations indicates that Palladius was not writing from personal experience.

## E. China

Reports of Chinese agriculture prior to the 14th century BCE are largely mythological because historical records from China begin very sparsely in about 1200 or 1250 BCE and do not get rich until about 400 BCE (Chang 1965; Arbuckle 1994; R. MacNeal pers. commun.). Pollan (2001) simply asserts that grafting originated in China sometime during the second millennium BCE. One dubious claim for the early origins of grafting is based on the mention of citrus fruits in the Chinese literature during the reign of Ta Yu (ca. 2205–2197 BCE). Cooper and Chapot (1977) mention that *chu* (a generic term for kumquats and small-fruited mandarins) are indigenous to the ancient Yanchow region and probably were included in tributes. Accounts of *chu* in early Chinese herbals indicate that they were a wild-growing loose-skinned fruit. One early (but unfortunately undated) Chinese tradition has *chu* grafted onto *chih* (*Poncris trifoliata*). Hartmann et al. (1997) put the date at 1560 BCE, but no evidence is presented. Juniper and Maberly (2006) speculate that grafting of mulberry may have originated in association with the development of a Chinese silk industry about 300 BCE, although it is not clear what would have motivated the development of this relatively elaborate means of cloning because the mulberry (*Morus alba*) is easily rooted from cuttings (Hartmann et al. 2002) and by layering (Anon. 2007a).

The earliest (indirect) credible evidence that grafting was being practiced in China may have been written about in the first century BCE in *The Book of Fan Sheng-Chih Shu.* According to Shih Sheng-Han (1959), the original book was lost long ago and only excerpts have been preserved in later agricultural treatises, especially in the all-comprehensive *Ch'I Min Yao Shu* (*Essential Techniques for the Farming Populace*) by Jia Sixie in the 6th century CE, and translated into English by Shih Sheng-Han (1962). According to Jia Sixie, the earlier *Book of Fan Sheng* describes grafting of bottle gourd (*Lagenaria siceraria*). The practice involved planting 10 seeds in one hole, tying the emerging stems together so that they fuse (approach graft), and then pruning to a single shoot, which would remain attached to 10 root systems. The purpose may have been to increase fruit size or lengthen the production season by delaying root system decline due to fungal diseases (10 root systems hold out longer than 1), rather than

invigoration of the scion since bottle gourd is extremely vigorous to begin with (H.C. Wien pers. commun.).

Most of the recommendations regarding the techniques and timing of grafting by Jia Sixie are reasonable and sound, but his advice regarding the limits of graft compatibility is not always accurate. The recommendation to graft pear onto ''crab apple'' (*Pyrus phaeocarpa*) or *P. betulifolia* is reasonable because they are different species within the same genus. However, he describes the combination of *Pyrus sp* (scion) and either jujube (*Zizyphus sp.*) or pomegranite (*Punica granatum* L.) rootstock. These species are not in the same family and hence are certain to be incompatible since there are no verifiable reports of successful interfamilial grafts in woody plants.

Advice is given in *Ch'I Min Yao Shu* pertaining to the use of grafting in the open orchard compared to the courtyard of the home: ''when grafting pear trees in an orchard, scions should be inserted sidewise; in a courtyard, insert upwards—sidewise scions facilitate fruit-picking while upright growth makes no trouble with the buildings.'' The author goes on to say that scions taken near the stump give better-looking trees but fruit later. This sensitivity to horticultural esthetics is in contrast to his disdain for beauty for its own sake: ''Flowers may certainly be pleasant for the eye, but (empty) blooms in spring without substantial autumn fruits are vain and fraudulent things. So there is no need to record them.''

## F. Medieval and Islamic Period

**1. Medieval Europe.** From the surviving records of agriculture from ancient Greece and Rome, it is clear that grafting was well known and widely practiced in the Mediterranean region by at least the fifth century BCE (see Section III.C). It is likely that the art of grafting survived in Christian monasteries after the fall of the Roman Empire. Grafting is mentioned in King Alfred's English translation of Pope Gregory's *Regula Pastoralis* around 897 CE (Juniper 2006). In the thirteenth century, Albert of Bollstadt (Albertus Magnus) wrote in *De Vegetabilibus* that grafting was one of the means by which to bring about cultivar improvement from wild species (Biewer 1992). He proposed that plant life was mutable and that new species could be produced by grafting.

**2. Islamic Period.** During the decline of the Roman Empire after the fifth century, a period often referred to as the Dark Ages, the Arabs were the major successors of the Greeks and Romans in all areas of science and technology, including horticulture. The Arabs took special

interest in gardens and gardening, probably because their ancestors originated in desert countries. This love of plants is clearly shown in a special genre of poetry, the *rawdiya* or (garden poems), which became the most common poetic themes. Islamic gardening was inspired and influenced by the traditional Persian fruit tree and ornamental gardening. Islamic rulers competed among themselves in the magnificence of their gardens. Basra, Cairo, Damascus, and later on Seville, Cordova, and Valencia were renowned for the size and beauty of their gardens, which preceded those of Christian Europe by several centuries; the earliest records of Italian gardens are from the fourteenth century. Numerous new crop plants were introduced during the Islamic period (Watson 1983); many were initially cultivated as ornamentals in the royal gardens of the Islamic rulers. Grafting undoubtedly was used extensively in the gardens of the Islamic era; Mazaheri (1951) reports that the garden of Il-Khans was directed by a Persian botanist who wrote a book on the grafting of fruit trees. Little is known, however, about developments in the understanding of grafting effects, and superstitions concerning grafting were common during this period. Thus, in his *Guide for the Perplexed* (Part III; Chapter 37), Maimonides (1137–1205) wrote:

> When a tree is grafted into another in the time of a certain conjunction of sun and moon, and incense is burned whilst a formula is uttered, that tree will allegedly produce something that will be exceedingly useful. The most remarkable witchcraft, as described in *The Nabatean Book of Agriculture* [Ibn-Whashiya's tenth century treatise] was the grafting of an olive branch on a citron tree. . . .They also said that when one species is grafted upon another, the branch which is to be grafted must be in the hand of a beautiful damsel, whilst a male person has disgraceful sexual intercourse with her: during that intercourse the woman grafts the branch into the tree. (Friedlander 1904, slightly edited)

Although considered by Maimonides to be trustworthy, the reliability of Ibn-Wahshiya, who allegedly describes the ''ancient'' agriculture, has been seriously questioned by modern investigators of Islamic literature. *The Nabatean Book of Agriculture* has been called a forgery, although the superstition may have long existed (Frazer 1935).

## G. Renaissance Europe

About 1440, Jon Gardener wrote *The Feate of Gardening*, which included a section on grafting, but the work was never published and only two copies are known today (Harvey 1985; Juniper, 2006). An

important grafting-related milestone was recorded by Champier in 1472. He mentioned the dwarfing Paradise apple for the first time in the horticultural literature (Tukey 1964), which implies a fairly sophisticated understanding of stock/scion interactions. Paradise, then as today, was presumably used primarily as a rootstock, not a scion cultivar since it has soft insipid fruit, in order to take advantage of its dwarfing effect on the scion and because it roots easily from cuttings. Vegetative propagation maintained its dwarfing character because apples do not come true to type from seed. Paradise may be the earliest examples of the use of clonal apple rootstocks in Europe. This is particularly significant since Paradise was the progenitor of the modern dwarfing rootstocks M.8 and M.9 (originally known as 'Jaune de Metz') and other dwarfing rootstocks (Webster 2003).

By the 16th century, the increased literacy after the widespread adoption of the printing press (invented by Gutenburg in 1440) led to increased demand for and availability of horticultural works that included descriptions of grafting. Some of these included the *Boke of Husbandry* in England by John Fitzherbert (1531), *Ein Neues Pflantzbüchlin* by the Bavarian Johann Domitzer (1531), and *De Natura stirpium libri tres* authored by the Parisian physician and botanist Jean Ruel (1536).

In 1558, the Italian Gambattista della Porta published a four-volume work in Latin entitled called *Natural Magick* (Porta 1558), which in 1584 was expanded into 21 volumes and translated into English. The subtitle, *Wherein Are Set Forth All the Riches and Delights of the Natural Sciences*, suggests the tone of the work. His subjects ranged from the fantastic (*Of changing metals*, *Of the generation of animals*), to the mundane (*Of cookery*). Scholars have concluded that he had a propensity for exaggeration and embellishment, ''to bring out the full wonder and marvel of the world'' (Price 1957). In the third volume, which was titled *Of the Production of New Plants*, he states in the subsection ''How to make new fruits compounded of many'': the Fig tree may be incorporated into the Plane tree, and the Mulberry tree,... likewise the Mulberry tree into the Chestnut tree, the Turpentine tree, and the White Poplar, whereby you may procure White Mulberries, and likewise the Chestnut tree into a Hazel, and an Oak, and likewise the Pomegranate tree into all trees, for that it is like to a common whore, ready and willing for all comers.'' Throughout the work Porta acknowledges using information on grafting from ancient scholars, including Virgil and Columella. Porta not only wildly overstated the limits of compatibility between stock and scion, as did Virgil 15 centuries earlier, but he went further with his claims that the stock

could dramatically alter the nature of the scion. For example, he asserted that mulberry scion on white poplar stock would generate white mulberry fruit. Although Porta's fantastic claims could easily be dismissed as the work of an uninformed, inexperienced pedant with a penchant for exaggeration, *Natural Magick* was widely read through-out Europe for over a century (Porta 1659). For example, Nicholas Bonnefons (1658) repeated the claim that grafting mulberry onto popular generated white mulberries.

A work by Leonard Mascall in 1572, *A Booke of The Arte and Manner How to Plant and Graffe All Sorts of Trees ... by one of the Abbey of S. Vincent in Fraunc* (Mascall 1589), was largely a translation from French to English based on a French manuscript by David Brossar (*L'art et Maniere de Semer Pepins et de Faire Pepiniere*) (Anon. 2007b). The introduction by Mascall explains: ''there is none that more doth refresh the vital spirits of men, nor more engender admiration in the effects of nature, or that is cause of greater recreation to the weary and traveyled spirit of man, or more profitable to mans life, than is the skill of planting and graffing.''

In his introduction, Mascall attempts to motivate a broad range of prospective grafters:

The poore man may with pleasure finde
Some thing to help his neede
So may the rich man reape some fruit
Where earth he had but weed
The noble man that needeth naught
May thereby have at will
Such pleasant fruit to serve his life
And give each man his fill

The book, although translated from the French, goes on to claim that earlier works on grafting from Greece, Barbarie, Italy, and France ''doeth very small profit for this our Realme of England.'' Mascall goes on to chide his country men for their lack of diligence: ''which I can blame nothing more then the negligence of our nation, which hath had small care heretofore in planting an graffyng ... but if we would endeavour our selves thereunto as other countries doe wee might florish and have many a strange kinde of fruit which now we have oftentimes the want therof.''

