

* 11

Principles of Grafting and Budding

INTRODUCTION

Since the beginning of civilization, fruit and nut trees have been grafted because of the difficulty in propagating by cuttings, and the superiority and high value of the grafted crop. *Grafting* is among the most expensive propagation techniques, surpassing even micropropagation. *Budding*, which is a form of grafting, is three times more costly than cuttings and fourteen times more expensive than seedling propagation (89). The horticulture and forestry industries have sought to develop clonal propagation systems that avoid labor-intensive graftage. Yet, traditional and highly efficient grafting and budding systems are essential for the propagation of many woody plant species. New markets continue to require grafted and budded plants for improved plant quality, fruit yield, superior forms, and better adaptation to greater ecological ranges. In the southeastern United States, where high temperatures and periodic flooding of soils (low soil oxygen) are the norm, cultivars of birch, fir, oak, and other species are grafted onto adapted rootstock (Fig. 11–1) (129). The propagator benefits via new markets, while the consumer gains a greater variety of better-adapted landscape plants. The acid-loving blueberry can be produced in more basic pH soils when grafted to pH-tolerant rootstock (Fig. 11–2).

With the greater reliance on integrated pest management and reduced availability of pesticides and soil fumigants, disease-tolerant rootstocks are playing a greater role not only with woody perennial fruit crops and ornamentals, but also with grafted vegetable crops (Figs. 11–3 and 11–4, page 417) (34, 39, 67, 82, 85, 86). Organic growers of high value heirloom tomatoes are using grafted plants as a management tool to reduce crop loss from soilborne diseases (131).

This chapter reviews the biology of grafting and budding. Chapters 12 and 13 describe the techniques of grafting and budding, respectively. Chapter 19 enumerates grafting and budding systems for selected fruit and nut trees, as Chapter 20 does for selected woody ornamental plants. A better understanding of the fundamental biology of grafting (and the causes of graft incompatibility) will enhance the development of superior cultivars and increase the ecological range of species for new markets in horticulture and forestry.

THE HISTORY OF GRAFTING

The origins of grafting can be traced to ancient times (110). There is evidence that the art of grafting was known to the Chinese at least as early as 1560 BC. Aristotle (384–322 BC) and Theophrastus (371–287 BC) discussed grafting in their

learning objectives

- Describe the role of grafting in human history.
- Distinguish between the use of seedling and clonal rootstocks.
- Describe how natural grafting can affect tree performance.
- Describe how the rootstock and scion heal together during grafting.
- Define how specific genetic, environmental, and management factors and polarity affect graft success.
- Determine what kinds of plants can be grafted.
- Define graft incompatibility—its symptoms, causes, and control.
- Describe important ways the rootstock (root system) influences the scion (shoot system) and vice versa.





(a)



(b)

Figure 11-1
Cleft-grafted-variegated English Holly on Ilex ‘Nellie Stevens’ rootstock adapted to the high temperature, periodic flooding, low oxygen soils of the southeastern United States.



(a)

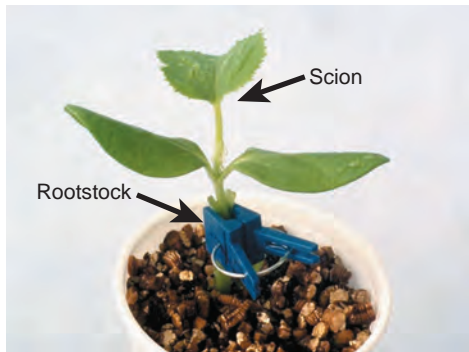


(b)

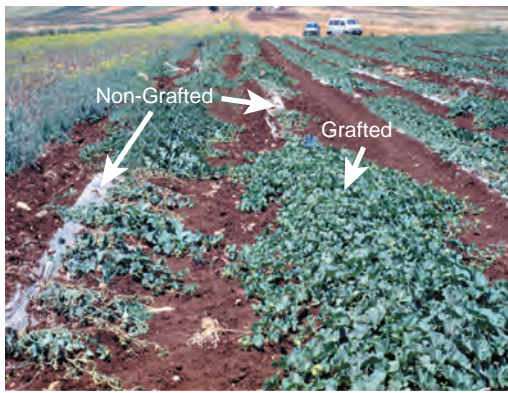


(c)

Figure 11-2
Pushing the ecological envelope. Using an inlay bark graft of ‘Tif Blue’ blueberry (*Vaccinium ashei*) on a farkelberry (*Vaccinium arboreum*) rootstock, which tolerates a more basic soil pH, allows the acid-loving blueberry to be produced in a site with higher soil pH. (a) New scion growth with aluminum foil and poly bag protecting the graft area. (b) Healed graft union, and (c) ‘Tif Blue’ blueberry crop.



(a)



(b)

Figure 11-3
Grafting vegetables is a common practice in Japan, Korea, the Mediterranean basin, and Europe. It is used for managing soil-borne diseases, enhancing tolerance of low temperature and salinity, and for increasing plant vigor and yield. (a) Grafted melon scion on curcubita rootstock with a grafting clip. (b) Melons grafted (white arrow) on Fusarium-resistant Curcubita rootstock in Israel, (b) compared to susceptible, non-grafted melons (black arrows). Courtesy M. Edelstein.

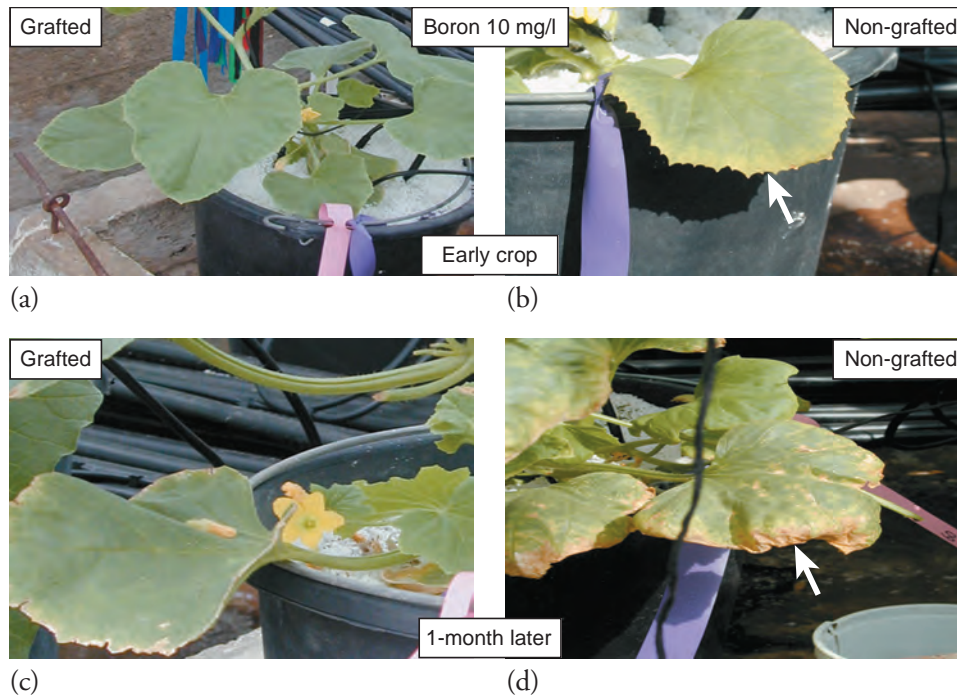


Figure 11-4
(a and c) Melon grafted onto boron-resistant *Cucurbita* rootstock. (b) Non-grafted melon showing boron susceptibility early in crop cycle and (d) 1 month later
Photos courtesy M. Edelstein.

writings with considerable understanding. During the days of the Roman Empire, grafting was very popular, and methods were precisely described in the writings of that era. Paul the Apostle, in his Epistle to the Romans, discussed grafting between the “good” and the “wild” olive trees (Romans 11:17–24).

The Renaissance period (AD 1350–1600) saw a renewed interest in grafting practices. Large numbers of new plants from foreign countries were imported into European gardens and maintained by grafting. By the 16th Century, the cleft and whip grafts were widely used in England and it was realized that the cambium layers must be matched, although the nature of this tissue was not then understood or appreciated. Propagators were handicapped by a lack of a good grafting wax; mixtures of wet clay and dung were used to cover the graft unions. In the 17th Century, orchards in England were planted with budded and grafted trees.

Early in the 18th Century, Stephen Hales, in his studies on the “circulation of sap” in plants, approach-grafted three trees and found that the center tree stayed alive even when severed from its roots. Duhamel studied wound healing and the uniting of woody grafts. The graft union at that time was considered to act as a type of filter that changed the composition of the sap flowing through it. Thouin (163), in 1821, described 119 methods of grafting and discussed changes in growth habit resulting from grafting. Vöchting (171), in the late 19th Century, continued Duhamel’s earlier work

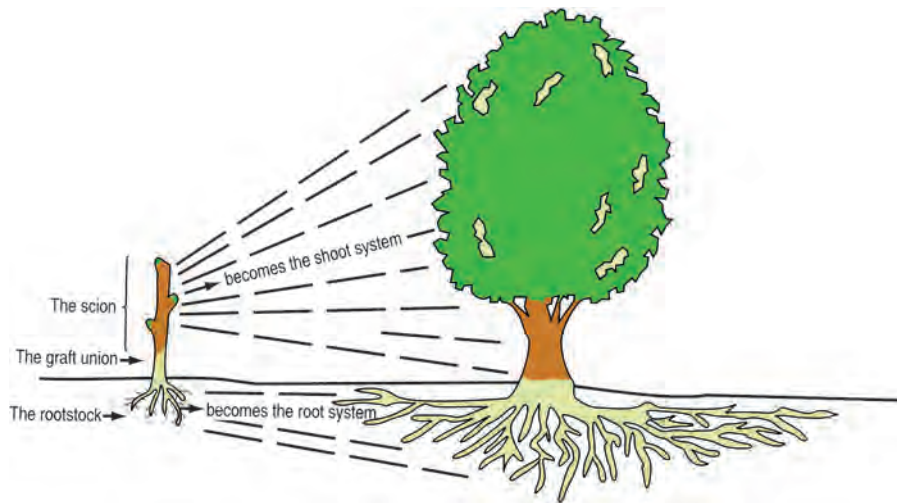
on the anatomy of the graft union. Development of some of the early grafting techniques have been reviewed by Wells (178).

Liberty Hyde Bailey in *The Nursery Book* (8), published in 1891, described and illustrated the methods of grafting and budding commonly used in the United States and Europe at that time. The methods used today differ very little from those described by Bailey.

TERMINOLOGY

Grafting is the art of joining two pieces of living plant tissue together in such a manner that they will unite and subsequently grow and develop as one composite plant. As any technique that will accomplish this could be considered a method of grafting, it is not surprising that innumerable procedures for grafting are described in the literature. Through the years, several distinct methods have become established that enable the propagator to cope with almost any grafting problem. These are described in Chapter 12 with the realization that there are many variations of each, and that there are other forms that can give similar results. Figure 11-5 illustrates a grafted plant and the parts involved in the graft.

grafting The union of a root system (**understock**) with a shoot system (**scion**) in such a manner that they subsequently grow and develop as one **composite** (compound) plant.

**Figure 11-5**

In grafted plants the shoot system consists of growth arising from one (or more) buds on the scion. The root system consists of an extension of the original rootstock. The graft union remains at the junction of the two parts throughout the life of the plant.

budding A form of grafting that uses a smaller scion piece—sometimes just a piece of the stem with an axillary bud.

Budding is a form of grafting. However, the scion is reduced in size and usually contains only one bud. An exception to this is patch budding of pecan, where secondary

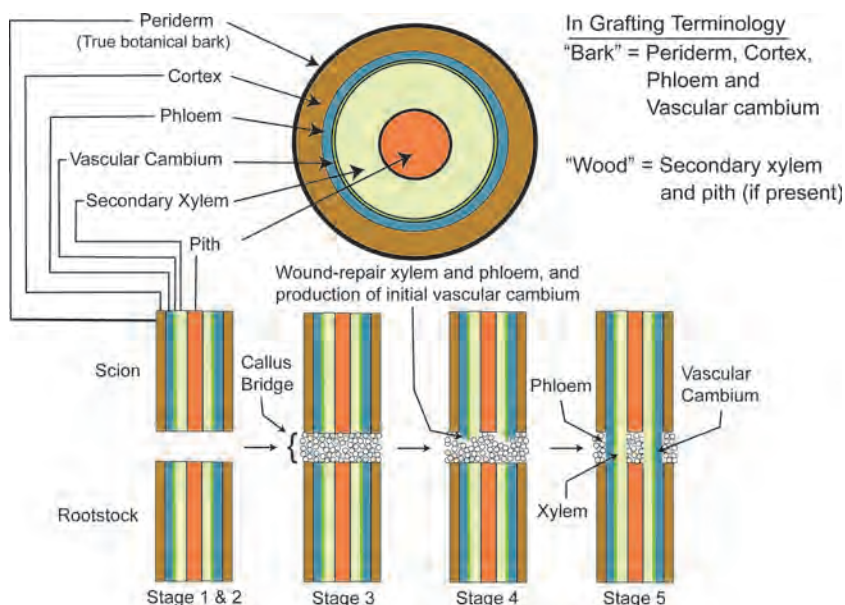
and tertiary buds are adjacent at the same node to the primary bud. The various budding methods are described in Chapter 13.

The **scion** becomes the new shoot system of the graft. It is composed of a short piece of detached shoot containing several dormant buds, which, when united with the rootstock, comprises the upper portion of the graft. The stem, or branches, or both, of the grafted plant will grow from the scion. The scion should be of the desired cultivar and free from disease.