Mascall expressed disdain for those who promoted the idea that the scion could take on the ''nature'' of the stock. He wrote: ''many which have written that if ye graft the medlar upon the quince tree, they shall

be without stones, which is abusive and mockery. For I have (saith he) proved the contrary myself.''

Mascall's book and many that followed in the late sixteenth and seventeenth centuries, is a practical, hands-on guide for the fruit tree gardener. It makes fewer fantastic claims than Porta about the limits of compatibility. The book recommends grafting cherry to cherry, and apple to apple or to pear, although Mascall suggests some incompatible interfamilial combinations (cherry on crabapple, fig on peach, and apricot on fig). An illustration on the title page of Mascall's work shows a top graft greatly exaggerated in size, illustrated in Juniper and Maberly (2006, p. 96). Exaggerations of size were not uncommon in illustrations of grafting of the sixteenth and seventeenth centuries (Anon. 1654; Mascall 1589; Sharrock 1672; Markham 1635; Meager 1688; Langford, 1699).

## H. Early Modern Europe

In 1618, William Lawson published a book on orchard gardening that was specific to the North of England: *A New Orchard and Garden: Or, the Best Way for Planting, Graffing, and to Make Any Ground Good for a Rich Orchard, Particularly in the North.* Most, if not all, of the seventeenth century books that covered propagation-related topics described various grafting and budding (inoculation) techniques in sufficient detail that, after allowing for the challenge of ''translating'' early modern English into contemporary English, could be faithfully executed today with reasonable expectation of success. However, as in earlier times, misinformation abounded during this period on the issue of the genetic limits of compatibility. A related consideration was extraordinary claims about the influence of the stock on the scion (mingling of traits). The principal fruit tree species of consequence to seventeenth century gardeners were apples, pears, medlars, quince, peach, cherry, plum, and apricot, but mulberries and figs were also mentioned. Most authors got the basics right: apple on apple or crabapple stock, pear on pear or quince stock, and even pear on apple stock, which was acknowledged, as is the case, to be a short lived combination. Thomas Barker (1651), in his book *The Country-mans Recreation, or the Art of Planting and Graffing,* copied Mascall's entire section (several pages) on compatibility verbatim without attribution.

More advice regarding red apples and other minor (secret) miracles was published in 1654 in *The expert gardener; or a treatise containing certaine necessary, secret, and ordinary knowledge* by an anonymous

author (who gave credit to "sundry Dutch, and French Authors"; Anon. 1654). In order to make red apple, the reader is advised to graft an apple scion upon an alder or cherry stock. Alternatively, soak the scion in pike's, blood. The book conveyed many other "secrets," such as a method for producing cherries without stones that involved using an iron to draw the "heart and marrow from both sides" of the stock cherry tree, followed by anointing with ox dung and then grafting another cherry scion to it. According to this author, there were essentially no limits to compatibility, and apples could be grafted to apple, pear, cherry, willow, fig, and chestnut.

Nearly all of the books published during this time were practical agricultural treatises written for the educated practitioner/landowner. A work by Robert Sharrock (1630–1684), *The History of the Propagation and Improvement of Vegetables...,* first published in 1659 and reprinted in 1672, was somewhat different. It attempted to be both practical as well to convey the natural history, botany, and natural philosophy related to the propagation of plants. Sharrock drew from his own "observations made from experience and practice," as did most garden writers of his time, but also incorporated his critical analysis of other published works and his speculations on natural philosophy and religion. "I gave myself the trouble to run over with my eye all books I could procure of the subjects, not intending to trust any." There he discovered "a multitude of monstrous untruths...in both Latin and English old and new writers."

Sharrock was a remarkably ecumenical scholar. In addition to work just mentioned, he wrote at least 12 others books on diverse topics, including theology, natural philosophy, physics, history, and even sexual deviancy. Sharrock was the archdeacon of Winchester Cathedral and fellow of New College, Oxford, and his theological orientation permeates his writing, which was not at all uncommon for scholars of the scientific revolution. The latter was no doubt reinforced by his friendship with Sir Robert Boyle (Arber 1960), one of the most influential contributors to the scientific revolution, best known for Boyle's gas law ($pV = k$). According to the book's Dedicatory Epistle, Boyle requested Sharrock to write this scientific treatise on plant propagation. Sharrock embraced a practical as well as a scholarly/experimental approach to the subject, and he specifically eschewed "natural Magick and romantic stories." He may have been referring to Porta's *Natural Magick* (1584) or more generally to any "magical" explanations of natural phenomenon, but he does mention Gambista della Porta in other sections of the book, unflatteringly. The title and subtitle of the book, *The History of the Propagation and*

*Improvement of Vegetables by the Concurrence of Art and Nature,* is elaborated on in the section ''Of Natural Propagation and Seminal Principles Latent from the Creation.'' He writes: ''Industry and art may bring materials and place them fitly for it, but nature works them. And therefore, as one sayeth, it is the great art of man to find out the arts of nature.''

Sharrock's fifth chapter is titled *Insitions*, which refers to grafting and budding. It begins with a core principle necessary for success in any and all types of grafting and budding: ''Grafting is an art of so placing the cyon upon a stock that the sap may pass the stock to the cyon without impediment. . . .The space that is between the bark and the stock is the great channel for conveyance and keeping of sap so that every one that grafts well so orders the manner that these spaces be so laid, that the passage may be easy.''

Concerning the recurrent issue of the limits of graft compatibility, Sharrock's views were consistent with some of the more enlightened writers of the time, stressing that: ''The cyon or thing implanted be of like nature to the stock.'' Rather than simply giving several examples of compatible (e.g., apple/apple) and less compatible (e.g., apple/pear) combinations, as most earlier authors had done, Sharrock added the caveat: ''But to tell what nearness in every kind is enough, is a matter of greatest Art.'' In the same chapter, he undertakes a critical analysis of some previous claims regarding compatibility. This section is titled ''Kirchers Experiments Concerning Insitions Examined.'' Sharrock writes: ''I have tried mulberries on Beech, Quinces, Apples, Pears, Elms, Poplars and by grafting they would not take, and yet he [Kircher] affirms they take easily.'' In addition to questioning Kircher's claims of excessively broad limits of compat-ibility, Sharrock addresses the assertions of several other authors back to and including Porta (1584), that the traits of stock and scion mingle within the new fruit on the scion. Sharrock writes (referring to Kircher): ''mulberries are by conjunction with white Poplars made to be of a white kind and bear white mulberries [a claim made by Porta in 1584]. . . .Pear being grafted on a mulberry bring a red colored pear . . .a white rose grafted upon a red, will bring the Rosa Mundi or a flower both red and white. This I have often prov'd false by mine own trial.'' Thus he exhibits not only healthy skepticism but introduces ''experimentation.''

It is tempting to perceive Sharrock as the voice of reason emerging from the intellectual chaos of the Middle Ages, but then he reverts so stunningly in his judgment about compatibility that it is difficult to imagine that this text was written by the same author:

> There are almost infinite stories of strange conjunctions which urge earnestly for credit, some of insitions made upon animal bodies: The Lord of Pieresh had a present made him of a plum-tree branch which bore blossoms and leaves, which sprang from a thorn that grew in the breast of a shepheard, this shepheard having got this thorn by falling upon a plum-tree. . . .The bodies of divers beasts be excoriated and planted anew with silk, fine wool, cotton, or the linen. When these new plantations shall have succeeded to any considerable advantage of the planters then we also will leave our vegetabnle and apply our selves by these rarer ways of insition to the improvement of animal bodies.

It is just possible that these lines betray his sense of humor rather than his gullibility because this is the only instance of extreme exaggeration in the book.

In many instances, Sharrock goes beyond his own observations and practices or those of his contemporaries and, in the spirit of the scientific revolution of which he was a part, he speculates on more mechanistic questions that border on natural philosophy. One of the issues he spends a significant amount of time on is the paradox originally addressed by Pseudo Hippocrates, about 2,000 years earlier, regarding the essence of plant growth. If a plant of a given species grows by extracting from the soil a fluid specific to its particular kind (and no other), how then does this fluid taken up by stock serve to provide for the growth of the scion of a different species? Or, as Sharrock put it: ''But how the sap of the stock (suppose a white thorn) can serve to make the wood, bark, leaves and fruit of its cyon, suppose a pear, is a difficult question. For grant there be an elective attraction of sap from the earth, yet how shall a white thorn choose that which is fit for a pear?''

The Greeks (*see* Pseudo Hypocrites translation, Section III.C) dealt with this paradox by asserting that the scion rooted itself into the stock and these scion roots grew down, all the way through the stock, and emerged into the soil, where they took up the growth fluid appropriate to the scion species. It is not clear if Sharrock knew of this ''Theory of Specific Fluids'' as described by Lonie (1981), but he chose to resolve the paradox in another, more metaphysical way. Sharrock writes, ''when the sap gathered in its roots comes to the place of conjuncture, it is there forced to undergo a total corruption and lapse into the bed of its first matter, from whence by a new generation, there arises a new sap, begot in the tree by specifick faculty, which in a pear graff may be called a pear-sap-making power.'' He goes on to generalize to a broad range of natural phenomena: ''it is equally applicable to all things in

The Exemplification of the Operations by the
Figure.

*a* Denotes the ordinary cutting of the Bark of Inoculation.
*b b* The fides of the Bark, lifted up for the puccing in of the Shield.
c The Shield taken off with the Bud, which lies under the Stalk
  of the Life cut off.
  In the Sheld put into the Stock to be bound up.
d The Bark cut out in an oblong fquare, according to another
  way of Inoculation
e The Shield cut out for the fitting the dit barke fquarec.
  in The fame Shield put into the Stock.
f A variation of the fore-mentioned way, by cutting off the upper
  part of the oblique fquare, and binding the lower part down upon
  the Shield.
e The Shield of put in to be bound up,
e Another varincion by flitting the Bark, that the Bud and Leaf
  may ftand forth are, and the Bark flit be bound down upon the
  Shield.
b Acrofs cut for Incculuion.
i The fame crofs cut lifted up in this Figure, fomewter to big.
k The Shield cut off to be put thercis.
p The Shield put in.
g or q The cut of the Cyon or Srock for whip-grafring.
m The cut of Cyon and Stock for Shoulder-grafting.
e The cut of the Cyons, and flit of the Stock for Grafting in the clcft.
a The Stock fet for Abledation or approche.
H The Cyon of the Brauch for the fame operation.
a The Branch that is to be taken off by cireuropofition.
3 the Branch that bears up the mould to the dif-barked place.
4 The Branch of a Caraction to be laid.
5 The joynt where the flit begins.
6 The next joynt where the fit is popped open with pcice
  of carartion Leaf put in.
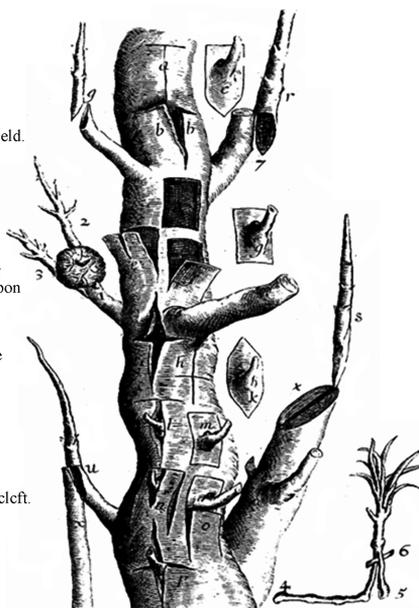
Adde this at the 60th Page.

**Fig. 9.6.** Different types of grafts (*Source*: Sharrock 1672).

the world, each thing being made by some such thing-making power. Diva Colchodea, the grand-general form-making-intelligence.''

One particularly useful and practical contribution was the single illustration in Sharrock's (1672) book (Fig. 9.6) of a stylized tree showing nine different grafting and budding techniques as well as ''circumposition'' (air layering), all applied to a single tree trunk. This, along with the detailed figure caption, goes far beyond other books of the 17th century and earlier in providing visual representation of grafting techniques described in the text. Seventeen years later, Langford's book (1696) included a very similar illustration, obviously derived from Sharrock's work.

At about the same time as Sharrock, the Frenchman Nicholas Bonnefons (1658), author of *The French Gardiner* (1658), wrote accurately about what could be grafted to what (regarding pears and apples) based on his own experience. When he speculated based on the words of others he, like Sharrock, succumbed to exaggeration: ''There are some curious persons who graffe Queen apple up the white mulberry, and hold that the fruit does surpasse in redness all others.''

In other respects, Bonnefons had a very sophisticated understanding of asexual propagation in the service of clonal rootstock production. He writes of the Paradise rootstock in particular: ''on Layers of the tree (called by the French Pommier de Parradis) and in particular the Queen apple does wonderfully prosper upon it, and more red within then those which are graffed upon the free (wild?) stock.''

He describes rootstock propagation by mound layering, and trench layering methods that are still used today. The use of clonal rootstocks, including the size-controlling Paradise, was more pre-valent in France than in England in the late seventeenth century. Neither the comprehensive work of the Englishmen Sharrock (1672) or that of Langford (1696) mentions clonal rootstock production, and Langford in particular recommend using crabapple seedlings as the preferred stock for apple. The English book *The Compleat Planter & Cyderist* by an anonymous ''Lover of Planting'' in 1685 (republished by Juniper and Juniper 2001) specifically mentions the Paradise rootstock.

In the eighteenth century, practical advice on grafting was a common theme in gardening books. The sixteenth edition of the *The Gardeners Kalendar* by Philip Miller (1775) has 14 references to grafting tasks throughout the year. In 1795, Thomas Andrew Knight would present a paper (I. Observations on the grafting of tree) to the Royal Society (Anon. 1844). In North America, the prevailing view was that grafting of fruit trees was time consuming, difficult, and unnecessary given that the primary goal was to produce fruit for hog feed or cider. The third President of the United States, Thomas Jefferson (1743–1826), was an avid fruit tree gardener (170 cultivars of fruit trees). At his home at Monticello, he preferred to grow most fruit trees from seed because he believed they were healthier than grafted trees, but he did have his gardener graft named cultivars of apples or bud cherries in order to preserve their dessert qualities (Hatch 1949).

## I.  Ninteenth Century

**1. French Wine Industry.** Grapes and olives are the most economically important temperate-zone fruit crops in the world. Because of the importance of wine, grapes have had an (arguably) greater impact on human history and culture than any other fruit crop. Nowhere is the latter more true than in France. Imagine the panic in the French wine industry in the latter half of the ninteenth century when an insect plague nearly wiped out grape production. The insect phylloxera (*Dactylosphaera vitifolii*) often kills the highly susceptible

vinifera grape (*Vitis vinifera*), from which most wines were and still are made. To this day the pest has never been eradicated or otherwise defeated and remains a problem in susceptible wine-grape-producing regions throughout the world.

From the French point of view, the phylloxera panic began in 1864 in the southeastern Midi region of France (Campbell 2005). Grape vines were observed to rapidly decline, as leaves turned from yellow to red and rapidly dried up and defoliated, while the root systems collapsed and rotted, resulting in death of the entire vine. It took an additional three years, while the malady continued to spread, before an aphidlike insect infesting the roots was observed to be the culprit. Thanks to detective work of an American entomologist, C. V. Riley, and several French scientists including a botanist, J. E. Planchon, entomologists V. Signoret, J. E. Westwood, and J. Lichtenstein, the pest was determined to have been introduced from eastern North America, where it occurs at low frequency on leaves and roots of American grape species (*V. labrusca* and other species) without killing the vines.

It was not lost upon the scientific community of the time that phylloxera was an object lesson in the evolutionary theory of natural selection that Charles Darwin had published a few years earlier in *On the Origin of Species.* Coevolution of the pest and its host in North America has resulted in American grape species with resistance to phylloxera, allowing the two to coexist. *Vinifera* grapes, however, having never been exposed to the pest, had no natural (genetic) resistance, and quickly succumbed to the onslaught. The phylloxera ''plague'' eventually destroyed a quarter to a third of all grape vineyards planted in France.

In the first few years after phylloxera's appearance on the French grape scene, the response of grape growers was to rip up the affected vines, roots and all, and burn them. Needless to say, this approach was completely unsuccessful, and infestation progressed from the Midi to other grape-producing regions. As it became widely acknowledged that phylloxera originated in North America and that American vines were phylloxera resistant, two opposing socioscientific movements emerged. The Americainistes, including Planchon and a rich wine connoisseur, Leo Laliman, believed that that importation of American stock should be encouraged either for direct production of wines from American grapes or to serve as rootstocks on which to graft French vines. The opposing point of view of the Sulfuristes, who advocated expensive soil injection with the chemical carbon bisulfide, was that American stock should be banned from France entirely lest the pest be

introduced to regions not yet infested. Furthermore, there was a great deal of prejudice against wines made from American grapes as they were (and by some still are) widely considered unpalatable. It was even feared that the American rootstock would impart an undesirable ''foxy'' character to wines from *Vinifera* cultivars grafted onto them. In his engaging narrative The Botanist and the Vintner—How Wine Was Saved for the World, Christopher Campbell (2005) put it this way: ''grafting proud French vines onto alien roots seemed the counsel of miscegenating madmen.'' Later attempts to cross French and American species in order to obtain phylloxera-resistant hybrids was never more than marginally successful as far as the French were concerned. Eventually the practice became strictly regulated in France and remains so. However, such French-American interspecific hybrids, although they are of intermediate hardiness, are important to wine production in some parts of the world, including eastern North America.

By 1890, the Sulfuristes had largely capitulated to the Americainistes, and grafting French cultivars onto American stocks became widespread. Laliman proclaimed far and wide that he had been the first to recommend the grafting solution in 1869, although it has been claimed that the American C. V. Riley was the first to suggest it in 1870. During the ensuing years when ''reconstruction'' (the practice of replanting vineyards with grafted grapes) was in full swing, grafting became all the rage, with people enrolling in special classes and proudly displaying their certificates of completion. Books and articles on grafting were abundant, and new grafting methods were invented, including machine grafting for mass production of grafted plants. Reconstruction was not without its problems, however. The two American grape species used as rootstocks, *V. riparia* ('Riparia Gloire') and *V. rupestris* ('Rupestris St. George'), were not well adapted to the chalky (high pH) soils of the better wine-producing regions of France, resulting in leaf chlorosis due to iron deficiency and less-than-optimal performance. In another transatlantic collaboration, a French plant pathologist, Pierre Viala and an American grape enthusiast and plant explorer, T. V. Munson, introduced an American species, *V. berlandieri,* which was phylloxera resistant as well as tolerant of high soil pH. This might have solved the problem, but *V. berlandieri* turned out to be unusually difficult to root from dormant cuttings, the standard means of propagation of grape rootstocks. The ultimate solution, which prevails today, was to hybridize *V. berlandieri* with the easier-to-propagate *V. riparia* and *V. rupestris* (Rieger 2006).

**2. Citrus Problems.** Evidence of citrus grafting goes back to the Roman era. Gallesio (1811) cites Palladius (fifth century CE) for grafting citron. Grafting of citrus was practiced during the Middle Ages and the Renaissance, while many types of citrus were considered exotic ornamentals and grown in orangeries throughout western Europe (Fig. 9.7). Gallesio (1811) was aware of the ideas that grafting can give rise to the appearance of new species but noted that his observations



**Fig. 9.7.**   Grafting of citrus grown in containers. (From Volkamer 1708).

did not support such notions. However, the introduction of grafting as a standard procedure in commercial citrus groves took place only during the middle and late 19th century. According to Chapot (1975), the advent of foot-rot, or gummosis, caused by various species of *Phytophthora* first in the Azores Islands in 1842 and later in almost all other citrus-growing countries, obliged the use of scions grafted on rootstocks tolerant of the disease. The sour orange (*C. aurantium*) was the universally favored citrus rootstock until the breakout of the Tristeza virus epidemic in South America during the 1930s and its subsequent spread to North America and the Mediterranean. Sweet orange grafted on the sour orange rootstock proved to be most susceptible to the Tristeza viral disease, which necessitated the replacement of sour orange by other rootstocks. The susceptibility to Tristeza and other virus and viruslike diseases became a major consideration in modern citriculture. The trifoliate orange (*Poncirus trifoliata*), which is a deciduous, cold-resistant citrus relative, and resistant to tristeza, is used as a rootstock in cool citrus-growing regions such as Japan.

## K. Twentieth Century

A number of innovations have occurred in grafting technology in the 20th century. These include in vitro grafting, herbaceous vegetable and ornamental grafting, flower bud grafting, and Mukabit grafting of cassava.

**1. In Vitro Grafting.**  One of the most ingenious grafting innovations of the 20th century has been in vitro grafting, which involves grafting a shoot tip about 1.5 mm high from a mature plant onto a seedling rootstock. This technique was developed by Toshio Murashige et al. (1972) with citrus and is now used in many species. The technique is used in citrus to rid plants of viruses and other systemic pathogens. The technique exploits two concepts: (1) meristems are relatively virus and pathogen free; and (2) meristems from mature plants retain the mature phase. Thus, the use of in vitro shoot tip grafting produces plants that are virus free and reproductively mature. This technique overcomes problems of producing virus-free plants from nucellar seedlings or by thermotherapy. Although nucellar seedlings of citrus are both clonal and virus free, the seedlings are juvenile and take many years to flower. In the case of thermotherapy, many viruses, such as exocortis viroid and stubborn virus, are difficult to clean up with this process (Roistacher 2004). In vitro grafting was used in Spain to produce

virus-free plants of all cultivars and is considered a major factor in improving the Spanish citrus industry (Navarro et al. 1975).