The **rootstock (understock, stock)** is the lower portion of the graft, which develops into the root system of the grafted plant. It may be a seedling, a rooted cutting, a layered or micropropagated plant. If the grafting is done high in a tree, as in topworking, the rootstock may consist of the roots, trunk, and scaffold branches.

The **interstock (intermediate stock, interstem)** is a piece of stem inserted by means of two graft unions between the scion and the rootstock. Interstocks are used to avoid incompatibility between the rootstock and scion, to produce special tree forms, to control disease (e.g., fire-blight resistance), or to take advantage of their growth-controlling properties.

Vascular cambium is a thin tissue located between the bark (periderm, cortex, and phloem) and the wood (xylem) (see Fig. 11-6). Its cells are meristematic; that is, they are capable of dividing and forming new cells.

**Figure 11-6**

Top: Grafting terminology of the "bark" and "wood" and associated tissues with schematic drawing of a stem cross section of a young woody plant stem. Bottom: Schematic longitudinal section of the stages of graft union formation: (Stage 1) Lining up vascular cambiums of the rootstock and scion, and (Stage 2) subsequent wound healing response. (Stage 3) Callus bridge formation. (Stage 4) Wound-repair xylem and phloem occur in the callus bridge just prior to initial cambium formation. (Stage 5) The vascular cambium is completed across the callus bridge and is forming secondary xylem and phloem.

For a successful graft union, it is essential that the cambium of the scion be placed in close contact with the cambium of the rootstock.

callus Tissue composed of parenchyma cells, which is a response to wounding. Callus development is important in graft union formation.

of these parenchyma (or callus) cells constitute one of the important steps in callus bridge formation between the scion and rootstock in a successful graft.

Callus is a term applied to the mass of parenchyma cells that develop from and around wounded plant tissues. It occurs at the junction of a graft union, arising from the living cells of both the scion and rootstock. The production and interlocking

SEEDLING AND CLONAL ROOTSTOCK SYSTEMS

Rootstocks can be divided into two groups: seedling and clonal.

Utilization and Propagation of Seedling Rootstock

Seedling rootstocks propagated from seed can be mass-produced relatively simply and economically. Viruses are transmitted from parent to progeny in very low percentages or not at all except in specific instances. Seedling plants tend to have deeper rooted and more firmly anchored plants than rootstocks grown from cuttings (e.g., plum and apple rootstock).

Seedling rootstock may show genetic variation leading to variability in growth and performance of the scion variety. The variation can arise from natural heterozygosity of the source or from cross-pollination—both are more likely if the rootstock is from an unknown, unselected source. Selection of special mother-tree (elite) seed source trees or a special clone can provide uniform, special seedling rootstocks for specific crops (see Chapter 5).

Uniformity of seedling variability can be controlled by managing production conditions in the nursery, including digging nursery trees of the same age, one row at a time, and discarding off-type or slow-growing seedlings or budded trees. In most nurseries, the young trees are graded by size, and all those of the same grade are sold together. Many fruit crops grown on uniform seedling rootstocks show no more variability resulting from the rootstock than from unavoidable environmental differences in the orchard—principally soil variability.

Utilization and Propagation of Clonal Rootstock

Clonal rootstocks are those vegetatively propagated by stool layering, rooted cuttings, or micropropagation. Micropropagation of clonal rootstocks makes possible the production of great numbers of such plants, upon which the scion cultivar can be grafted or budded (76, 77). Rootstock of citrus is produced from apomictic seed and is genetically uniform; this is a more cost-effective method of propagating clonal rootstock than traditional asexual techniques.

Clonal rootstocks are desirable not only to produce uniformity, but also to utilize special characteristics such as disease resistance. Clonal rootstock also influence the size and growth habit of the grafted plant and flowering and fruit development of the scion. Each particular scion-rootstock combination requires an extensive evaluation period in different environments before its future performance can be predicted.

Historically, clonal rootstocks for fruit crops received much attention in European and Middle Eastern countries, going back centuries. Today, much of the apple production around the world is on clonal rootstocks for size control and fruit yield. Other fruit crops, such as pear, quince, plum, cherries, grapes, citrus, and others are routinely propagated on clonal rootstock (179).

Only pathogen-free scions and rootstock material should be utilized in the nursery. To maintain rootstock influence, deep planting of the nursery tree or grafted vegetable—which may lead to “**scion rooting**”—must be avoided, as illustrated in Figure 11–7. The deeper the graft union below the soil surface, the higher the incidence of scion rooting is likely to be (31).

REASONS FOR GRAFTING AND BUDDING

Grafting and budding serve many different purposes:

- Perpetuating clones desired for their fruiting, flowering, or growth characteristics that cannot be readily maintained or economically propagated by other asexual means
- Combining different cultivars into a composite plant as scion, rootstock, and interstock—each part providing a special characteristic
- Changing cultivars of established plants (topworking), including combining more than one scion cultivar on the same plant
- Repairing graftage for injuries—including inarching and bridge graftage



Figure 11-7

An incompatible graft with the melon scion forming adventitious roots above the grafted *Cucurbita* rootstock. The melon will establish its own roots above graft, which is not desirable. Courtesy M. Edelstein.

- Disease indexing—testing for virus diseases
- Study of plant developmental and physiological processes

Each of these reasons is discussed in detail in the following pages.

Perpetuating Clones Desired for Their Fruiting, Flowering, or Growth Characteristics That Cannot Be Readily Maintained or Economically Propagated by Other Asexual Means

Cultivars of some groups of plants, including most fruit and nut species and many other woody plants, such as selected cultivars of fir, eucalyptus, beech, oak, and spruce, are not propagated commercially by cuttings because of poor rooting. Additional individual plants often can be started by the slow and labor-intensive techniques of layering or division. But for propagation in large quantities, it is necessary to resort to budding or grafting scions of the desired cultivar on compatible seedling rootstock plants.

In forestry, grafting is used almost exclusively for the clonal production of genetically improved seed orchards of Monterey pine (*Pinus radiata*), hoop pine

(*Araucaria cunninghamii*), slash pine (*P. elliottii*), Caribbean pine (*P. caribaea*), eucalyptus (*Eucalyptus nitens*), Douglas-fir (*Pseudotsuga menziesii*), and others (120). The major advantage of using grafts is that superior germplasm from older, elite trees can be clonally regenerated as parent trees for seed orchards. Frequently, trees selected for breeding or seed orchard purposes are so old (often greater than 15 or 20 years) that clonal production by rooted cuttings is either impossible or far more costly than grafting. Where graft incompatibility is not a serious problem, grafting scions of elite trees onto established seedling rootstock is a quick, straightforward, and cost-effective way of developing seed orchards.

Combining Different Cultivars into a Composite Plant as Scion, Rootstock, and Interstock—Each Part Providing a Special Characteristic

Obtaining the Benefits of Certain Scions Grafting selected cultivars can enhance plant growth rates, fruit characteristics and yield, and plant form. “Weeping” forms of landscape plants can be obtained by grafting (Fig. 11-8). Cactus and succulents are easily grafted to produce unusual plant forms, as shown in Figure 11-9.

Obtaining the Benefits of Certain Rootstocks There are a number of benefits of grafting onto selected rootstock, including greater plant resistance to biotic and



Figure 11-8

“Weeping” plant forms may be obtained by grafting. Rootstock of an upright willow is grafted at the top by a side graft with another cultivar having a hanging growth pattern.



(a)



(b)

Figure 11-9

Grafted ornamental (a) cactus and (b) succulents. An easily rooted cultivar is used as the rootstock and an unusual attractive type is used as the scion. These grafts are made in large quantities in Japan and Korea, and shipped to wholesale nurseries in other countries for rooting, potting, and growing until ready for sale in retail outlets.

abiotic stress

A condition caused by environmental factors such as drought, low temperature, low oxygen, and salinity, which reduce growth and can sometimes kill plants.

biotic stress

A condition caused by living organisms such as insects, pathogens, and nematodes that reduce growth and can sometimes kill plants.

11-4) (47, 124-126, 129). Other rootstocks may resist **biotic stresses** such as soil-borne insect, nematodes, viruses, or pathogens (34, 86) better than the plant's own roots (Fig. 11-3). See Chapters 19 and 20 for detailed discussions of the rootstocks available for the various fruit and ornamental species. Special rootstocks for glasshouse, poly-covered high tunnel production and field production of vegetable crops are used in Europe, the Middle East, Asia, and North America to avoid root diseases such as *Monosporascus*, *Fusarium* and *Verticillium* wilt (34, 131). In the Netherlands, greenhouse cucumbers are grafted onto *Cucurbita ficifolia*, and commercial tomato cultivars are grafted onto vigorous F₁ hybrid, disease-resistant rootstocks (21).

Controlling Size of Grafted Plant. For some species, size-controlling rootstocks are available that can cause the composite grafted plant to have exceptional vigor or

abiotic stress, size control, enhanced reproductive growth, reduction in nursery production time, and increased transplanting success.

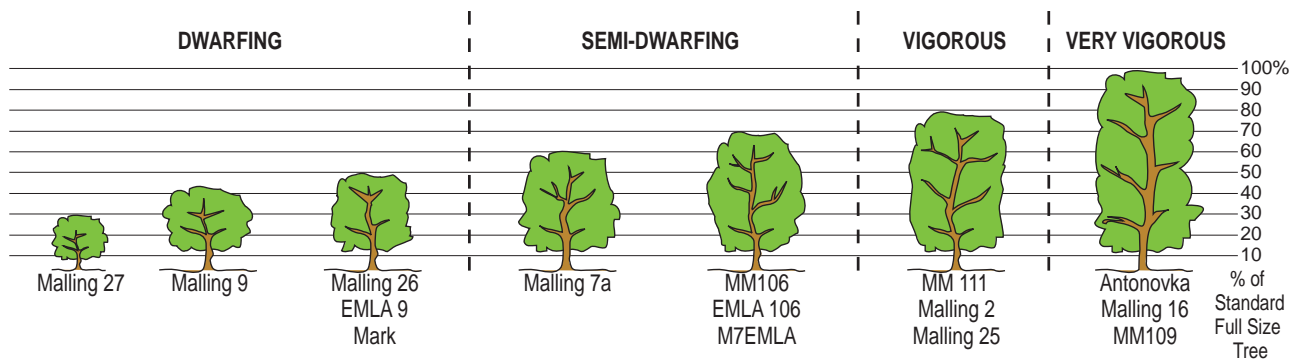
Greater Resistance to Environmental Stress and Disease. For many kinds of plants, rootstocks are available that tolerate unfavorable **abiotic stress** conditions—such as heavy, wet soils, salinity, and drought (Figs. 11-1, 11-2, and

to become dwarfed (Fig. 11-10). Scions grafted onto selected rootstock of some citrus, pear, and apple rootstocks produce larger size and/or better-quality fruit than when grafted onto other rootstock (179).

Hastening Reproductive Maturity. Scions of many fruit crops can be established more quickly in the orchard and come into bearing more rapidly when grafted onto dwarfing rootstock (169), as opposed to being grown as seedlings or as rooted cuttings. (An exception to this is peach production in Mexico, where very vigorous seedlings are selected for fruit production—seedling plants fruit as rapidly as grafted plants.) It is also possible to hasten the onset of maturity by grafting cultivars onto larger, established trees. Such grafting takes advantage of an existing large root system of the rootstock plant to speed up maturation of the scion.

Hastening Plant Growth Rate and Reducing Nursery Production Time. In nursery production of shade trees, budded or grafted trees grow more rapidly than seedling or cutting-produced trees; for example, *Acer platanoides* 'Crimson King' budded on a vigorous rootstock (see Fig. 13-4), and budded *Tilia cordata* or budded *Zelkova serrata* grow more in 1 year than rooted cuttings will in 3 or 4 years (53).

Improving Transplanting Success. Some plants rooted by cuttings make such poor root systems that they are difficult or impossible to transplant; for example, the Koster spruce (*Picea pungens*) can be rooted in commercial numbers, but cannot be successfully transplanted unless the root system is produced from grafted plants (53). Many Asiatic maples form poor root systems from cuttings and must be grafted (170).

**Figure 11-10**

Relative size of apple trees on different rootstock. The reduction in tree size ranges from dwarfing (25 to 50 percent of a standard full-size tree) to semi-dwarfing (60 to 70 percent) to vigorous to very vigorous (same size as a seedling tree). With the exception of Antonovka, all listed are clonal rootstock. The absolute size of the mature, composite tree is determined by soil, climate, culture, and the vigor of the scion cultivar (e.g., the scions of the vigorous cultivar ‘Mutsu’ are twice as large as ‘Golden Delicious’ on ‘Malling 9’ dwarfing rootstock).

Obtaining the Benefits of Certain Interstocks (Double-Working)

In addition to the rootstock and scion, one may insert a third plant system between them by grafting. Such a section is termed an **interstock, interstem, intermediate stock, or intermediate stem section**. This is done by making two grafts (see Fig. 12–50), or double budding. For example, a thin plate (minus the bud) of ‘Old Home’ pear interstock is budded on the quince rootstock, then a shield bud of the ‘Bartlett’ scion is inserted directly over the ‘Old Home’ plate and wrapped with a budding rubber (see Fig. 13–21).

double-working The grafting or budding of an interstock (interstem) between the rootstock and scion.

There are several reasons for using **double-working** in propagation:

- The interstock makes it possible to avoid certain kinds of incompatibility.
- The interstock may possess a particular characteristic (such as disease resistance or cold-hardiness) not possessed by either the rootstock or the scion.
- A certain scion cultivar may be required for disease resistance in cases where the interstock characteristics are the chief consideration, such as in the control of leaf blight on rubber trees (*Hevea*) (84).
- The interstock may reduce vegetative growth and enhance reproductive growth of the tree. For example, when a stem piece of the dwarfing ‘Malling 9’ apple rootstock is used as an interstock and inserted between a vigorous rootstock and a vigorous scion cultivar, it reduces growth of the composite tree and stimulates flowering and fruiting in comparison with a similar tree propagated without the interstock [Fig. 11–11 (132)].