A successful technique in citrus involves growing 2-week-old, dark-grown seedlings (often 'Troyer' citrange) as rootstocks and 0.14- to 0.17-mm-long shoot tips of any cultivar as scions (Navarro et al. 1975). A scion that includes three-leaf primordia is cut with a razor blade attached to a handle as a scalpel. Shoot tips are inserted in an inverted T made at the top of the decapitated rootstock epicotyl. Highest success is obtained with the shoot tip set on the vascular ring tissue on top of the decapitated epicotyl. Nutrient solution was a modified Murashige and Skoog media with high sucrose (7.5%). Light is maintained during growth of grafts.

**2. Herbaceous Vegetable and Ornamental Grafting.** Although the use of grafting of vegetables is an ancient practice (*see* Section II.E), grafting was not been a common practice in herbaceous vegetables and ornamentals until the 20th century (Lee 2003; Lee and Oda 2003). Information on grafting scions of watermelon (*Citrullus lanatus*) on bottle gourd (*Lagenarias scieraria*) rootstock to overcome yield decline was described in the 1920s by Japanese workers in Korea. Since that time there has been an explosion of the use of this technique in watermelon, cucumber, melons, tomato, eggplant, pepper, and ornamental cactus, especially in Korea and Japan. The advantages of vegetable grafting are attributed principally to resistance of the understock to soilborne diseases, such as verticillium wilt, fusarium wilt, bacterial wilt, and nematodes, but also to increase of vigor and stress tolerance. The problems associated with banning methylbromide for soil fumigation have increased vegetable grafting in Europe and the United States, and this technique is now considered to be an environmentally sustainable practice. Grafting of ornamental cactus has created a large industry in Korea. Ten million grafted cacti are exported from that country each year.

Because of the increased expenses associated with grafting, grafted seedlings are mostly used in greenhouses and tunnels but also are used in field production for watermelon, cucumbers, and tomato. In Korea and Japan, practically all greenhouse production of watermelon, cucumbers, and melons are from grafted plants. The increased use of grafting has resulted in breeding programs to produce specific disease-resistant rootstocks, many involving various formerly noncultivated species.

Most grafting is done by hand using various modifications of the detached scion and approach grafting techniques and insertion

techniques (whip and tongue, cleft, hole insertion, splice), often held together by various clips and pins. Experienced grafters can perform an average of 1,000 grafts per day. Special techniques used to heal the graft union involve environmental control (temperature, light, and humidity). In order to reduce the cost of grafting, various machines and robots have been developed to perform the grafting operation. A simple grafting machine can produce 600 grafts per hour per two-person team; more costly grafting robots can perform 600 to 1,200 grafts per hour, but highly uniform seedlings are required in order to increase grafting efficiency, and robots are costly. The creation of the plug seedling industry produced by specialized nurseries has increased the potential for machine grafting, and the vegetable grafting technique is increasing rapidly throughout the world (Cantliffe 2009).

**3. Flower Bud Grafting.** A unique use of grafting has been developed in the service of the Taiwan pear industry (Kuniyama 1996; Gemma 2002). The Japanese pear, or nashi (*Pyrus pyrifolia*), is a favorite in Taiwan, but some cultivars cannot be grown in the subtropical areas there because of insufficient chilling. This is overcome by flower bud grafting. After trees in Japan have received chilling nearly sufficient to break dormancy, budwood is harvested and shipped to Taiwan, where it is held at $2°$ to $4°C$ to complete the chilling requirement. The prechilled scions are grafted into 'Heng Shan' pear trees and produce two to four marketable fruits per cluster. Grafting must be renewed each year. The technique benefits Japanese growers, who obtain an additional source of revenue from exporting buds, and Taiwanese growers, who profit by early crops of marketable fruit that receive very high prices.

**4. Mukibat Grafting of Cassava.** Not all modern innovations necessarily involve cutting-edge technology. Mukibat grafting is an example of horticultural innovation by a peasant subsistence farmer. In 1958, a farmer named Mukibat, living on the island of Java, Indonesia, took an extension grafting course and shortly thereafter began to experiment with grafting of cassava, which is an important food crop in Indonesia and many other tropical countries. He grafted an inedible relative of cassava, the Ceara rubber tree (*Manihot glaziovii*), onto a cassava (*Manihot esculenta*) stock (De Foresta et al. 1994). The resulting yield of cassava tubers was dramatically increased, on the order of 30% to 100% or more, compared to ungrafted cassava (De Bruijn and Dharmaputra 1974). The potential agronomic significance of this enhanced yield for food sufficiency is obvious. Unlike apples in

which selected rootstocks are used to dwarf or otherwise control the size of the scion cultivar (*see* Section IV), Mukibat grafting uses a selected scion to invigorate the rootstock. Effects of the scion on rootstock vigor have not been generally reported.

## IV. HISTORY OF CLONAL ROOTSTOCKS

For more than 2,000 years, the most important reason for grafting has been to asexually propagate scion cultivars. This could be accomplished by grafting a scion cultivar onto any compatible seedling rootstock. Across many centuries, however, there was a belief that certain rootstock genotypes affected the scion cultivar differently from others. In some cases, this was based on accurate empirical observation. For example, in China in the sixth century, Jia Sixie wrote in *Qi Min You Shu* (Sheng-Han 1962) that pear grafted onto ''*tang*'' (*Pyrus phaeocarpa* or *P. betulifolia*) would produce large pears with fine flesh, as compared to pear grafted onto ''*du*'' ( *P. calleryana* or *P. ussuriensis*), which were not as good. As early as the 17th century, it was known that quince (*Cydonia oblonga*) had a dwarfing effect on pear, and was the recommended rootstock for espalier pears (Tukey 1964).

   In other cases, the alleged rootstock effect was based on wishful thinking. For example, Gambista della Porta (1584) wrote that mulberry grafted onto white poplar would produce white mulberry fruit, and in 1563 the anonymous author of *The Crafte of Graffynge & Plantynge of Trees* (republished by Juniper and Juniper 2001) wrote that an apple grafted onto elm would produce red apples.

   Whether accurate or otherwise, these alleged rootstock effects involved interspecific (*Pyrus phaeocarpa/P. calleryana*), intergeneric (*Pyrus/Cydonia*), or even interfamilial (*Malus/Ulmus*) scion/rootstock combinations. Exploitation of the observation that selected scion/ rootstock combinations could have profound effects on scion cultivar development is one of the most significant advances in pomology over the last 1,000 years. In modern terminology, such compound genetic systems involve the independent optimization (selection and breeding) and asexual propagation of both the scion genotype and the rootstock genotype. The oldest and even today the most apparent criterion for clonal rootstock optimization has been rootstock effects on scion vigor (size control). For particular horticultural applications, dwarf fruit trees have been an important goal, apparently since ancient Greece. In about the fourth century BCE, Alexander the Great is said to

have sent low growing dwarf apple trees, "Spring Apples," to the Lyceum (gymnasium with a wooded area), where Aristotle and later Theophrastus was the director. Given that grafting was known by Theophrastus (Janick 1989) and that this Spring apple was easy to root, it may be that it was used as a dwarfing rootstock for other apples. The same low-growing (dwarf) apple was later used by Roman agriculturists, and it is likely that they used it as a dwarfing rootstock. Bunyard (1920) felt that the Spring apple was the progenitor of the Paradise apple. Juniper and Mabberly (2006) suggest that apple genotypes that were eventually selected as size-controlling rootstocks migrated from wild populations in the Tian Shan Mountains of Kazakhstan, westward through Persia and Armenia into Europe. They point out that the low-growing, easily rooted 'French Paradise' is very similar to the Armenian rootstock 'Marga Khndzor'. The gene(s) for the horticulturally important dwarfing phenotype is (are) being identified and cloned in New Zealand by S. Gardiner (pers. commun).

'Paradise' apple, however it arrived in Europe, was first mentioned in print by the Frenchman Champier in 1472 and later by Dalechamps in 1507 (Tukey 1964). 'French Paradise' was first introduced into England in 1696 and into America during the early 19th Century. Tukey argues that its ease of rooting was initially more important than its dwarfing effect to European growers, but why bother to clone a rootstock at all if it was not dwarfing? Paradise as described above refers to a dwarfing rootstock that is easily propagated asexually, but eventually a distinction arose between 'French Paradise' and 'English Paradise'. 'French Paradise' referred to the centuries-old (if not millennia-old) dwarfing, easily cloned genotype, whereas 'English Paradise' or 'Doucin', first described in 1519, referred to a somewhat more vigorous (semi-dwarfing) rootstock that was more difficult to clone. These genotypes represented some of the genetic diversity that would become the basis for later rootstock selection and breeding during the early 20th century. In the meantime, the issue of genotype nomenclature was becoming increasingly confused. In part this was due to deliberate selection of new genotypes (e.g., 'Jaune de Metz', a chance seedling selected in Metz, France, in 1879). More prominently, though, the confusion was due to frequent, location-dependent renaming of established clones (e.g., 'Red Paradise', 'River's Paradise', 'Holstein Doucin') or due to mislabeling in the nursery. In 1870, Thomas Rivers noted 14 different kinds of 'Paradise.' By the early 20th century, this situation had become untenable, and efforts to bring order to chaos were undertaken independently in Germany, the Netherlands, France, and England.

The rootstock standardization and selection program that got under way at the East Malling Research Station at Kent, England, proved to have a profound effect on apple production that persists today (Tukey 1964). Initially (1912) station director R. Wellington and subsequently (1914) R. G. Hatton assembled a collection of 'Paradise' apple rootstocks, including 71 collections from 35 sources including Britain (29), France (3), Germany (1), and the Netherlands (1). Each of these was evaluated with respect to size control, propagation, and productivity. Nine of them were renamed to eliminate confusion and released in 1917 ('M I', 'M II', 'M III', etc.). 'Doucin' ('English Paradise') was renamed 'M II', 'French Paradise' as 'M VIII', and 'Jaune de Metz' as 'M IX'. Eventually the number of East Malling releases was increased to 27. These were categorized into size classes from Very Dwarf, Semi Dwarf, Vigorous, Very Vigorous. Currently the number after the prefix M is presented as an Arabic numeral (Fig. 9.8).

Although rootstock disease and pest resistance were not key selection criteria for these initial efforts, they were the focal points of subsequent collaborative efforts. In 1917 (Ferree and Carlson, 1987), the East Malling Research Station and the John Innes Horticultural Institute at Merton, England, participated in collaborative effort to solve a critical problem faced by apple growers in Australia and New Zealand where wooly apple aphid (*Eriosoma lanigerium*) was a limiting factor in apple production. Capitalizing on progress that had
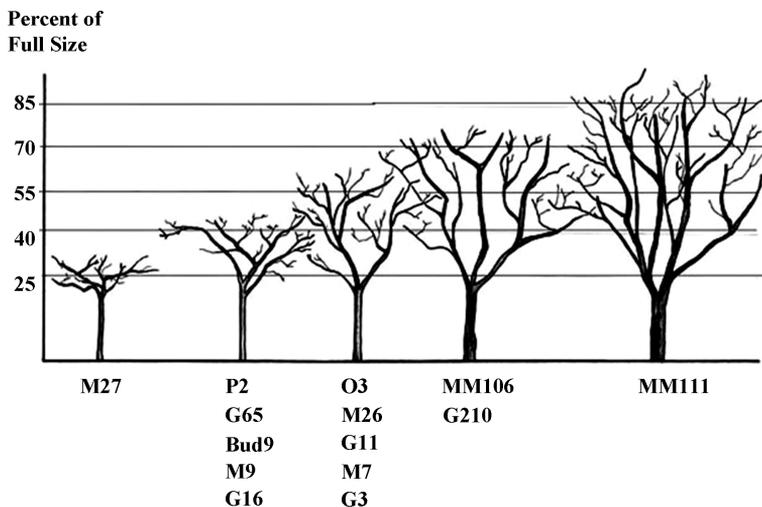


Fig. 9.8.   Size control in apple with clonal rootstocks. (Courtesy Vanessa Gray).

been made with the EM selections, they crossed these (and a few others) with the 'Northern Spy' apple, which was known to be resistant to the wooly apple aphid. By screening 3,758 seedling for wooly aphid resistance and characterizing the survivors for size control, propagation, compatibility, precocity, and field performance on two different soils, a total of 15 selections were made, numbered Malling-Merton 101 through 115. Several of these are still in use in various parts of the world.

Another rootstock improvement program involving the East Malling Research Station in collaboration with the Long Ashton (LA) Research Station had to do with elimination of latent viruses that had accumulated in the original East Malling (EM) rootstocks over time, resulting in declining vigor and graft incompatibility. By the process of micropropagation combined with heat treatment of the original M series and MM series, the EMLA series were created. As would be expected, virus elimination resulted in increased vigor. Perhaps unexpectedly, the elimination of latent viruses did not always improve horticultural attributes such as scion yield efficiency for these rootstocks.

## V.  GRAFT HYBRIDS

The effect of grafting on the genetic integrity of the scion has been an issue in biology and horticulture since antiquity. In the 16th century, Jewish law prohibited the use of citron fruit for the feast of Tabernacles if the citron tree had been grafted onto lemon root stock (Nicolosi et al. 2005). Some rabbis even went so far as to express the view that citron fruit from an ungrafted tree originally propagated from cutting taken from a tree that had been grafted was not permissible. This view was derived in part from a general belief that the rootstock influences the nature (genotype) of the scion so that a fruit from a grafted tree or from a tree propagated from a grafted tree was in some sense a hybrid between the stock and scion and hence religiously forbidden.

William Shakespeare alludes to the influence of stock on scion in *The Winter's Tale*:

You see, sweet maid, we marry
A gentler scion to the wildest stock
And make conceive a bark of baser kind
By bud of nobler race. This is an art
Which does mend Nature—change it rather;
But the art itself is Nature.

The fact that scions of high-quality fruits maintained their ''noble'' nature even when grafted on wild (''degenerate'') plants is a constant biblical theme, and provided anecdotal evidence that rootstock did not profoundly affect fruit morphology. Although it has been widely accepted as a horticultural truism that grafted plants retain their own genetic identity, the Bible is rife with mention of spontaneous development of ''degenerate plants,'' implying that there could be a genetic effect through the graft union (*see* Section II.B). Such references mistakenly imply a change in the nature (genotype) of the scion due to the influence of the stock, when in reality such ''degenerations'' are more likely due to suckering of the rootstock. Nevertheless, the observed rootstock effects on performance of the scion (e.g., dwarfing) were difficult to explain fully and suggested to some a genetic change of the scion associated with grafting. In the 13th century, Albert of Bollstadt (Albertus Magnus) wrote in *De Vegetabilibus* that grafting was one of the means by which to bring about cultivar improvement from wild species, intuitively believing that the close physical contact between stock and scion ought to have some ''genetic'' effect, but clear experiments were never performed (Biewer 1992). Furthermore, it was long observed that grafted scions from trees on dwarfing rootstocks revert to normal size when regrafted onto nondwarfing rootstocks. Thomas Langford (1696) was equivocal about grafting not changing the integrity of the scion: ''if you graff a scion on a stock differing from it in kind, whether the fruit of this new tree will be anything better than the fruit of the tree from whence the scion was taken . . .may be held in the negative. . . because the stock only conveys food and nourishment to the scion and then when the scion hath received it, it converts it perfectly into its own nature.''

However, he goes on to make a case for the opposing point of view: ''graff in natural bodies is hardly conceivable without some commixture of their natures and there as some reasons from experience that make this probable. 1) seeds take after the stock, and if the seeds are influenced by the stock, the fruit must also be, and 2) in the same orchard all planted to the same scion variety some are better than others, and this can be attributed to differences in the seedling rootstocks.''

## A. Graft Chimeras

The occurrence of plants containing a mixture of phenotype involving sectors of tissue known as graft chimeras (named after a mythological beast, part lion, goat, and dragon) suggested a novel genetic effect of

grafting. Confusingly, graft chimeras have been referred to as graft hybrids, but we will use the latter term only for alleged graft-induced direct genetic transformation as discussed later. It was long noticed that in rare cases grafting produced new types of plants (horticultural curiosities) composed of mixtures of stock and scion characteristics. In the 16th century, the Italian Giambattista della Porta (1584) declared that the scion of an orange grafted on a lemon stock could produce lemons ''half sweet, half sour.'' Gervase Markham (1635) stated: ''if you take an apple graft and a pear graft of like bigness and having cloven them join them as one body in grafting, the fruits they bring forth will be half apple and half pear.'' In 1672, Robert Sharrock described with skepticism an experiment of Kircher, who found that a white rose grafted upon red roses will bring a ''flower both red and white.'' In 1674, Pietro Nati (1625–1685), director of the Botanical Garden of the University of Pisa, published *De malo limonia citrata-aurantia vulgo la bizzarria* (On the citron-orange lemon, called the bizzarria), in which he described a lemon-orange ''graft chimera,'' a tree that bears oranges, lemons, and citrons and combinations thereof. Its leaves and flowers are also a mixture of different citrus.

One of the best-known chimeral hybrids arose in 1825, when a Parisian nurseryman grafted *Chamaecytisus purpureus* onto *Laburnum anagyroides.* From the junction between stock and scion, an adventitious bud developed, and the shoot that developed from this had leaf and floral characteristics that were intermediate between the stock and scion phenotype. This oddity, named *Laburnocytisus Adamii*, was widely regarded a true hybrid of the two ''parental'' species. Propagated by grafting, the clone is still in existence (Cowles and Chamberlin 1911).

These mixtures of two genetic tissues or genotypes have been explained as a special type of genetic mosaic (Marcotrigiano and Gradziel 1997) where the lineage of genetically dissimilar apical cells continues into developing plant organs. Chimeras based on the structure of the meristem may be classified as sectoral (a wedge of tissue), mericlinal (a wedge of tissue in one or more layers of the meristem), and periclinal, (hand-in-glove type) confined to one or more layers of the apical meristem. The periclinal chimeras are stable. The Bizzaria orange first described in 1674 was proved to be a periclinal chimera composed of sour orange and citron (Cowles and Chamberlin 1911). They also summarized evidence that disputed the contention that *Laburnocytisis* and others were true hybrids. For example, seeds from *Laburnocytisis* always gave rise to *Laburnum* seedlings rather that the segregation of phenotypes that would

expected from a true hybrid. Earlier research by E. Baur (1910, cited in Cowles and Chamberlin 1911) established that *Laburnocytisis* and other alleged graft hybrids were periclinal hybrids with the outer tissues layers of the stem and other organs consising of cells that were of the *Chamaecytisus* genotype, whereas cells of the inner core were *Laburnum.* Since floral organs, including gametes, arise in the inner core tissue, which was genetically *Laburnum*, only *Laburnum* seedlings grew from seed obtained from the graft chimera. Thus the explanation of graft chimeras as mixtures of tissues with genetically preserved identities refuted the contention that grafting induced genetic change at the cellular level. The concept of chimeral engineering involving graft insertion of epidermal cells of an insect-resistant genotype has been suggested in Solancaceae (tomato and nightshade) and Brassicaceae (Goffreda et al. 1990; Lindsay et al. 1995).

## B. Graft Transformation

In the early 20th century, genetic dogma proclaimed that although the stock may influence the phenotype of the scion (e.g., size control), the scion and stock maintain their genetic identity (Bailey 1928). This paradigm, which might be called conservation of genetic identity, was then challenged by reports of graft transformation. The theory of graft transformation has an infamous history in the former Soviet Union. The Russian pomologist and fruit breeder Ivan Vladimirovich Michurin (1855–1935), with a popular reputation similar to Luther Burbank in the United States, made the neo-Lamarkian assertion that genetic effects, could be induced by the environment, including grafting, although this assertion was not based on specific experiments. The issue became profoundly political when Trofim Lysenko, a Soviet crop physiologist best known for his explanation of the vernalization of winter wheat (cold induction of wheat flowering through seed treatment), developed a theory of environmentally induced genetic effects. He held the position that formal genetics based on the gene, which he termed Mendelian-Morganism, was reactionary and bourgeois and contrasted it with Darwinism-Michurinism, the reconciliation of inheritance of acquired characters with Marxist dialectical materialism. Supported by Stalin, the Lysenko faction succeeded in making genetics a political issue (Glass 1948). In 1940, N. I. Vavilov, the plant breeder and botanist best known for his work on the domestication and centers of origin of crop plants, was relieved of his position as head of the Institute of Genetics and imprisoned in 1943. There he later

died of starvation, to become a martyr for science. In 1964, the physicist Andrei Sakharov spoke out against Lysenko in the General Assembly of the Academy of Sciences and charged him with being ''responsible for the shameful backwardness of Soviet biology and of genetics in particular'' (Gorelik 2005). Vavilov's reputation has been restored in Russia, and he is now considered one of the most revered personalities in science.