- Obtaining special forms of plant growth. By grafting certain combinations together it is possible to produce unusual types of plant growth, such as “tree” roses (Fig. 11–12) or “weeping” cherry, birch, or willow cultivars (Fig. 11–8).

Nurseries supplying trees on seedling or clonal rootstocks, or with a clonal interstock, should identify such stocks on the label just as they do for the scion cultivar.

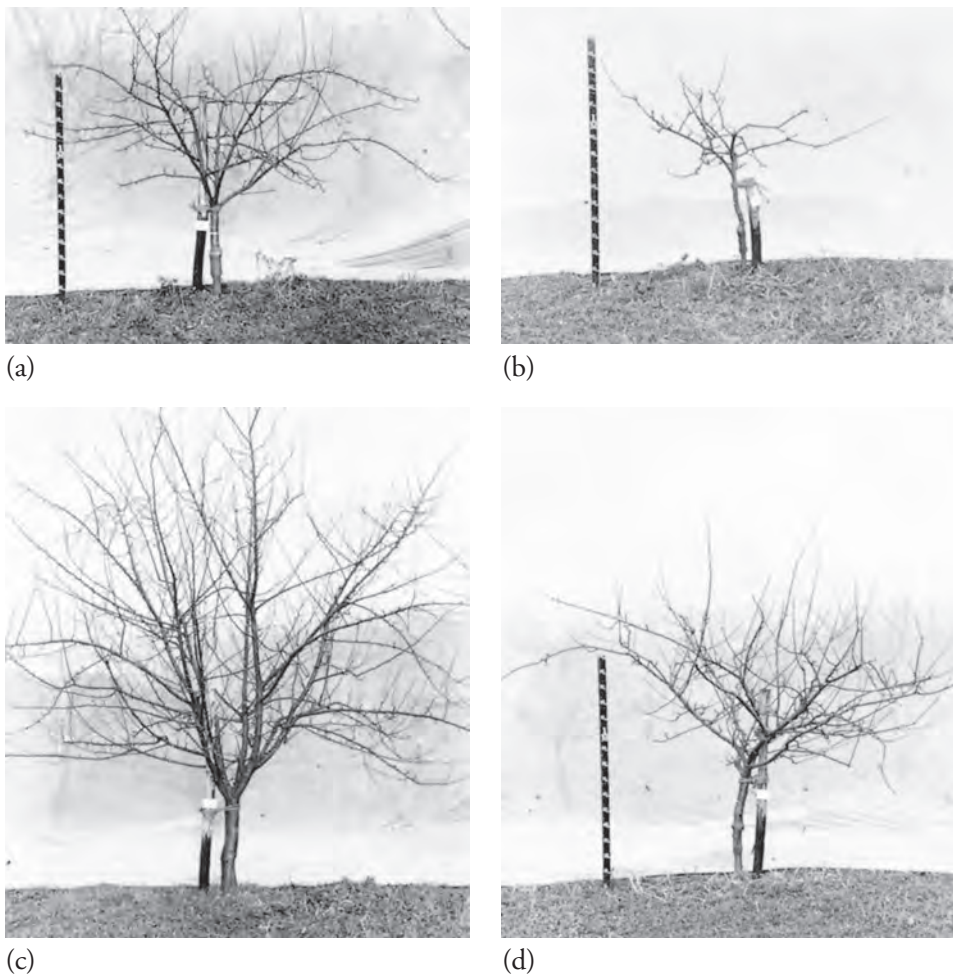
Changing Cultivars of Established Plants (Topworking)

A fruit tree, or an entire orchard, may be replaced with a more desirable cultivar. It could be unproductive, or an old cultivar whose fruits are no longer in demand; it could be one with poor growth habits, or possibly one that is susceptible to prevalent diseases or insects. **Topworking** has sometimes been done by California producers of peach, plum, and nectarine every 2 to 3 years to take advantage of newer, more promising cultivars and thus remain competitive on the market. Examples of topworking are shown in Figure 11–13, page 424.

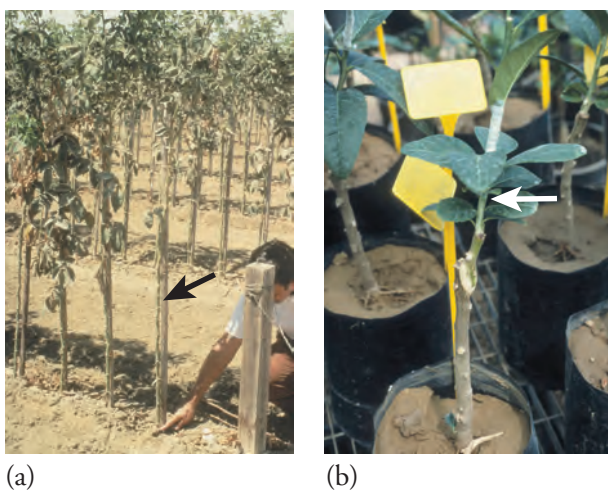
topworking

The grafting of a new cultivar onto established trees in the orchard.

In an orchard of a single cultivar of a species requiring cross-pollination, provision for adequate cross-pollination can be obtained by topworking scattered trees throughout the orchard to a proper pollinating cultivar. A single pistillate (female) plant of a dioecious (pistillate and staminate flowers borne on separate individual plants) species, such as the hollies (*Ilex*), may be unfruitful because of the lack of a nearby staminate (male) plant to provide proper pollination. This problem can be

**Figure 11-11**

Effect of interstock on the size of six-year-old 'Cox's Orange Pippin' apple scion grafted on a vigorous 'MM 104' rootstock: (a) Cox/'M 9' dwarfing interstock/'MM 104', (b) Cox/'M 27' dwarfing interstock/'MM 104', (c) Cox/'MM 104' vigorous interstock/'MM 104', (d) Cox/'M 20' dwarfing interstock/'MM 104'.

**Figure 11-12**

Double-working. (a) Used in the production of specialty "tree" roses, where the interstock (arrow) of Multiflore de la Grifferaie forms the straight trunk of the tree rose. (b) Doubleworking citrus in Sicily with micrografted scion grafted on Troyer citrange interstock (arrow) grafted onto sour orange rootstock.

corrected by grafting a scion taken from a staminate plant onto one branch of the pistillate plant.

The home gardener may be interested in growing several cultivars of a fruit species together on a single tree of that species by topworking each primary scaffold branch to a different cultivar. In a few cases, different species can be worked on the same tree. For example, a single citrus tree would grow oranges, lemons, grapefruit, mandarins, and limes; or plum, almond, apricot, and nectarine can be grafted on peach rootstock. Some different cultivars (or species), however, grow at different degrees of vigor, so careful pruning is required to cut back the most vigorous cultivar on the tree to prevent it from becoming dominant over the others.

Walnut and pistachio are difficult to transplant. Producers will plant seedling rootstock in the orchard and then graft 2 years later.

Repair Graftage for Injuries

Occasionally, the roots, trunk, or large limbs of trees are severely damaged by winter injury, cultivation implements, diseases, or rodents. By the use of bridge

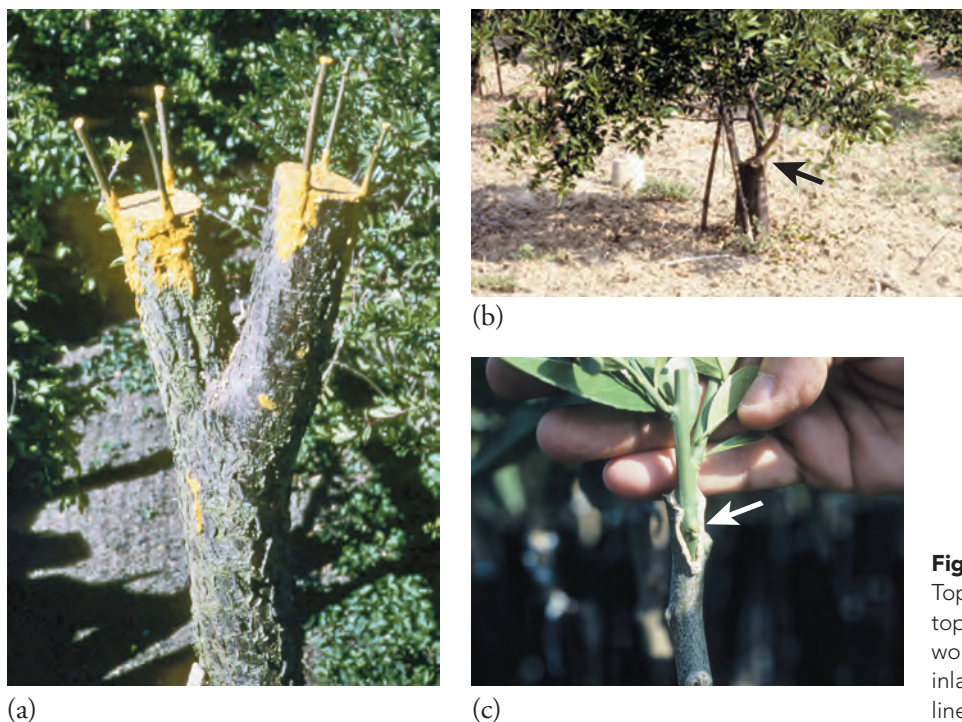


Figure 11-13
TopWorking. (a) Inlay bark graft in top working an orchard. (b) Top worked citrus grove in Sicily using an inlay bark graft. (c) Smaller citrus liner with inlay bark graft.

grafting, or inarching, such damage can be repaired and the tree saved. This is discussed in detail in Chapter 12.

Disease Indexing—Testing for Virus Diseases

Virus diseases can be transmitted from plant to plant by grafting. This characteristic makes possible testing for the presence of the virus in plants that may carry the pathogens but show few or no symptoms. By grafting scions or buds on a plant suspected of carrying the virus onto an indicator plant known to be highly susceptible, and which shows prominent symptoms, detection is easily accomplished. This procedure is known as indexing (see Chapter 16).

In order to detect the presence of a latent virus in an asymptomatic carrier, it is not necessary to use combinations that make a permanent, compatible graft union. For example, the ‘Shirofugen’ flowering cherry (*Prunus serrulata*) is used to detect viruses in peach, plum, almond, and apricot. Cherry does not make a compatible union with these species, but a temporary, incompatible union is a sufficient bridge for virus transfer (see Fig. 16–30).

Thermotherapy Thermotherapy is a heat treatment used to rid scion material of viruses (see Fig. 16–34). After the virus-free material is indexed, as indicated previously, or tested with serological techniques, it can be multiplied by traditional grafting/budding techniques. Micrografting under aseptic tissue culture conditions is

another technique used to clean up viruses and bacterial problems with budwood (112).

Study of Plant Developmental and Physiological Processes

Grafting has enabled plant biologists to study unique physiological and developmental processes, beginning in the 1700s with Stephen Hale’s studies on the circulation of plant sap. Grafting has been used successfully to study transmissible factors (98) in flowering (42), tuber initiation, the control of branching (20), and promotion of cold-hardiness between induced and noninduced organs. The use of multiple graft combinations, including reciprocal and autografting, has facilitated studies on promoters and inhibitors in adventitious rooting (57), root regeneration potential, and rejuvenation of mature phase plant material (119).

NATURAL GRAFTING

Occasionally, branches become naturally grafted together following a long period of being pressed together without disturbance. In commercial orchards, limbs of fruit trees are sometimes deliberately “braced” together and allowed to naturally graft, forming a stronger scaffold system to better support the fruit load of the tree (see Fig. 12–34).

Natural grafting of roots is not as obvious but is more significant and widespread, particularly in



stands of forest species of pine, hemlock, oak, and Douglas-fir (59, 97). Such root grafts are common between roots of the same tree or between roots of trees of the same species. Grafts between roots of trees of different species are rare. In the forest, living stumps sometimes occur, kept alive because their roots have become grafted to those of nearby intact, living trees, allowing the exchange of nutrients, water, and metabolites (95, 97).

The anatomy of natural grafting of aerial roots has been studied (128). Natural root grafting also permits transmission of fungi, viruses, and phytoplasmas from infected trees to their neighbors (128). This problem can occur in orchard and nursery plantings of trees and in urban shade tree sites where numerous root grafts may result in the slow spread of pathogens throughout the planting. Natural root grafting is a potential source of error in virus-indexing procedures where virus-free and virus-infected trees are grown in close proximity (60). In addition, fungal pathogens causing oak wilt and Dutch elm disease can be spread by such natural root connections.

FORMATION OF THE GRAFT UNION

A number of detailed studies have been made of graft union formation, with woody (9, 11, 35, 49, 133, 156, 168) and herbaceous plants (52, 91, 101, 105, 123, 152, 159, 164, 188). Just as *de novo meristems* are

de novo meristems
New meristematic areas initiated from parenchyma cells such as the vascular cambium that must develop in the callus bridge of a grafted plant.

necessary for adventitious bud and root formation, a *de novo*-formed meristematic area (new vascular cambium) must develop between the scion and rootstock if successful graft union formation is to occur (188). The parts of the graft that are originally prepared and placed in close contact do not themselves move about or grow together. Rather, the union is accomplished entirely by cells that develop after the actual grafting operation has been made. The graft union is initially formed by rapidly dividing callus cells, originating from the scion and rootstock, which later differentiate to form the vascular cambium (a lateral meristem) and the associated vascular system.