The claims of graft transformation were generally unreproducible by appropriate methods of experimentation (Stubbe 1954; Bohme, 1957; Topoleski and Janick 1963). However, over the past several decades, many papers have been published in peer reviewed journals, such as *Science*, *Proceedings of the National Academy of Science* (USA), *Genetics*, *Journal of Heredity*, *Euphytica*, and *Theoretical and Applied Genetics*, reporting observations that appear to support the concept of graft hybridization, particularly a series of papers published by Japanese researchers using a range of species including red pepper, eggplant, tomato, tobacco, and soybean. The most intensive analysis focused on changes observed in grafted *Capiscum annum* cultivars with varying fruit morphology (Hirata et. al. 1986; Yagishta 1961; Kashara et al. 1971). This work employed ''mentor grafting'' in which a very young seedling that is continually defoliated is grafted to a mature rootstock, so that the scion is a sink for stock-derived nutrients. A range of stocklike phenotypic characteristics were observed in the scion fruit, and in some case, these characteristics were transmitted to seedling progeny (Taller 1998). Another Japanese scientist repeated this work (Ohta 1991) with largely similar results. Among the stocklike phenotypes reported to be inherited in the scion progeny were alterations of fruiting direction, fruiting habit, and pericarp color. Ohta states that genetic analysis indicates that these three traits are due to independently inherited Mendelian genes that are highly stable in the cultivars used in the grafting studies. The frequency of transmission of stocklike traits in the progeny of the scion was reported to be highly variable across different experiments, but with an average rate of 0.84%.

A second line of experimentation with graft-induced variation involves the generation of cytoplasmic male sterility through grafting of petunia (Frankel 1956; Edwardson and Corbett 1961), sugarbeet (Curtis 1967), and alfalfa (Thompson and Axtell 1978). In these studies, cytoplasmic male sterile plants were used as rootstock and lines expressing nuclear maintainer/restorer genes were the scions. The scions were observed to flower normally; however, a significant percentage of progeny plants were scored as male sterile.

All of these studies run against the mainstream understanding of genetics and are viewed with considerable skepticism. None of the authors cited has proffered an explanation for these observations that can be supported by modern molecular biology. Ohta (1991) specified that the mechanism responsible for graft-induced variation was ''graft transformation,'' in which chromatin was translocated from the stock to the scion. A variant of this model was offered by Liu (2006) in a review in which he states: ''I propose that the stock mRNA molecules are being transferred to the scion—then reverse transcribed into cDNA that can be integrated into the genome of the scions germ cells, embryonic cells, as well as the somatic cells of juvenile plants—may be the main mechanism of graft hybridization.''

The evidence provided for the transfer of chromatin or DNA sequences is highly questionable. Ohta (1991) built his case on a microhistological analysis that he interpreted as showing chromatin masses moving through the cell walls of dying cells. Taller et al. (1998) presented random amplified polymorphic DNA (RAPD) analyses indicating that a stock-specific DNA marker could be detected in graft-induced variants; however, it must be noted that standard controls for RAPD experiments were not included in the data presented. It is difficult to assess the significance of observations associated with graft transformation given the lack of rigorous experimental characterization and, with the exception of Ohta, the absence of independent experimental replication. If these observations are in fact artifactual, the most likely explanation may be pollen contamination, although efforts to avoid this were noted in some of the papers. Modern plant molecular biology has certainly not provided support for the models involving translocation of DNA from one cell to another.

However, before leaving this topic, it is worth considering how the recent insights into RNA-mediated gene silencing might apply to grafting and could provide a plausible mechanism for some of the phenomena associated with graft-induced variation. It is now known that the accumulation of double-stranded RNA (dsRNA) activates a homology-dependent mechanism that cleaves the dsRNA into 21 to 25 base-pair fragments, known as small interfering RNAs (siRNAs). These are utilized to direct the sequence-specific degradation of mRNA or to suppress transcription via DNA methylation (Baulcombe 2005). A particularly fascinating aspect of this process is that the silencing signal can be propagated through the phloem so that gene silencing occurs elsewhere in the plant (Tournier et al. 2006). It should be noted that such movement would be stimulated in mentor grafting. This was

demonstrated by experiments in which transgenic tobacco plants expressing green fluorescent protein (GFP) were grafted onto rootstock containing another GFP construct that was silenced. In this case, the rootstock GFP transgene was silenced because it produces dsRNA homologous to the GFP coding sequence. In these grafted plants, the silencing signal is propagated into the scion where GFP expression is consequently abolished via degradation of the mRNA.

The demonstration of the transmission of silencing across the graft junction raises the question whether it could be involved in graft-induced variation. Several reports describing graft hybrids claim that graft-induced variation can be inherited. Heritable genetic changes can also result from the RNA-mediated gene silencing mechanism. One of the actions known to result from production of siRNAs is sequence-specific methylation of DNA. Heritable transcriptional silencing of GFP genes in transgenic tobacco has been observed when siRNAs target methylation to the promoter (Jones et. al 2001). Approximately 30% of seedlings that display GFP silencing will maintain this state throughout their life cycle; plants that remain fully silenced give rise to silenced progeny, the majority of which will eventually revert to being nonsilenced.

Although all of this experimentation involves the silencing of transgenes rather than endogenous genes, most aspects of the silencing mechanism apply to naturally occurring genes and transgenes alike. Based on what is now known, RNA-mediated silencing could provide an explanation for variation reported in graft hybrids, provided the phenotypic changes result from gene inactivation. If this mechanism does underlie such variation, several conditions would be predicted to exist in the rootstock and scion. It would be predicted that the gene in the rootstock responsible for triggering the graft-induced variation would be silenced and have a configuration such that it produces dsRNA. If graft-induced variation is heritable, it would also be predicted that the homologous gene, which becomes silenced in the scion, would not be transcribed in the progeny and would display DNA methylation.

The point we want to make is that although the topic of graft-induced variation has been surrounded by much controversy and generated much skepticism, aspects of the phenomena associated with it have interesting parallels with RNA-mediated gene silencing. We certainly are not prepared to state that any of the graft-induced changes reported in these papers result from RNA-mediated gene silencing. However, if similar observations could be produced in a model plant like Arabidopsis, the resources would be available to rapidly

determine which genes were being affected. Given the wealth of tools available for studying RNA-mediated gene silencing, this system could be employed to carry out a rigorous reexamination of graft-induced variation (Brosnan et al. 2007).


## VI. CONCLUSION

Grafting is an ancient horticultural technology that is essential to modern horticulture. The practice of joining together two living organisms that then function as one has long been considered a mysterious process and craft secret. This review sheds light on the origins of this process and considers how its history relates to current and future advances in our understanding and application of modern grafting. Given the abundance of natural grafting in the wild, it is reasonable to assume that deliberate grafting arose by discovery rather than invention. The earliest definite written evidence of grafting dates to Pseudo Hippocrates discussion of the graft union, which was written about 412 BCE, indicating that the introduction of grafting predated Alexander's excursions to the East in the fourth century BCE. This detailed discussion of the graft union suggests that grafting was an established technology at the time. Since grafting is not directly discussed in the Hebrew Bible, it was probably not a common practice in Mesopotamia but derived instead from the East, perhaps in Central Asia. A Chinese report from the sixth century referring back to grafting in China in the first century suggests that grafting may have been a common practice there even before this time. Whether the Chinese and Greek references to grafting represents separate independent ''inventions'' or more likely an Asian discovery that migrated, East and West, along with other components of agricultural technology (Carter 1977) still cannot be resolved.

Regardless of modern advances in propagation technology, such as the use of rooting hormones, misting of cuttings, and micropropagation, grafting still remains a common and essential method of plant cloning for a wide range of purposes and a wide range of species.. Not only is grafting still used for traditional tree fruit crops and woody ornamentals, but it is increasingly used for herbaceous vegetables. The goal of much of the modern breeding of disease-resistant rootstocks is to reduce the use of chemical pesticides for disease management, thus contributing to the goal of sustainable agricultural production.

During the twentieth century, the independent breeding of clonal fruit tree (especially apple) rootstocks and scion genotypes has

allowed for the construction, by grafting, of compound genetic systems that allow an unprecedented level of size control and other desirable rootstock and scion characteristics. Despite the fact that size control (dwarfing) is one of the most important selection criteria in rootstock breeding, the mechanism by which this occurs is just beginning to be unraveled at the molecular level. Resolving this question will allow even greater control over compound genetic systems.

Stock/scion compatibility has been one of the most persistently misunderstood aspects of grafting from its earliest record until at least the 18th century. In about 50 BCE, Virgil wrote ''swine crunched acorns 'neath the boughs of elms,'' suggesting an impossible interfamilial (Ulmaceae/Fagaceae) graft combination. Similar fantastic claims were made by the Chinese writer Jia Sixie in the sixth century, the Italian Gambista Dela Porta in the 16th century, and the Englishman Leonard Mascall in 1572, to name a just a few. All these fundamental misunderstandings of the need for taxonomic affinity between stock and scion suggest that those who wrote about grafting historically were not always the ones actually practicing the method, which is a reminder of the gulf between the educated class and their gardeners.

There does not appear to be one overall explanation for graft incompatibility among different taxa. We suggest that the anatomical, physiological, and genetic bases for compatibility need to be examined in a wider biological context. The ability of some parasitic higher plants including mistletoes to form an efficient graft union (as some choose to interpret it) is an example of not only interfamilial but interorder ''graft'' compatibility (e.g., Santalales/Fagales in the case of a mistletoe/oak association). A better understanding of this association could shed some light on the basis of compatibility among nonparasitic plants. Over 4,000 species of angiosperms are able to directly invade and parasitize other plants (Nickrent et al. 1998; Joel et al. 2007).

Not only were the limits of graft compatibility consistently misunderstood over millennia; during the same period there were frequent fantastic claims of commingling stock and scion traits, particularly the scion taking on characteristics of the stock. One notable exception appears in the earliest known writings on grafting by Pseudo Hippocrates in 430 BCE, which acknowledged that the stock and scion remained unique. It is now widely accepted that stock and scion each retain their own identity. The introduction of the concept of genetics in the 20th century has made it clear that there is a difference between environmental, external effects and inherent, hereditary cues.

Thus, while the physiological influences of grafting are well recognized and indisputable, it is still debatable whether grafting induces genetic changes across the graft union. In the first half of the 20th century, persistent claims of heritable graft ''transformation'' were reported by Michurin, Lysenko, and others, but such claims were treated skeptically by most scientists. Yet claims of graft transformation continue to be reported and published, in reputable journals, and the evidence of genetic effects of grafting have not been unequivocally discounted. The recent recognition that gene silencing signals, perhaps small RNAs, can pass across the graft union has reopened up the issues concerning the genetic effects of grafting. We suggest that the book on this interesting paradox has many chapters that remain unwritten.

## VII.  LITERATURE CITED

Andrews, P.K., and C.S. Marquez. 1993. Graft incompatibility. Hort. Rev. 15:183–231.

Anon, 1654. The expert gardener; or a treatise containing certaine necessary, secret, and ordinary knowledge in grafting and gardening. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:18775177.

Anon. 1844. A selection from the physiological and horticultural papers by the late Thomas Andrew Knight. Longman, Orme, Brown, Green, and Longman, London. (Facsimile edition, ASHS Press, 2001).