The development of a compatible graft is typically comprised of three major events: **adhesion** of the rootstock and scion, proliferation of callus cells at the

graft interface or **callus bridge**, and **vascular differentiation** across the graft interface (106).

The scion will not resume its growth successfully unless a vascular connection has been established so that it may obtain water and mineral nutrients. Likewise, degeneration of the rootstock will occur if the phloem in the graft union is disrupted from sending carbohydrates and other metabolites from the scion to the root system. In addition, the scion must have a terminal meristematic region—a bud—to resume shoot growth and, eventually, to supply photosynthate to the root system.

Considering in more detail the **steps involved in graft union formation** (Figs. 11–6 and 11–14), the first one listed below is a preliminary step, but nevertheless, it is essential, and one over which the propagator has control.

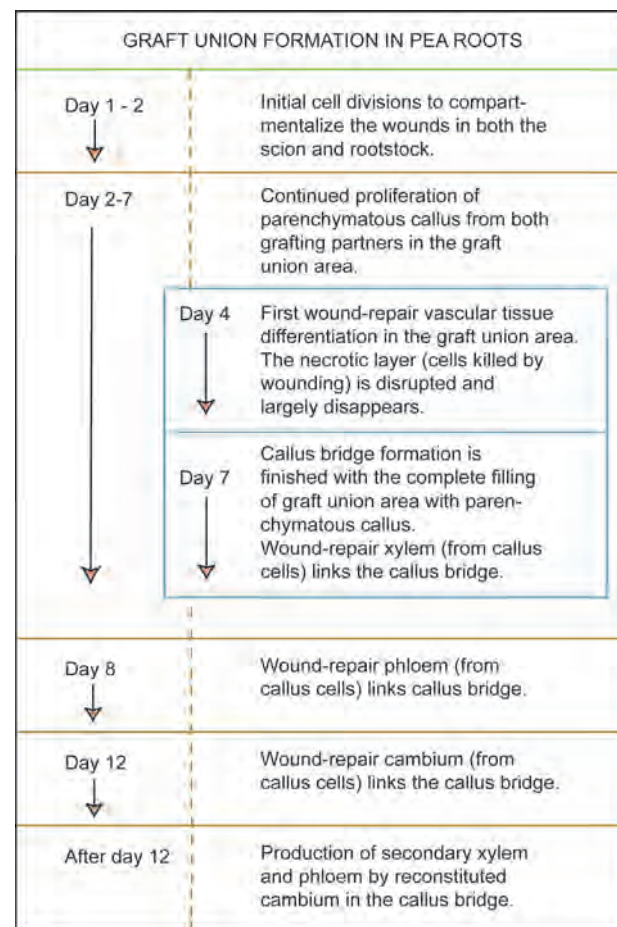


Figure 11-14

Graft union formation in grafted pea roots (91, 159). This sequence of grafting events is common to topgrafting and root grafting in many other woody and herbaceous plant species. What will vary is the time period in grafting events with different species.

1. Lining Up Vascular Cambiums of the Rootstock and Scion

The statement is often made that successful grafting requires that the cambium layers of rootstock and scion must “match.” Although desirable, it is unlikely that complete matching of the two cambium layers occurs since they are only one to several cell layers thick. In fact, it is only necessary that the cambial regions be close enough together so that the parenchyma cells from both rootstock and scion produced in this region can become interlocked. In a **mismatched rootstock and scion**, where one partner has a greater diameter than the other, lining up the periderm on at least one side of the rootstock and scion generally assures that their vascular cambia are close enough to interconnect through the callus bridge (see Figs. 12–5 and 13–6). The cambium is critical for maintaining vascular connections in the callus bridge.

Two badly matched cambial layers may delay the union or, if extremely mismatched, prevent the graft union from taking place, leading to graft failure (152). With vanilla, which is a herbaceous, monocotyledonous plant, the cambium layer is not necessarily required for forming the graft union, since any parenchyma cells capable of dividing will produce callus tissue and lead to the formation of a union between the rootstock and scion (111). However, a continuous cambium layer in the graft union is necessary for successful graft union formation with woody perennial angiosperms and gymnosperms.

It is essential that the two original graft components be held together firmly by some means, such as wrapping, tying, stapling, or nailing, or better yet, by wedging (as in the cleft graft, or machine-notched chip budding)—so that the parts will not move about and dislodge the interlocking parenchyma cells after proliferation has begun.

2. Wounding Response

A **necrotic layer** or **isolation layer** forms from the cell contents and cell walls of the cut scion and rootstock cells. Cells are killed at the cutting of the scion and rootstock at least several cell layers deep. Much of the necrotic layer material later disappears, or it may remain in pockets between subsequently formed callus produced by actively dividing parenchyma cells. Undifferentiated **callus tissue** is produced from uninjured, rapidly dividing parenchyma cells (adjacent and internal to the necrotic layer). The callus tissue initially forms a **wound periderm**.

3. Callus Bridge Formation

Callus formation is a prerequisite for successful graft union formation. New parenchymatous callus proliferates in 1 to 7 days from both the rootstock and scion (Figs. 11–6, 11–14, 11–15, and 11–16) (164, 168). The callus tissue continues to form by further cell divisions of the outer layers of undamaged parenchyma cells [in the *cambial region*, *cortex*, *pith* (159)—or *xylem ray parenchyma* (9)] in the scion and rootstock. The actual cambial tissue plays a lesser role in callus formation of the wound periderm and callus bridge formation than originally supposed (146, 159). New parenchyma cells produced are adjacent and internal to the necrotic layer; soon they intermingle and interlock, filling up the spaces between scion and stock (Fig. 11–17, page 428).

In grafting scions on larger, established rootstocks (e.g., topworking in the field), the rootstock produces most of the callus. However, when the graft partners are of equal size, the scion forms much more callus than does the rootstock (35, 159, 164). This difference is explained by natural polarity, since the root-tip-facing end of the scion (proximal end) forms more callus than the shoot-tip-facing (distal end) (see Fig. 11–26, page 437) (24). In budding, the sizes of the cut surfaces are so different that it is difficult to distinguish which grafting partner contributes the most callus (28).

Adhesion between cells of the scion and rootstock is aided by “cement” or binding material, which projects in a beadlike manner from the surface of the callus cells of both grafting partners. A general fusion of the cell walls then follows (9, 72, 159). The beadlike projections are a mix of pectins, carbohydrates, and proteins (96). The cells do not need to divide to produce the cement, and the cement can bond the graft partners, regardless of the absence or presence of the necrotic layer (159).

It is not clear if a specific cell-to-cell recognition in grafting is required as part of adhesion and the events that follow successful graft union formation.

The formation of superimposed sieve areas and sieve plates (in phloem sieve elements), pits and perforation plates (in xylem elements), and the **plasmodesmata** (in vascular parenchyma) may require cellular

plasmodesmata Minute cytoplasmic threads that extend through openings in cell walls and connect the protoplasts of adjacent living cells at the graft interface.

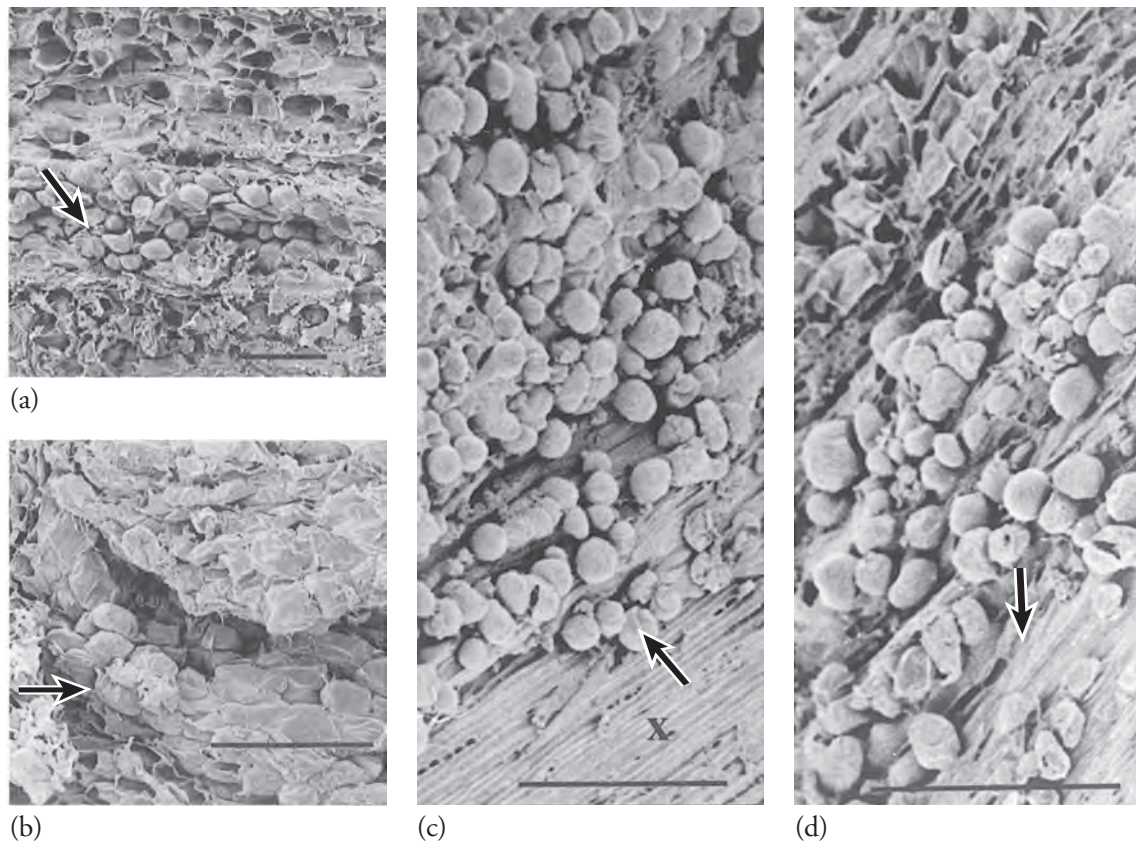


Figure 11-15

Early callus bridge formation in Sitka spruce (*Picea sitchensis*). (a) Scanning electron photos of a cross section of rootstock wound surface at seven days with a cluster of callus cells (arrow) formed in the cortical region. (b) Scion wound surface at seven days with callus cells (arrow) associated with the needle trace (nt) in the outer cortex. (c) Rootstock wound surface of a nine-day-old graft with well-established callus originating from ray cells in the xylem (x) close to the cambium (arrow). (d) Scion wound surface of a nine-day-old graft showing callus formation mainly in the cambium region. Callus is also produced from ray cells in the xylem (arrow), and from phloem parenchyma cells. Courtesy of J. R. Barnett (9).

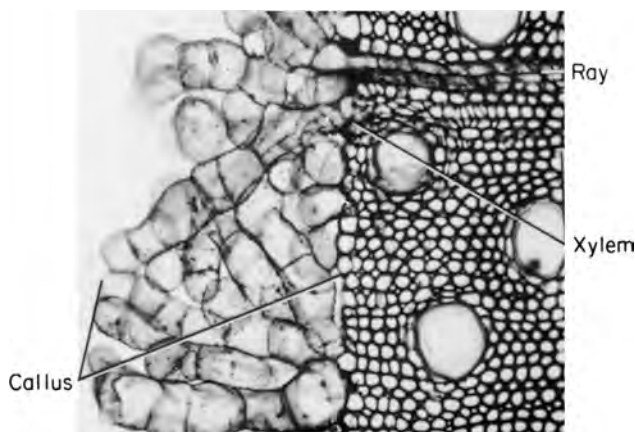


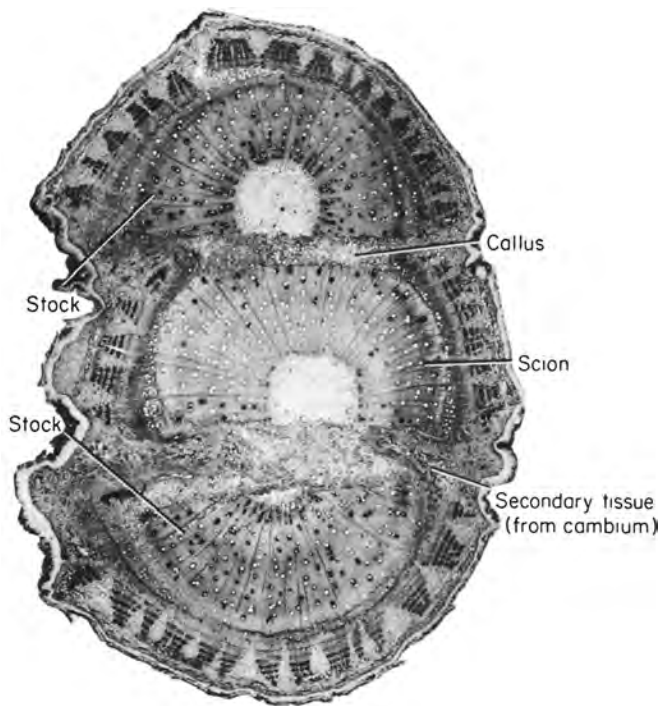
Figure 11-16

Callus production from incompletely differentiated xylem, exposed by excision of a strip of bark. $\times 120$. Photo courtesy K. Esau.

recognition or cellular communication (101). For cell recognition, the pectin fragments during the adhesion process may act as signaling molecules. Cell recognition is discussed later in the section on graft compatibility-incompatibility.