Anon. 2007a. *Morus alba.* Agroforestry Tree Database, World Agroforestry Center, Nairobi, Kenya. (cited 10 Janurary 2008). Available at www.worldagroforestry.org/Sites/TreeDBS/aft/speciesPrinterFriendly.asp?Id=1170.

Anon. 2007b. Herbals and early gardening books. Patten Collection, Arizona State Univ. (cited 10 January 2008). Available at www.asu.edu/lib/speccoll/patten/html/authors.html.

Arber, A. 1960. Robert Sharrock (1630–1684): A precursor of Nehemiah Grew (1641–1712) and an exponent of ''Natural Law'' in the plant world. Isis 51:3–8.

Arbuckle, G. 1994. Literacy and orality in early China. Text of lecture at Calgary Institute for the Humanities, Feb. 15, 1994, David C. Lam Institute for East-West Studies (cited 10 January 2008). Available at www.cic.sfu.ca/nacc/articles/litoral/loral.html.

Autio, W.R., J.L. Anderson, J.A. Barden, G.R. Brown, R.M. Crassweller, P.A. Domoto, A. Erb, D.C. Ferree, A. Gaus, P.M. Hirst, C.A. Mullins, and J.R. Schupp. 2001. Location affects performance of Golden Delicious, Jonagold, Empire, and Rome Beauty apple trees on five rootstocks over ten years in the 1990 NC-140 cultivar-rootstock trial. J. Amer. Pom. Soc. 55:138–145.

Bailey, L.H. 1914. The nursery-book, a complete guide to the multiplication of plants. Macmillan, New York.

Bailey, L.H. 1928. The standard cyclopedia of horticulture. Macmillan, New York.

Barker, T. 1651. The country-mans recreation, or the art of planting, graffing, Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/open-url?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:99866534.

Basnet, K., F.N. Scatena, G.E. Likens, and A.E. Lugo. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest Puerto Rico. Biotropica 25:28–35.

Baulcombe, D. 2005. RNA silencing. Trends Biochem Sci. 30(6): 290–293.

Biewer, K. (trans.) 1992. Albertus Mangus. De vegetabilibu Buch VI. Traktat 2. Lateinisch-deutsch. Wissenschaftgliche. Verlasgesellschaft, Stuttgart.

Böhme, H. 1945. Weitere Untersuchungen zum Problem der genetischen Bedeutung von Pfropfungen zwischen genotypisch verschiedenen Pflanzen. Z. Pfanzenzg 38:367–418.

Bonnefons, N. 1658. The French gardiner instructing how to cultivate all sorts of fruit-trees and herbs for the garden, Early English Books Online (cited 10 January, 2008). Available atgateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:10618174.

Bornman, F.H. 1966. The structure, function, and ecological significance of root grafts in *Pinus strobus.* L. Ecol. Monogr. 36:1–26.

Bormann, F.H., and B.F. Graham. 1959. The occurrence of natural root grafting in eastern white pine, *Pinus strobus* L., and its ecological implications. Ecology 40:677–691.

Bostock, J., and H.T. Riley. 1855. Pliny's natural history complete in 5 volumes. Bohn, London.

Brasier, C.M. 1991. *Ophiostoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. Mycopathologia 115:151–161.

Brosnan, C.J., N. Mitter, M. Christie, N.A., Smith, P.M. Waterhouse, and B.J. Carroll. (2007) Nuclear gene silencing directs reception of long-distance mRNA silencing in Arabidopsis. Proc. Natl. Acad. Sci. USA 104:14741–14746.

Bunyard, E.D. 1920. The history of the paradise stocks. J. Pom. 1:166–176.

Campbell, C., 2005. The botanist and the vintner: How wine was saved for the world. Algonquin Books of Chapel Hill, Chapel Hill, NC.

Cantliffe, D. 2009. Plug transplant technology. Hort. Rev 35:397–436.

Carter, G.F. 1977. A hypothesis concerning a single origin of agriculture. pp. 89–133. In: C.A. Reed. (ed.), The origin of agriculture. Mouton Publ., The Hague, the Netherlands.

Chang, Chun-shu. 1965. Review of: written on bamboo and silk: The beginning of Chinese books and inscriptions by Tsuen-hsuin Tsien, Harvard J. Asiatic Studies 25:265–268.

Chapot, H. 1975. The citrus plant.pp.6–13 in: Citrus. CIBA-GEIGY Agrochemicals Tech. Monog. 4. CIBA-GEIGY Ltd., Basel, Switzerland.

Childe. V.G. 1958. The dawn of European civilization. Routledge & Kegan Paul, London.

Cowles, H., and C.J. Chamberlain. 1911. Graft hybrids and chimeras. Bot. Gaz. 51:147–153.

Coetzee, B.A., and B.A. Fineran. 1989. Translocation of lysine from the host Melicope simplex to the parasitic dwarf mistletoe *Korthalsella lindsayi* (Viscaceae). New Phytologist 112:377–381.

Cooper, W.C., and H. Chapot. 1977. Fruit production with special emphasis on fruit for processing. In: S. Nagy, P.E. Shaw, and M.K. Veldhuis (eds.), Citrus Sci. Technol., AVI Publ. Co., Westport, CT.

Courbesier, L., and G. Coupland. The quest for florigen: A review of recent programs. J. Expt. Bot. 57:3395–3403.

Curtis G.J. 1967. Graft-transmission of male sterility in sugarbeet (*Beta vulgaris* L.). Euphytica 16:419–424.

De Bruijn, G.H., and T.S. Dharmaputra. 1974. The Mukibat system, a high-yielding method of cassava production in Indonesia, Neth. J. Agr. Sci. 22:89–100.

De Foresta, H., A. Basri, and Wiyone. 1994. A very intimate agroforestry association. Cassava and improved homegardens: the Mukibat technique. Agroforestry Today 6:12–14.

Dodds, J.A., D. Mathews, M.L. Arpaia, and G. W. Witney. 2007. Recognizing avocado sunblotch disease. AvoResearch (cited 10 January 2008). Available at www.avocado. org/growers/pdf/avoresearch_oct2001_Sunblotch_Disease.pdf.

Domitzer, J. 1531. Ein Neues Pflantzbuchlin, von Mancherley Artiger Propffung, und Beltzung der Baum. Augsburg, Germany.

Edwardson, J.R., and M.K. Corbett. 1961. Asexual transmission of cytoplasmic male sterility. Proc, Natl. Acad. Sci. (USA) 47:390–396.

Eis, S. 1972. Root grafts and their silvicultural implications, Can. J. For. Res. 2:111–120.

Epstein, A.H. 1978. Root graft transmission of tree pathogens. Annu. Rev. Phytopath. 16:181–192.

Ewing, E.E., and P.C. Struik. 1992. Tuber formation in potato: Induction, initiation, and growth. Hort. Rev. 14:89–197.

Feliks, Y. 1967. Mixed sowing, breeding and grafting: A study of the Halachic topics and their botanical-agricultural background (in Hebrew). Dvir, Tel Aviv.

Ferree, D.C., and R.F. Carlson, 1987. Apple rootstocks, In: R.C. Rom and R.F. Carlson (eds.), Rootstocks for fruit crops. John Wiley & Sons, New York.

Fitzherbert, J. 1531. The boke of husbandry, London. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:99838088

Foo, E., S. Morris, K. Parmenter, N. Young, W. Huiting, J. Wang, C. Rameau, C. Turnbull, and C. Beveridge. 2007. Feedback regulation of xylem cytokinin content is conserved in pea and arabidopsis, Plant Physiol. 143:1418–1428.

Frankel, R. 1956. Graft-induced transmission to progeny of cytoplasmic male sterility in petuna. Science 124:684–685.

Frazer, J.G. 1935. The magic art and the evolution of kings. Vol 2. Macmillan, New York.

Friedlander, M. (transl.). 1904. The guide to the perplexed by Moses Maimonides. Dover Publ. (1956)

Gallesio, G. 1811. Traite du Citrus. Louis Fantin, Paris.

Garmer, R.J. 1988. The grafters handbook, 5th ed. Oxford Univ. Press, New York.

Gemma, H. 2002. The nashi industry in Japan. Acta Hort. 596:101–107.

Glass, B. 1948. Review: Dialectical materialism and scientific research. Quart. Rev. Biol. 23:333–335.

Goffreda, J.C., E. J. Szymkowiak, I.M. Sussex, and M.A. Mutschler. 1990. Chimeric tomato plants show that aphid resistance and triacylglucose production epidermal autonomous characters. Plant Cell 2:643–649.

Gorelik, G., and A.W. Bouis. 2005. The world of Andrei Sakharov: A Russian physicist's path to freedom. Oxford Univ. Press, New York.

Graham, B., and F.H. Bornman. 1966. Natural root grafts, Bot. Rev. 32:255–292.

Harlan, J.R. 1995. The living fields, Our agricultural heritage. Cambridge University Press, Cambridge, UK.

Harris, S.A., J.P. Robinson, and B.E. Juniper. 2002. Genetic clues to the origin of the apple. Trends Genet. 18:426–430.

Hartman, H.T., D.E. Kester, F.T. Davies, and R. Geneve. 1997. Plant propagation, principles and practices, 6th ed. Prentice-Hall, Englewood Cliffs, NJ.

Hartman, H.T., D.E. Kester, F.T. Davies and R. Geneve. 2002. Plant propagation, principles and practices, 7th ed. Prentice-Hall, Englewood Cliffs, NJ.

Harvey, J.H. 1985. The first English garden book: Mayster Jon Gardener's treatise and its background, Garden History 13:83–101.

Hatch, P.J. 1949. The fruits and fruit trees of Monticello. Univ. Press of Virginia, Charlottesville, VA.

He, C.X., W.B. Li, A.J. Ayres, J.S. Hartung, and V.S. Miranda. 2000. Distribution of *Xylella fastidiosa* in citrus rootstocks and transmission of citrus variegated chlorosis between sweet orange plants through natural root grafts. Plant Dis. 84:622–626.

Heftmann, E. 1983. Biogenesis of sterols in Solanaceae. Phytochemistry 22:1843–1860.

Hirata, Y. 1986. Graft-induced changes in eggplant (*S. melongena* L.) I. Appearance of the changes. Euphytica 35:395–401.

Hooper, W.D. (transl.) 1935. Marcus Porcius Cato: On agriculture. Harvard Univ. Press, Cambridge, MA.

Janick, J. 1983. Horticultural science, 4th ed. W.H. Freeman, New York.

Janick, J. 1989. Theophrastus (300 BC). The modes of propagation in woody and herbaceous plants. Propagation in another tree. pp. 3–13. In: J. Janick (ed.), Classic papers in horticultural science, Prentice-Hall, Englewood Cliffs, NJ.

Janick, J. 2005. The origins of fruits, fruit growing, and fruit breeding. Plant Breed. Rev. 25:255–320.