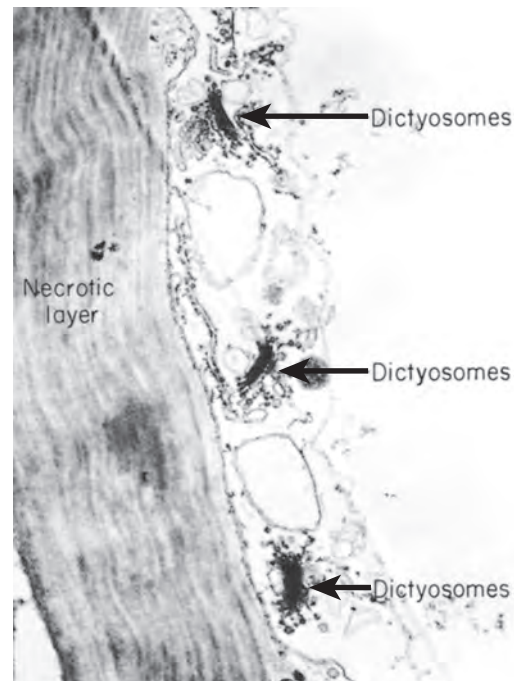
Underneath the necrotic layer, parenchyma cells show an increase in **cytoplasmic activity** with, in some plants at least, a very pronounced accumulation of **dictyosomes** along the graft interfaces (Fig. 11-18) (101,

dictyosomes A series of flattened plates or double lamellae that accumulate along the graft interface—one of the component parts of the Golgi apparatus. They secrete materials into the cell wall space between the graft components via vesicle migration to the plasmalemma.

**Figure 11-17**

Cross section of a Hibiscus wedge graft showing the importance of callus development in the healing of a graft union. Cambial activity in the callus has resulted in the production of secondary tissues that have joined the vascular tissues of the stock and scion $\times 10$. Photo courtesy K. Esau.

105, 106). These dictyosomes appear to secrete materials into the cell wall space between the graft components via vesicle migration to the **plasmalemma**, resulting in a rapid adhesion between parenchymatous cells at the graft interface.

**Figure 11-18**

Accumulation of dictyosomes along the cell walls adjacent to the necrotic layer at six hours after grafting in the compatible autograft in *Sedum telephoides*. $\times 17,500$. Courtesy R. Moore and D. B. Walker (101).

4. Wound-Repair Xylem and Phloem: Differentiation of Vascular Cambium Across the Callus Bridge

In both woody and herbaceous plants, the initial xylem and phloem are generally differentiated prior to the bridging of vascular cambium across the callus bridge (Figs. 11-6 and 11-14) (35, 56, 159).

BOX 11.1 GETTING MORE IN DEPTH ON THE SUBJECT WOUNDING RESPONSE



Some literature refers to a "wound healing response" (25), "wound healing process" (33), or "healing of the graft union." A wounded area of a plant is not healed per se by the replacement of injured tissues; rather, it is compartmentalized or walled-off from the rest of the plant as a defensive mechanism to eliminate invasion of pathogens, and so on (139, 142, 150, 151). This is all part of the *response* or *reaction* to wounding, which occurs in grafting, budding, or the propagation of a cutting. A *necrotic plate* or *isolation layer* at the graft interface is first formed, which helps adhere the grafted tissues together, especially near the vascular bundles (164). Wound repair occurs by meristematic

activity, which results in the initial formation of a wound periderm between the necrotic layer and uninjured tissue—the wound periderm becomes suberized to further reduce pathogen entry (33). In grafting, the close physical contact of scion and stock cells, and pressure exerted on the graft union area from the scion and rootstock tied or wedged together prevents the necrotic layer from forming a barrier to graft union formation. Profuse callusing causes the majority of the necrotic layer to disappear (in most situations) (159, 164). Further meristematic activity occurs in graft union formation, culminating with the formation of a vascular cambium in the callus bridge area.



BOX 11.2 GETTING MORE IN DEPTH ON THE SUBJECT SYMPLASTIC AND APOPLASTIC CONNECTIONS BETWEEN THE SCION AND ROOTSTOCK



In the callus bridge, parenchyma cells of the graft partners are interconnected by plasmodesmata (72, 104); these cytoplasmic strands form continuous, *symplastic cell connections*, linking cell membranes that form a potential pathway of communication among cells in the graft bridge. This pathway may be important in cell recognition and compatibility/incompatibility response, which is discussed later. *Apoplastic connections* occur during adhesion of the graft with cell walls of both graft partners coming together and adhering by means of their extracellular pectin-containing beads.

In a compatible graft, the wound response is followed by dissolution of the necrotic layer, perhaps as a prerequisite to the formation of secondary plasmodesmata between cells of the graft partners (164).

The secondary plasmodesmata are formed *de novo* across the fused callus walls, particularly near cut vascular

strands (80). In the *de novo* formation of plasmodesmata, development of continuous cell connections starts with the thinning and loosening of local wall regions, opening the chance of fusion of *plasmalemma* (cell or protoplast membrane) and **endoplasmic reticulum** between the adjoining cells (80). Golgi vesicles bud off from individual dictyosomes and secrete cell wall material as part of this process (Fig. 11–19). Sieve elements in the connecting phloem of the grafting partners are also interconnected, further demonstrating *symplastic connections* between the graft partners (100).

Endoplasmic reticulum (ER) A membrane system that divides the cytoplasm into compartments and channels. Rough ER is densely coated with ribosomes, whereas smooth ER has fewer ribosomes.

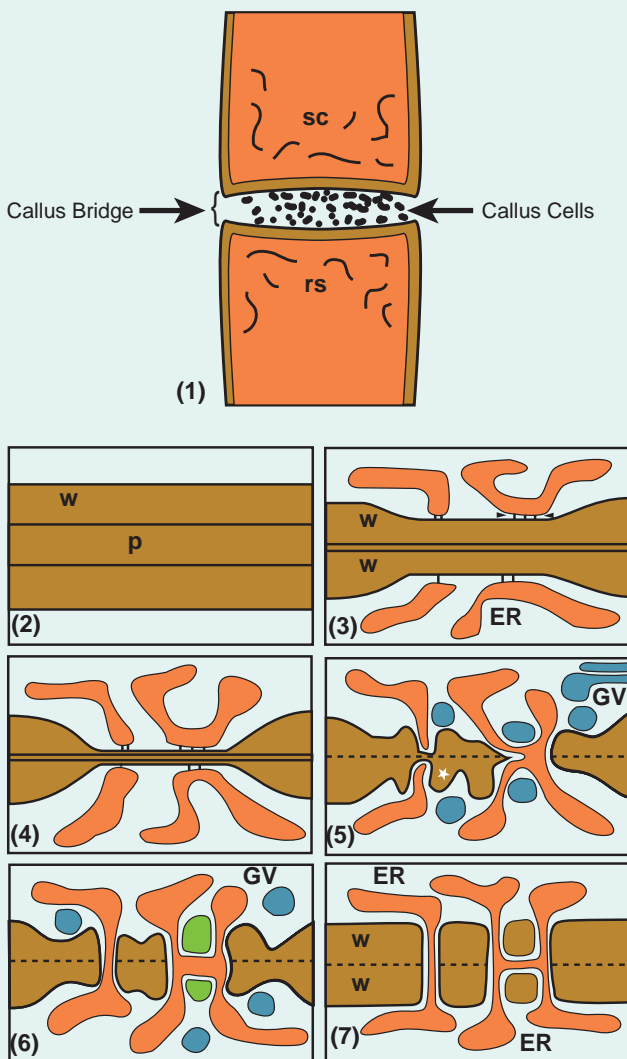


Figure 11–19

Schematic diagram of secondary (*de novo*) formation of plasmodesmata at the graft interface (callus bridge). (1) Approaching callus cells of scion (sc) and rootstock (rs). Pectic material (p) between adjoining callus cell walls. Region between arrows: wall parts where secondary plasmodesmata will be formed, as shown in detail. Formation of continuous cell connections (2 to 7) by plasmalemma and endoplasmic reticulum (ER) fusion of adjoining cells (5, 6) within wall parts that have been thinned synchronously with both cell partners. Elongation of the branched and single strands during rebuilding the modified wall parts (6, 7). W = cell wall, GV = golgi vesicles, *new deposited wall material. Redrawn from Kollman and Glockmann (80).

The **wound-repair xylem** (wound-type vascular elements) is generally the first *differentiated* tissue to bridge the graft union, followed by **wound-repair**

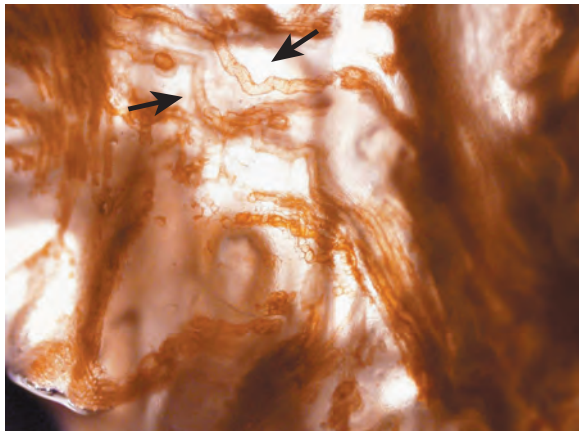
phloem (Fig. 11–20). Initial xylem tracheary elements and, frequently, initial phloem sieve tubes form directly by differentiation of callus into these vascular elements. A vascular cambium layer subsequently forms between the vascular systems of the scion and rootstock.

Exceptions to this developmental sequence are in bud graftage in citrus, apple, and rose where a

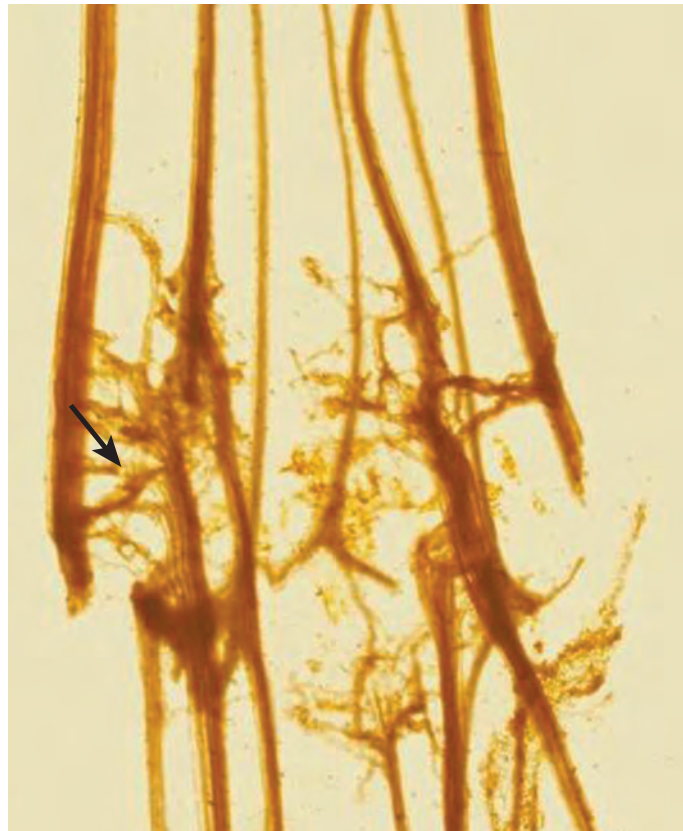
wound-repair xylem

(Wound-type vascular elements) generally the first *differentiated* tissue to bridge the graft union, followed by **wound-repair phloem**.

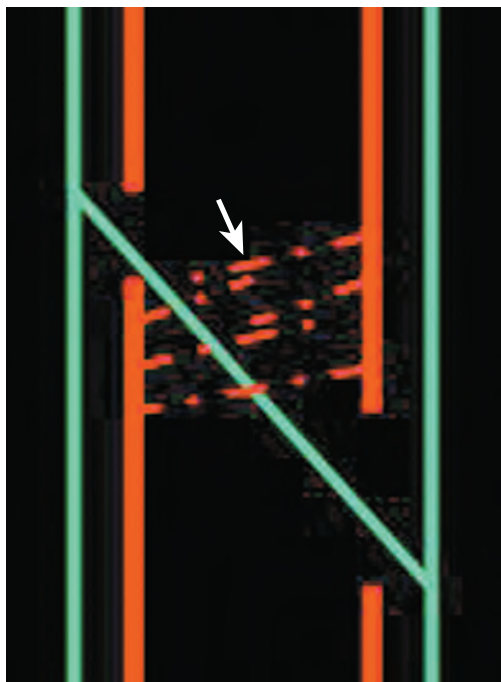
wound cambium differentiates prior to the bridging of vascular tissue, and in autografts of *Sedum* (*Crassulaceae*) where procambial differentiation occurs before vascular differentiation (101). With budding, the scion is considerably smaller and normally limited to one bud and a short shoot piece; hence, any early vascular differentiation from callus cells is probably limited by lower phytohormone levels. The vascular cambium can form independent of any xylem or phloem (28), or the cambium may differentiate between the wound-bridging xylem and phloem (159). It is important that the vascular cambium unite so that the continuity of wound-bridging xylem and phloem can be maintained, and so that secondary vascular development occurs for successful graft union formation.



(a)



(b)



(c)

Figure 11–20

Vascular connections between melon and Cucurbita rootstock. (a) Early vascular strands in callus bridge area which are from wound-repair xylem and wound-repair phloem. (b) Vascular connections after 14 days. (c) Schematic of vascular connections (dotted red lines between scion and rootstock). Courtesy M. Edelstein.



BOX 11.3 GETTING MORE IN DEPTH ON THE SUBJECT

CORRELATIVE EFFECTS OF SCION BUDS AND LEAVES ON XYLEM AND PHLOEM FORMATION



The first vascular tissues produced in the callus bridge are wound-repair xylem and phloem. The new wound-repair xylem tissue originates from the activities of the scion tissues, rather than from that of the rootstock (147, 187). The amount of initial graft-bridging xylem is strongly influenced by the presence of leaves and branches on the scion, and not by the presence of the rootstock (159). The scion buds are effective in inducing differentiation of vascular elements in the tissues onto which they are grafted. Such bud influence has been shown by inserting a scion bud into a root piece of *Cichorium* rootstock. Under the influence of auxin produced by the bud, the old parenchyma cells differentiate into groups of conducting xylem elements (59).

Induction of vascular tissues in callus is under the control of phytohormones (principally auxins) and other metabolites originating from growing points of shoots (166). Auxins (IAA or NAA) will cause the induction of wound-repair xylem, while auxins and carbohydrates can induce wound-repair phloem in callus tissue (3, 115). Auxin can also induce cambial formation when applied to wounded vascular bundles of cactus rootstock (152). For successful graft union formation of *in vitro* grafted internodes, auxin is an absolute requirement, cytokinin stimulates graft development, but gibberellic acid is inhibitory (118). Auxins enhance grafting success in root-grafting pecan trees (186). In cactus grafts, auxin can also promote vascular connections (Fig. 11–21) (152).

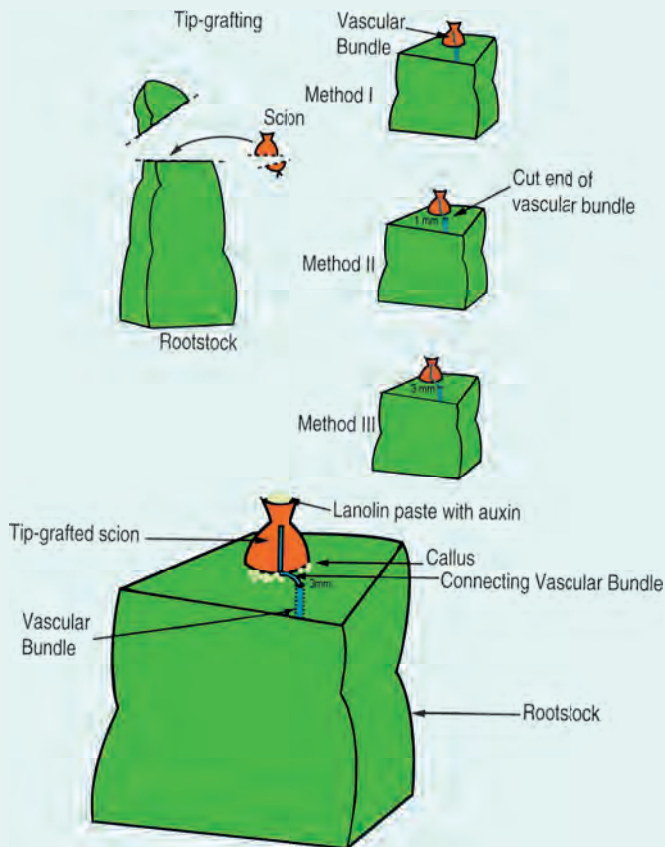


Figure 11–21

Schematic of tip grafting of cactus. Top: In Method I, the vascular bundles of the scion and rootstock were placed together, or 1 mm (Method II) or 3 mm (Method III) apart. Bottom: Auxin in lanolin paste promoted vascular connections between misaligned graft partners and increased the diameter of the connecting vascular bundle. Redrawn from Shimomura and Fuzihara (152).

At the edges of the newly formed callus mass, parenchyma cells touching the cambial cells of the rootstock and scion differentiate into new cambium cells within 2 to 3 weeks after grafting. This cambial formation in the callus mass proceeds farther and farther inward from the original rootstock and scion cambium, and on through the **callus**

bridge, until a continuous cambial connection forms between rootstock and scion.

5. Production of Secondary Xylem and Phloem from the New Vascular Cambium in the Callus Bridge

The newly formed cambial layer in the callus bridge begins typical cambial activity, laying down

new secondary xylem toward the inside and phloem toward the outside.

In the formation of new vascular tissues following cambial continuity, the type of cells formed by the cambium is influenced by the cells of the graft partners adjacent to the cambium. For example, xylem ray cells are formed where the cambium is in contact with xylem rays of the rootstock, and xylem elements where they are in contact with xylem elements (122).

Production of new xylem and phloem thus permits the vascular connection between the scion and the rootstock. It is essential that this stage be completed before much new leaf development arises from buds on the scion. Otherwise, the enlarging leaf surfaces on the scion shoots will have little or no water to offset that which is lost by transpiration, and the scion quickly will become desiccated and die. It is possible, however, even though vascular connections fail to occur, that enough translocation can take place through the parenchyma cells of the callus to permit survival of the scion. In grafts of vanilla orchid, a monocot, scions survived and grew for 2 years with only union of parenchyma cells; however, the grafted plants did not survive when subjected to transpirational stress (111).

GRAFT UNION FORMATION IN T- AND CHIP BUDDING

bark (In grafting) composed of tissues from the periderm, cortex, phloem, and vascular cambium.

wood (In grafting) composed of secondary xylem with some pith (in younger woody plants).

In T-budding, the bud piece usually consists of the **“bark”** (periderm, cortex, phloem, cambium), and often some **“wood”** (xylem tissue). Attached externally to this is a lateral bud subtended, perhaps, by a leaf petiole. In budding, this piece of tissue is laid against the exposed xylem and cam-

bium of the rootstock, as shown diagrammatically in Figure 11–22.

Detailed studies of the grafting process in T-budding have been made for the rose (28), citrus (93, 94), and apple (108).

In the apple, when the flaps of bark on either side of the “T” incision on the rootstock are raised, separation occurs from the young xylem. The entire

cambial zone remains attached to the inside of the bark flaps. Very shortly after the bud shield is inserted, a necrotic plate or layer of material develops from the cut cells. Next, after about two days, callus parenchyma cells start developing from the rootstock xylem rays and break through the necrotic plate. Some callus parenchyma from the bud scion ruptures through the necrotic area in a similar manner. As additional callus is produced, it surrounds the bud shield and holds it in place. The callus originates almost entirely from the rootstock tissue, mainly from the exposed surface of the xylem cylinder. Very little callus is produced from the sides of the bud shield (scion).

Cell proliferation continues rapidly for 2 to 3 weeks until all internal air pockets are filled with callus. Following this, a continuous cambium is established between the bud and the rootstock. The callus then begins to lignify, and isolated xylem tracheary elements appear. Lignification of the callus is completed between 5 to 12 weeks after budding (108, 172). The developmental stages and time intervals for graft union formation in T-budded citrus are listed in Box 11.4.

More Rapid Union Development in Chip Budding

Anatomical studies (155) have been made comparing graft union formation in T- and chip budding. Early union formation between ‘Lord Lambourne’ apple scion and ‘Malling 26’ dwarfing rootstock showed a more rapid and complete union of xylem and cambial tissues of the scion and rootstock after chip budding compared to T-budding. This is probably due to a much closer matching of the scion tissue to the rootstock stem (Fig. 11–22). Also in T-budding, the cambium of the rootstock is lifted in the flap of “bark,” so considerable callus in-filling and development of new cambium must occur. There is more flexibility in chip budding, which can be done over longer periods on either an active or dormant rootstock, than T-budding, which requires an active rootstock. In part this advantage to chip budding is due to less callus filling being needed, and because there is no requirement for an active cambium to lift the flap of rootstock bark, as there is with T-budding.

The previously mentioned advantages of chip budding compared with T-budding have also been demonstrated with ‘Crimson King’ maple on *Acer platanoides* rootstock, ‘Conference’ pear on ‘Quince A’ rootstock, and ‘Rubra’ linden on *Tilia platyphyllos* rootstock.

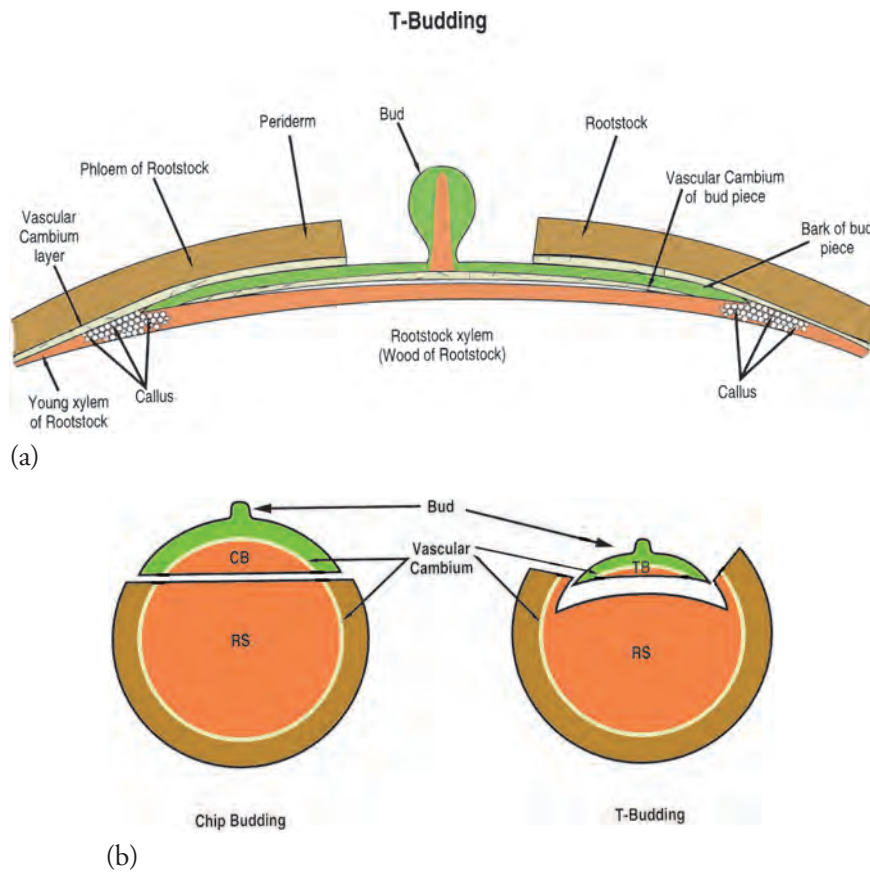


Figure 11-22
 (a) Tissues involved in healing of an inserted T-bud as prepared with the “wood” (xylem) attached to the scion bud piece. Graft union formation occurs when callus cells developing from the young xylem of the rootstock intermingle with callus cells forming from exposed cambium and young xylem of the T-bud piece. As the bark is lifted on the rootstock for insertion of the bud piece it detaches by separation of the youngest xylem and cambial cells.
 (b) A cross section of a chip bud (CB), T-bud (TB), and rootstock (RS). Because the chip bud substitutes exactly for the part of the rootstock that is removed, the cambium of the roots and scion are placed close together, resulting in a rapid and strong union. When a T-bud (right) is slipped under the “bark,” the cambium of the rootstock and scion are not adjacent, and the initial union formation can be weak and slow. Redrawn from B. H. Howard (68).

BOX 11.4 GETTING MORE IN DEPTH ON THE SUBJECT
 STAGES AND TIME INTERVALS IN GRAFT UNION FORMATION OF T-BUDDED CITRUS (94)



Stage of development	Approximate time after budding
• First cell division	24 hours
• First callus bridge	5 days
• Differentiation of cambium	
a. In the callus of the bark flaps (rootstock)	10 days
b. In the callus of the shield bud (scion)	15 days
• First occurrence of xylem tracheids	
a. In the callus of the bark flaps	15 days
b. In the callus of the shield	20 days
• Lignification of the callus completed	
a. In the bark flaps	25 to 30 days
b. Under the shield	30 to 45 days

FACTORS INFLUENCING GRAFT UNION SUCCESS

As anyone experienced in grafting or budding knows, the results are often inconsistent. An excellent percentage of “takes” occur in some operations, but in others the results are disappointing. A number of factors can

influence the healing of graft unions. Factors that influence graft union success include:

- Incompatibility
- Plant species and type of graft
- Environmental conditions during and following grafting



- Growth activity of the rootstock
- Polarity
- The craftsmanship of grafting
- Virus contamination, insects, and diseases
- Plant growth regulators and graft union formation
- Post-graftage—bud-forcing methods

Incompatibility

One of the symptoms of incompatibility in grafts between distantly related plants is a complete lack, or a very low percentage, of successful unions. Incompatibility is discussed in greater detail starting on page 441. Grafts between some plants known to be incompatible, initially will make a satisfactory union, even though the combination eventually fails.