Joel, D. M., H. Hershenhorn, H. Eizenberg, R. Aly, G. Ejeta. P.J. Rich, J.K. Ransom, J. Sauerborn, and D. Rubiales. 2007. Biology and management of weedy root parasites Hort. Rev. 33:267–349.

Jones, L., F. Ratcliff, and D.C. Baulcombe. 2001. RNA-directed transcriptional gene silencing in plants can be inherited independently of the RNA trigger and requires Met1 for maintenance. Current Biol. 11:747–757.

Juniper, B.E., and S.B. Juniper (eds.). 2001. The compleat planter & cyderist by a (anonymous) lover of planting (1685). National Gallery, London

Juniper, B.E., and J. Maberly. 2006. The story of the apple. Timber Press, Portland, OR.

Kashara, J., T. Nakamura, and Y. Yoneyam, 1973. Graft-induced variation in red peppers (in Japanese). Rec. Adv. Breed. 13:73–89.

Kite, P. 1980. The tree circus. Garden (Nov./Dec.):13–18.

Kuniyama, T. 1996. Pear growing under sub-tropical meterological conditions in Taiwan (in Japanese). Kisho Riyou Kenkyu 9:16–19.

Lammerts Van Bueren, E. 2007. Values in organic agriculture and their consequences for a process-oriented evaluation of plant breeding techniques. HortScience 42:813 (Abstr.).

Langford, T. 1699. Plain and full instructions to raise all sorts of fruit-trees that prosper in England. Early English Books Online (cited 9 January 2008). Available at http://gateway. proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:12496927.

La Rue, C. 1934. Root grafting in trees. Am. J. Bot. 21:121–126.

Lawson, W. 1618. A new orchard and garden, or the best way for planting, grafting and to make any ground good for a rich orchard. Early English Books Online (cited 9 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri: eebo&rft_id=xri:eebo:citation:99828379.

Lee, J.-M. 2003. Advances in vegetable grafting. Chronica Hort. 43 (2):13–19.

Lee, J.-M., and M. Oda. 2003. Grafting of herbaceous vegetable and ornamental crops. Hort. Rev. 28:61–124.

Leinfelder, M.M, and I.A. Merwin. 2006. Rootstock selection, preplant soil treatments, and tree planting positions as factors in managing apple replant disease. HortScience 41:394–401.

Lindsay, G.C., M.E. Hopping, H. Bindina, and G.K. Burge. 1995. Graft chimeas and somatic hybrids for new cultivars. 1995. New Zeal. J. Bot. 33:79–92.

Lion, B. 1992. Vignes au royaume de Mari [Vines of the kingdom Mari]. Mem. Nouvelles Assyriologies Breves Utilitaires 1:107–113.

Liu, Y. 2006. Historical and modern genetics of plant graft hybridization. In: J.C. Hall, J.C. Dunlap, T, Friedmann, and V. van Heyningen (eds.). Adv. Genet. 56:101–129.

Loehle, C., and R.H. Jones. 1990. Adaptive significance of root grafting in trees. Funct. Ecol. 4:268–271.

Lonie, I. M. 1981. The Hippocratric treatises. ''On generation,'' ''On the nature of the child,'' ''Diseases,'' IV. Walter de Gruyter, Berlin.

Marcotrigiano, M., and T. Gradziel. 1997. Genetic mosaics and plant breeding. Plant Breed. Rev. 15:43–84.

Markham, G. 1635. A way to get wealth containing six principal vocations, or callings, in which every good husband or house-wife may lawfully imploy themselves. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:cita-tion:99827985.

Mascall, L. 1589, A booke of the arte and manner how to plant and graffe all sorts of trees. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:cita-tion:22143348.

Mazaheri, A.A. 1951. La vie quotidiennedes Musulmans au Moyen Age. Paris.

Meager, L. 1688. The English gardener: Or a sure guide to young planters and gardeners. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:cita-tion:12351192.

Mendel, R. 1953. The development of our knowledge on transplantations in plants. Acte du Septième Congres International d'Histoire des Sciences, Jerusalem.

Meyer, E.H. 1854. Geschichte der Botanik Studien, Erster Band. Konigsberg. Buch I. Kap. 2. #10.

Miller, P. 1775, The gardeners calendar, 16th ed.. John and Francis Rivington, London.

Mosse, E.B. 1962. Graft incompatibility in fruit trees. Tech. Comm. Bur. Hort. Plant Crops, East Malling, England.

Murashige, T., W.P. Bitters, T.S. Rangan, E.M. Nauer, C.N. Roistacher, and P.B. Holliday. 1972. A technique of shoot apex grafting and its utilization towards recovering virus-free *Citrus* clones. HortScience 7:118–119.

Navarro, L., C.N. Roistacher, and T. Murashige. 1975. Improvement of shoot-tip grafting *in vitro* for virus-free citrus. J. Am. Soc. Hort. Sci. 100:471–479.

Nelson, S.H. 1968. Incompatibility survey among horticultural plants, Intl. Plant Prop. Soc. Comb. Proc. 18:343–393.

Nickrent, D.L. R.J. Duff, A.E. Colwell, A.D. Wolfe, N.D. Yung, K.E. Steiner, and C.W. dePamphilis. 1998. In: D.E. Soltis, P.S. Soltis, and J.J. Doyle (eds.), Molecular systema-tics of plants. II. DNA sequencing. Kluwer Academic Publ., Boston.

Nicolosi, E., S.L. Malfa, M. El-Otmani, M. Negbi, and E.E. Goldschmidt. 2005. The search for the authentic citron (*Citrus medica* L.): Historic and genetic analysis. HortScience 40:1963–1968.

Ohta, Y. 1991 Graft-transformation, the mechanism for graft-induced genetic changes in higher plants. Euphytica 55:91–99.

Osman S.F. 1979. Glycoalkaloids of the Solanaceae. Recent Adv. Phytochem. 14:75–96.

Owen, T. 1897. The fourteen books of Palladius, Rutilius Taurus Milianuas, on agricul-ture. J. White, London.

Pease, A.S. 1933. Notes on ancient grafting. Trans. Proc. Am. Philological Assoc. 64: 66–76.

Pina, P., and P. Errea. 2005. A review of new advances in mechanism of graft compatibility-incompatibility. Scientia Hort. 106:1–11.

Pollan, M. 2001. Botany of desire. Random House, New York.

Porta, Giambattista della. 1558. Magia naturalis (Natural magic) (cited 10 January 2008). Available at http://homepages.tscnet.com/omard1/jportat5.html.

Porta, Giambattista della. 1659. Natural magick. Early English Books Online (cited 10 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:99829574.

Price, D. 1957. Giambattista della Porta and his natural magick. Available at http://homepages.tscnet.com/omard1/jportat3.html#price.

Rao, A.N. 1966. Developmental anatomy of natural root grafts in *Ficus globosa.* Austral J. Bot. 14:269–276.

Rieger, M. 2006. Grapes—*Vitus* species (cited 10 January 2008). Available at www.uga.edu/fruit/grape.html.

Roistacher, C.N. 2004. Diagnosis and management of virus and virus like diseases of citrus. In: S. Naqvi (ed.), Diseases of fruits and vegetables, Vol. 1, Springer, the Netherlands.

Ruel, J. 1536. De natura stirpium. Libri Tres, Paris.

Sharrock, R. 1672. The history of the propagation & improvement of vegetables by the concurrence of art and nature: shewing the several ways for the propagation of plants usually cultivated in England. Early English Books Online (cited 8 January 2008). Available at http://gateway.proquest.com/openurl?ctx_ver=Z39.88-2003&res_id=xri:eebo&rft_id=xri:eebo:citation:13785953.

Shih Sheng-Han. 1959. On Fan Sheng-Chih Shu. An agricultural book of China written by Fan Sheng-Chih in the first century B.C. Science Press, Peking, China.

Shih Sheng-Han. 1962. A preliminary survey of the book Ch'i Min Yao Shu, An agricultural encyclopedia of the 6th century. Science Press, Peking, China.

Stubbe, H. 1954. Ber die vegetative Hybridisierung von Pflanzen. Versuch an Tomatemutanten. Kulturepflanze 2:185–236.

Taller, J., Y. Hirata, N. Yagishita, M. Kita, and S. Ogata. 1998. Graft-induced genetic changes and the inheritance of several characteristics in pepper (*Capsicum annuum* L.). Theor Appl. Genet. 97:705–713.

Thoday, D. 1956. Modes of union and interactions between parasite and host in the Loranthaceae. I. Viscoideae, not including Phoradendreae. Proc. Royal Soc. London, Series B, Biological Sciences 145:531–548.

Thompson, T.E., and J.D. Axtell. 1978. Graft-induced transmission of cytoplasmic male sterility in alfalfa. J. Hered. 69:159–164.

Tidemann, R. 1989. Graft union development and symplastic phloem contact in the heterograft *Cucumis sativus* on *Cucurbita ficifolia.* J. Plant Physiol. 134:427–440.

Topoleski, L.D., and J. Janick. 1963. A study of graft-induced alterations in eggplant. Proc. Am. Soc. Hort. Sci. 83:559–570.

Tournier B. M. Tabler, and K. Kalantidis. 2006. Phloem flow strongly influences the systemic spread of silencing in GFP *Nicotiana benthamiana* plants. Plant J. 47:383–394.

Tukey, H. 1964, Dwarfed fruit trees. Macmillan, New York.

Tully, M. 2007. Johnny Appleseed (cited 10 January 2008). Available at www.nwta.com/Spy/winter00/johnny.html.

Virgil. 1953. The georgics. Translated into English verse by John Dryden. Heritage Press, New York.

Vochting, H. 1892. Uber Transplantation Am Pflanzenkorper, Untersuchungen zur Physiologie und Pathologie. Verlag der H. Lauppschen Buchhandlung, Tubingen.

Volkamer, J.C. 1708. Nuernbergische Hesperides oder Gruendliche Beschreibung der edlen Citronat Citronen und Pomeranzen-Fruechte, Vol. Nuernberg.

Watson, A.M. 1983. Agricultural innovation in the early Islamic world. Cambridge Univ. Press, Cambridge, UK.

Webster, A.D. 2003. Breeding and selection of apple and pear rootstocks. Acta Hort. 622:499–512.

Wilson, P.M.W. 1952. Distribution of solanaceous Alkaloids in some new graft combinations, New Phytol. 51:260–263.

Yagishita, N. 1961. Studies on graft hybrids of *Capsicum annum* L. II. Variation in fruit shape caused by grafting of three successive generatons and effects in the progeny. Bot Mag. 881:480–489.

Zeevaart, J. 2006. Florigen coming of age after 70 years. Plant Cell 18:1783–1789.

Zohary, D. and P. Spiegel-Roy. 1975. Beginning of fruit groing in the Old World. Science 187:319–327.