Plant Species and Type of Graft

Some plants—including hickories, oaks, and beeches—are much more difficult to graft than others even when no incompatibility is involved. Nevertheless, such plants, once successfully grafted, grow very well with a perfect graft union. In grafting apples, grapes, and pears (Figs. 11-23 and 11-24), even the simplest techniques usually give a good percentage of successful unions, but

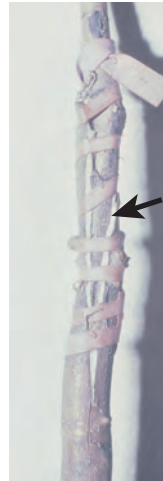


Figure 11-23

Some species form profuse callusing (arrow), which helps increase graft union success. Pear is easily grafted by a whip-and-tongue graft.

grafting certain stone fruits, such as peaches and apricots, requires more care and attention to detail. Strangely enough, grafting peaches to some other compatible species, such as plums or almonds, is more successful than reworking them back to peaches. One method of grafting may give better results than another, or budding may be more successful than grafting, or vice versa. For example, gymnosperms are grafted, whereas many angiosperm cultivars tend to be budded,



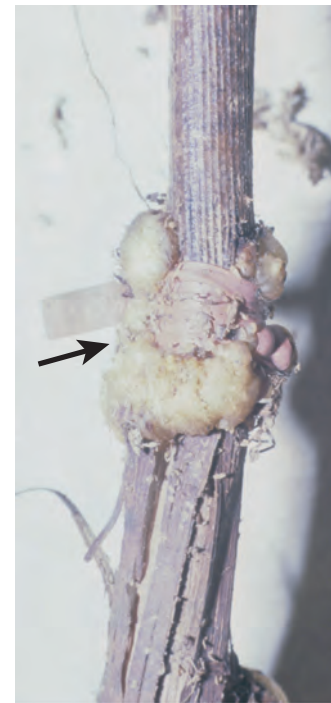
(a)



(b)



(c)



(d)

Figure 11-24

A high take occurs when grapes are saddle grafted, but the same graft is unsuccessful with roses, which did not form sufficient callus. (a) Heitz saddle graft bench graft tool. (b) Unsuccessful saddle graft with rose. (c and d) Successful saddle-grafted grape with profuse callusing in the callus bridge area.



rather than grafted (19). In topworking native black walnut (*Juglans regia*) to the Persian walnut (*Juglans hindsii*) in California, the bark graft method is more successful than the cleft graft. In nursery propagation of pecans, patch budding in Texas is preferred to the whip graft, which does better in climates with higher humidity, such as Mississippi.

Some species, such as mango (*Mangifera indica*) and camellia (*Camellia reticulata*) are so difficult to propagate by the usual grafting and budding methods that they are **approach grafted** (see Fig. 12–27, page 437). Both graft partners are maintained for a time after grafting onto their own roots as containerized plants. This variation among plant species and cultivars in their grafting ability is probably related to their ability to produce callus parenchyma, and differentiate a vascular system across the callus bridge.

The genetic limits of grafting are discussed on page 439.

Environmental Conditions During and Following Grafting

Certain environmental requirements must be met for callus tissue to develop.

Temperature Compared to field grafting and budding, temperature levels for greenhouse containerized rootstock and **bench grafting** can be readily controlled, thereby permitting greater reliability of results and more flexibility of scheduling grafting and budding over a longer period of time. Temperature has a pronounced effect on

bench grafting

A grafting procedure that is done on a bench in a protected environment with bare-root or containerized rootstock.

the production of callus tissue (Fig. 11–25). In apple grafts, little, if any, callus is formed below 0°C (32°F) or above about 40°C (104°F). At 32°C (90°F) and higher, callus production is retarded and cell injury increases with higher temperatures. Cell death occurs around 40°C (104°F). In bench grafting, callusing may be allowed to proceed slowly for several months by storing the grafts at relatively low temperatures, 7 to 10°C (45 to 50°F), or, if rapid callusing is desired, they may be kept at higher temperatures for a shorter time. Maintaining too high a temperature in order to induce rapid callus development of bench-grafted plants can deplete needed carbohydrate reserves, which limits field survival (see Fig. 10–3) (38).

Following bench grafting of grapes, a temperature of 24 to 27°C (75 to 80°F) is about optimal; 29°C

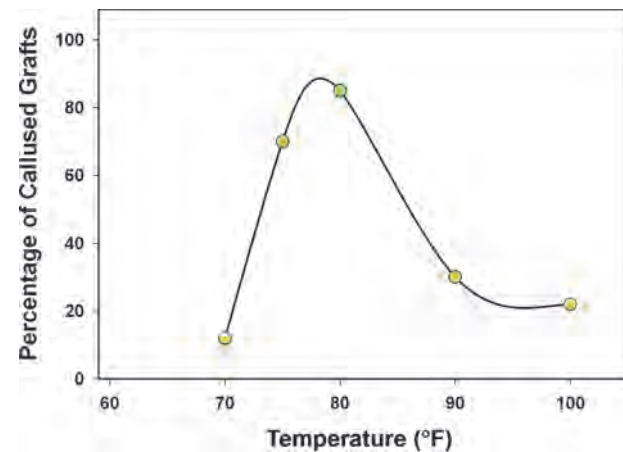


Figure 11–25

Influence of temperature on the callusing of walnut (*Juglans*) grafts. Callus formation is essential for the healing of the graft union. Maintaining an optimum temperature following grafting is very important for successful healing of walnut grafts. Adapted from data of Sitton (154).

(85°F) or higher results in profuse formation of a soft type of callus tissue that is easily injured during transplanting operations. At 20°C, callus formation is slow, and below 15°C (60°F) it almost ceases. Mango (*Mangifera indica*) is a tropical evergreen species that can be grafted year-round, provided the temperature is suitable for callusing. Optimum grafting temperature for mango is comparable to temperate-zone grape cultivars (24 to 28°C) (4). However, callusing of mango is somewhat more tolerant to high temperature than grapes [i.e., at 38°C (100°F) unions formed within 20 days, even though further high temperature exposure caused tissue injury and death of callus cells]. Conversely, mangoes are less tolerant of low temperatures—grafts failed to develop at 20°C or lower (4).

Outdoor grafting operations should thus take place at a time of year when favorable temperatures are expected and the vascular cambium is in an active state. These conditions generally occur during the spring months. Delay of outdoor grafting operations performed late in the spring (e.g., in the southern United States where excessively high temperatures may occur) often results in failure. For top-grafting walnut in California during high temperature conditions, whitewashing the area of the completed graft union promoted healing of the union. The whitewash reflected the radiant energy of the sun, which lowered the bark temperature to a more optimal level.

Moisture and Plant Water Relations The cambium of the graft partners and parenchyma cells comprising the important callus tissue are thin-walled and tender,

with no provision for resisting desiccation. If exposed to drying air they will be killed. This was found to be the case in studies of the effect of humidity on the healing of apple grafts. Air moisture levels below the saturation point inhibited callus formation; desiccation of cells increased as the humidity dropped. *In vitro* studies (43) of stem pieces of ash (*Fraxinus excelsior*) have shown that callus production on the cut surfaces was markedly reduced as the water potential decreased.

Water is one of the driving forces for cell enlargement and is necessary for callus bridge formation between the stock and scion. Water must be utilized initially from scion tissue, and if below a certain water potential, insufficient water is available for callus formation. Failed grafts of well-hydrated Sitka spruce rootstocks produced no callus at the graft union, suggesting that callus formation at the cut surface is controlled or dependent on the formation of callus from the scion (10). Until vascular connections are formed between the rootstock and scion, the callus bridge provides the initial pathway for water, bypassing damaged xylem vessels and tracheids of the scion and rootstock. Within the first 3 to 4 days of callus bridge formation, there is a recovery of scion water potential (10); with maturation of the connecting tracheids, water potential and osmotic potential continue to increase (15, 16). Photosynthesis declines and does not increase until xylem connections become reestablished (18).

Unless the adjoining cut tissues of a completed graft union are kept at a very high humidity level, the chances of successful healing are poor. With most plants, thorough waxing of the graft union or sealing of the graft union with polyethylene grafting tape, Parafilm, or Buddy Tape (Aglis & Co. Ltd.) helps retain the natural moisture of the tissues, which is all that is necessary. Often root grafts are not waxed but stored in a moist (not overly wet) packing material during the callusing period. Slightly damp peat moss or wood shavings are good media for callusing, providing adequate moisture and aeration.

Growth Activity of the Rootstock

Some propagation methods, such as T-budding and bark grafting, depend on the bark “slipping,” which means that the vascular cambium is actively dividing, producing young thin-walled cells on each side of the cambium. These newly formed cells separate easily from one another, so the bark “slips” (Fig. 11–22). Chip budding can be done on a dormant or active rootstock. Hence, there is much more flexibility in scheduling chip budding, because there is no requirement for an active cambium to lift the flap of rootstock bark, as with T-budding.

Initiation of cambial activity in the spring results from the onset of bud activity, because shortly after the buds start growth, cambial activity can be detected beneath each developing bud, with a wave of cambial activity progressing down the stems and trunk. This stimulus is due, in part, to production of auxin originating in the expanding buds (175). Callus proliferation—essential for a successful graft union—occurs most readily at the time of year just before and during “bud-break” in the spring, because auxin gradients diminish through the summer and into fall. Increasing callus proliferation takes place again in late winter, but this is not dependent upon the breaking of bud dormancy.

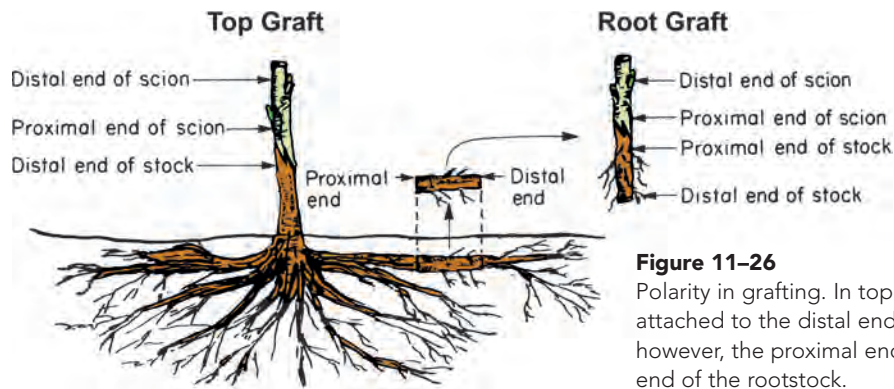
When T-budding seedlings in the nursery in late summer, it is important that they have an ample supply of soil moisture just before and during the budding operation. If they should lack water during this period, active growth is checked, cell division in the cambium stops, and it becomes difficult to lift the bark flaps to insert the bud. At certain periods of high growth activity in the spring, plants exhibiting strong root pressure (such as the walnut, maple, and grape) show excessive sap flow or “bleeding” when cuts are made preparatory to budding and grafting. Grafts made with such moisture exudation around the union will not heal properly. Such “bleeding” at the graft union can be overcome by making slanting knife cuts below the graft around the tree. Cuts should be made through the bark and into the xylem to permit such exudation to take place below the graft union. Containerized rootstock plants of *Fagus*, *Betula*, or *Acer* are relocated to a cool place with reduced watering until the “bleeding” stops. Then plants are grafted after the excessive root pressure subsides.

On the other hand, dormant containerized rootstocks of junipers or rhododendrons, when first brought into a warm greenhouse in winter for grafting, should be held for several weeks at 15 to 18°C (60 to 65°F) until new roots begin to form. Then the rootstocks are physiologically active enough to be successfully grafted.

When the rootstock is physiologically overactive (excessive root pressure and “bleeding”), or underactive (no root growth), some form of side graft can be used, in which the rootstock top is initially retained. On the other hand, **top-grafting**, in which

bleeding A process in which a plant has strong root pressure that causes excess sap flow that can reduce grafting success.

top-grafting A form of grafting in which the shoot of the rootstock is completely removed at the time the graft is made (e.g., in-lay bark graft of pecan).

**Figure 11-26**

Polarity in grafting. In topgrafting, the proximal end of the scion is attached to the distal end of the rootstock. In root grafting, however, the proximal end of the scion is joined to the proximal end of the rootstock.

the top of the rootstock is completely removed at the time the graft is made, is likely to be successful in plants in which the rootstock is neither overactive nor underactive (44).

Polarity in Grafting

Distal and Proximal Ends Correct polarity is strictly observed in commercial grafting operations. As a general rule, (and as shown in Fig. 11-26), in *top-grafting*, the *proximal end* of the scion should be inserted into the *distal end* of the rootstock. But in normal *root grafting*, the *proximal end* of the scion should be inserted into the *proximal end* of the rootstock.

Should a scion be inserted with reversed polarity “upside-down,” it is possible for the two graft unions to be successful and the scion to stay alive for a time (Fig. 11-27). But in bridge grafting, the reversed scion does not increase from its original size, whereas the scion with correct polarity enlarges normally (Fig. 11-28).

Nurse-Root Grafting *Nurse-root grafting* is a **temporary graft system** to allow a difficult-to-root plant to form its own adventitious roots. The rootstock may be turned upside-down, its polarity reversed, and then grafted to the desired scion. A temporary union will form, and the rootstock will supply water and mineral nutrients to the scion, but the scion is unable to supply necessary organic materials to the rootstock, which eventually dies.

In nurse-root grafting, the graft union is purposely set well below the ground level, and the scion itself produces adventitious roots, which ultimately become the entire root system of the plant. See Figure 12-26, page 487 for greater detail of nurse-root grafting systems.

In T-budding or patch budding, the rule for observance of correct polarity is not as exacting. The buds (scion) can be inserted with reversed polarity and

**Figure 11-27**

Inverse graft of grape with graft union forming between the distal end of the scion to the distal end of the rootstock. Notice that the shoot reorients itself via gravitational response.

BOX 11.5 GETTING MORE IN DEPTH ON THE SUBJECT PROXIMAL AND DISTAL ENDS



The **proximal end** of either the shoot or the root is that which is nearest the stem-root junction (crown) of the plant. The **distal end** of either the shoot or the root is that which is farthest from the stem-root junction of the plant and nearest the tip of the shoot or root.

Proximal end The end closest to the crown of the plant, whereas the **distal end** is farthest away from the crown.

Crown The junction of the root and shoot system of a plant.



Figure 11-28

Bridge graft on a pear tree five months after grafting. Center scion was inserted with reversed polarity. Although the scion is alive it has not increased from its original size. The two scions on either side were inserted with normal polarity and have grown rapidly.

still make permanently successful unions. As shown in Figure 11-29, inverted T-buds start growing downward, then the shoots curve and grow upward. In the inverted bud piece, the cambium is capable of continued functioning and growth. There is a twisting configuration in the xylem, phloem, and fibers formed from cambial activity that apparently allows for normal



Figure 11-29

Two-year-old 'Stayman Winesap' apple budded on 'McIntosh' seedling by inverted T-bud (reversing the scion bud polarity). Note the development of stronger, wide-angle crotches. Courtesy Arnold Arboretum, Jamaica Plain, MA.

translocation and water conduction. However, it is still desirable to maintain polarity when budding.

The Craftsmanship of Grafting

The art and craftsmanship in grafting and budding is critical for successful grafting. This is particularly true with difficult-to-graft species, such as conifers (e.g., *Picea pungens*), which callus poorly, making alignment of the cambial layers of the rootstock and scion critical. Conversely, the grafting technique is less critical in grape or pear grafts, which callus profusely and have high grafting success (Figs. 11-23 and 11-24).

Sometimes the techniques used in grafting are so poor that only a small portion of the cambial regions of the rootstock and scion are properly aligned. Graft union formation may be initiated and growth from the scion may start; however, after a sizable leaf area develops, and if high temperatures and high transpiration occurs, water movement through the limited conducting area is insufficient, and the scion subsequently dies. Other errors in technique resulting in graft failure include insufficient or delayed waxing, uneven cuts, use of desiccated scions, and girdling that occurs when polyethylene wrapping tape is not removed expeditiously after graft "take" occurs.

Virus Contamination, Insects, and Diseases

Some delayed incompatibilities are caused by viruses and phytoplasma (mycoplasma-like organisms). The cherry leaf roll virus causes blackline in walnut when it is initially spread by virus-infected pollen of the symptomless English walnut (*Juglans regia*). The virus then travels down the scions of *J. regia* into the susceptible rootstocks—California black walnut (*J. hindsii*) or Paradox walnut (*J. hindsii* × *J. regia*). The black walnut rootstock (used for resistance to *Phytophthora* root-rot in the soil) has a hypersensitive reaction and puts down a chemical barrier to wall-off the virus, which causes the graft to fail, and a characteristic black line forms at the graft union. Apple union necrosis and decline (AUND) (37) and brownline of prune (99) is caused by the tomato ring-spot virus that is transmitted by soil-borne nematodes to the rootstock and then to the graft union. Graft unions appear to be normal until the virus has moved, either from the rootstock or the fruiting branches to the graft union. Because of tissue sensitivity and death of the scion cells (in prunes and apples) or rootstock cells (in walnut), the graft union deteriorates and graft failure occurs. Virus and phytoplasma-induced delayed incompatibility is probably more common than expected (142).

Using virus-infected propagating materials in nurseries can reduce bud "take," as well as the vigor of

the resulting plant (121). In stone fruit propagation, bud-wood, free of ring-spot virus, has consistently greater “takes” than infected bud-wood.

Top-grafting olives in California is seriously hindered in some years by attacks of the American plum borer (*Euzophera semifuneralis*), which feeds on the soft callus tissue around the graft union, resulting in the death of the scion. In England, nurseries are often plagued with the red bud borer (*Thomasiniana oculiperda*), which feeds on the callus beneath the bud-shield in newly inserted T-buds, causing them to die.

Plant Growth Regulators and Graft Union Formation

Plant growth regulators, particularly auxin, applied to tree wounds or to graft unions give variable results in wounding response and graft union formation (93, 118, 152). Auxin (IBA, NAA) and cytokinin (BA) enhance graft success when applied to the base of side-grafted *Picea* scions, while the plant growth retardant, dikegulac, stimulated scion growth by retarding rootstock development (17). Cytokinins enhance patch budding of Persian walnut. The eloquent work of Shimomura (152) in tip grafting of cactus demonstrated how auxins enhanced vascular connections of deliberately misaligned scions (Fig. 11–21). TIBA, a well-known inhibitor of basipetal transport of auxin, inhibited vascular connections in the graft union; however, by subsequent reapplication of auxin, the inhibitory effect of TIBA was eliminated and vascular connections occurred.

However, unlike auxin usage in cutting propagation, no plant growth regulators are routinely used in commercial grafting and budding systems. In general, plant growth regulators do not uniformly enhance grafting, nor do they overcome graft incompatibility.

Post-Graftage—Bud-Forcing Methods

After graft union formation has occurred in grafting or budding, it is often necessary to force out the scion or the scion bud. In field budding of roses, 2 to 3 axillary buds of the rootstock remain distal to the scion bud. The axillary buds of the rootstock, which develop into photosynthesizing branches,

crippling The bending (restriction) or cutting halfway through the rootstock stem above the bud union to help force out the bud and maintain growth of the grafted plant.

are initially important for the growth of the composite plant. But they can inhibit growth of the scion through apical dominance, which is an auxin response. By “**crippling**” (cutting

halfway through the rootstock shoot above the bud union and breaking the shoot over the rootstock stem), girdling, or totally removing the rootstock above the scion bud union, apical dominance is broken and the scion bud rapidly elongates (Fig. 11–30) (50).

With budded citrus, plants on which rootstock shoots remained attached (lopping, or bending the rootstock shoot to its base and tying it in position) had the greatest gains in scion growth. This was due to the greater transfer of photosynthate from the rootstock leaves to scion shoots during growth flushes, and to roots during periods between growth flushes (181, 182).

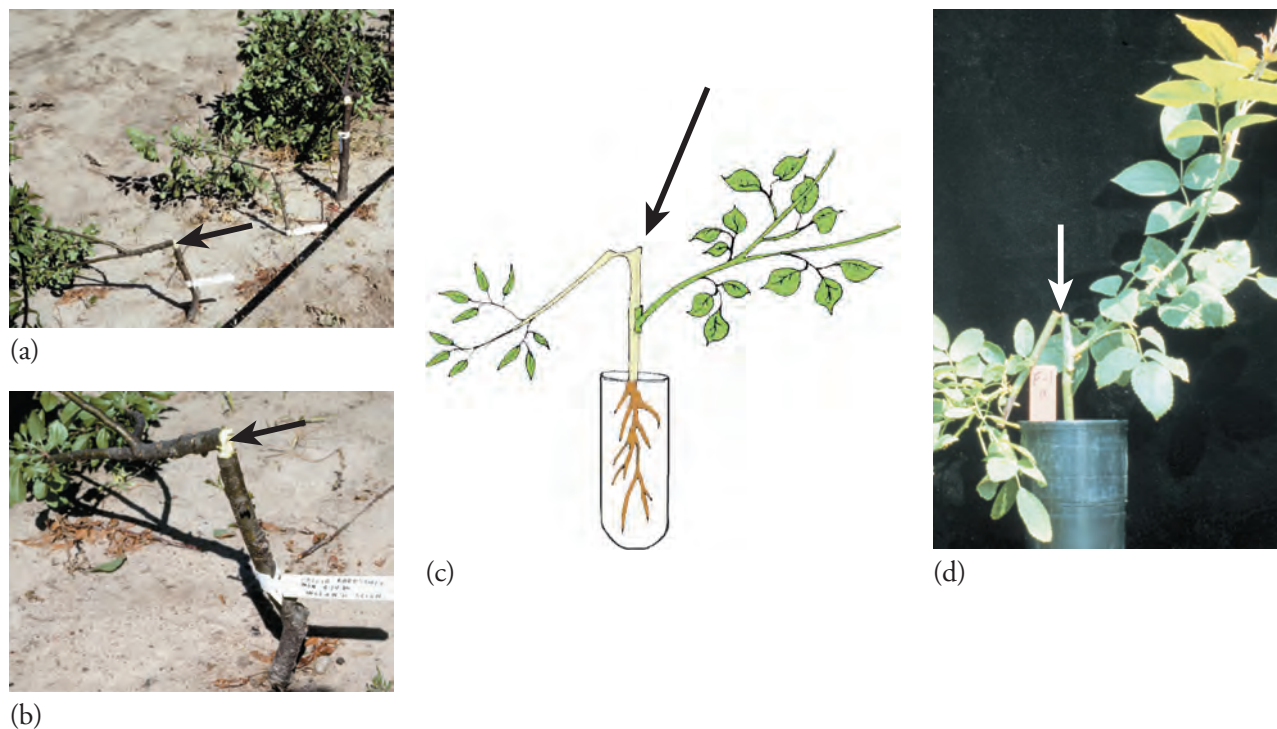
GENETIC LIMITS OF GRAFTING

Since one of the requirements for a successful graft union is the close matching of the callus-producing tissues near the cambium layers, grafting is generally confined to the dicotyledons in the angiosperms, and to gymnosperms. Both have a vascular cambium layer existing as a continuous tissue between the xylem and the phloem. Grafting is more difficult, with a low percentage of “takes” in monocotyledonous plants. Monocots have vascular bundles scattered throughout the stem, rather than the continuous vascular cambium of dicots. However, there are cases of successful graft unions between monocots. By making use of the meristematic properties found in the intercalary tissues (located at the base of internodes), successful grafts have been obtained with various grass species as well as the large tropical monocotyledonous vanilla orchid (111).

Before a grafting operation is started, it should be determined that the plants to be combined are capable of uniting and producing a permanently successful union. There is no definite rule that can exactly predict the ultimate outcome of a particular graft combination except that the more closely the plants are related botanically, the better the chances are for the graft union to be successful (71). However, there are numerous exceptions to this rule.

Grafting Within a Clone

A scion can be grafted back onto the plant from which it came, and a scion from a plant of a given clone can be grafted onto any other plant of the same clone. For example, a scion taken from an ‘Elberta’ peach tree could be grafted successfully to any other ‘Elberta’ peach tree in the world.

**Figure 11-30**

Forcing or “cripling” of (a and b) T-budded apples; (c and d) Chip budded roses. The rootstock is partially severed on the same side (arrows) that the rootstock was budded. This breaks the apical dominance of the rootstock shoot system on the scion, and helps force out the scion bud. By not totally severing the rootstock top, growth of the composite plant is maximized, since the shock of total severance to the composite plant is avoided, and photosynthate is still produced by the rootstock (182). The rootstock shoot system will be totally severed later, and the scion will fully develop into the shoot system of the composite plant.

Grafting Between Clones Within a Species

In tree fruit and nut crops, different clones within a species can almost always be grafted without difficulty and produce satisfactory trees. However, in some conifer species, notably Douglas-fir (*Pseudotsuga menziesii*), incompatibility problems have arisen in grafting together individuals of the same species, such as selected *P. menziesii* clones onto *P. menziesii* seedling rootstock (36). Incompatibility is also a problem in grafting clones of deciduous species, such as red maple (*Acer rubra*), Chinese chestnut (*Castanea mollissima*), and red oak (*Quercus rubra*).

Grafting Between Species Within a Genus

For plants in different species but in the same genus, grafting is successful in some cases but unsuccessful in others. Grafting between most species in the genus *Citrus*, for example, is successful and widely used commercially. Almond (*Prunus amygdalus*), apricot (*Prunus armeniaca*), European plum (*Prunus domestica*), and Japanese plum (*Prunus salicina*)—all different species—are grafted commercially on rootstock of peach (*Prunus*

persica). But on the other hand, almond and apricot, both in the same genus, cannot be intergrafted successfully. The ‘Beauty’ cultivar of Japanese plum (*Prunus salicina*) makes a good union when grafted on almond, but another cultivar of *P. salicina*, ‘Santa Rosa,’ cannot be successfully grafted on almond. Thus, compatibility between species in the same genus depends on the particular genotype combination of rootstock and scion.

Reciprocal interspecies grafts are not always successful. For instance, ‘Marianna’ plum (*Prunus cerasifera* × *P. munsoniana*) on peach (*Prunus persica*) roots makes an excellent graft combination, but the reverse—grafts of the peach on ‘Marianna’ plum roots—either soon die or fail to develop normally (2, 90).

Grafting Between Genera Within a Family

When the plants to be grafted together are in the same family but in different genera, the chances of a successful union become more remote. Cases can be found in which such grafts are successful and used commercially, but in most instances such combinations are failures. Intergeneric grafts are rarely used in conifers. However, high success rates occur between Nootka cypress

(*Chamaecyparis nootkatensis*) grafted on Chinese arborvitae (*Platycladus orientalis*) rootstock (71).

Trifoliolate orange (*Poncirus trifoliata*) is used commercially as a dwarfing rootstock for the orange (*Citrus sinensis*), which is a different genus. The quince (*Cydonia oblonga*) has long been used as a dwarfing rootstock for certain pear (*Pyrus communis* and *P. pyrifolia*) cultivars. The reverse combination, quince on pear, though, is unsuccessful. The evergreen loquat (*Eriobotrya japonica*) can be grafted on deciduous and dwarfing quince rootstock (*Cydonia oblonga*). See Westwood (179) for other examples of graft compatibility between related pome genera.

Intergeneric grafts in the nightshade family, Solanaceae, are quite common. Tomato (*Lycopersicon esculentum*) can be grafted successfully on Jimson weed (*Datura stramonium*), tobacco (*Nicotiana tabacum*), potato (*Solanum tuberosum*), and black nightshade (*Solanum nigrum*).

Grafting Between Families

Successful grafting between plants of different botanical families is usually considered to be impossible, but there are reported instances in which it has been accomplished. These are with short-lived, herbaceous plants, though, for which the time involved is relatively brief. Grafts, with vascular connections between the scion and rootstock, were successfully made (114) using white sweet clover, *Metilotus alba* (Leguminosae) as the scion, and sunflower, *Helianthus annuus* (Compositae) as the rootstock. Cleft grafting was used, with the scion inserted into the pith parenchyma of the stock. The scions continued growth with normal vigor for more than 5 months. To date, there are no reported instances in which woody perennial plants belonging to different families have been successfully and permanently grafted together.

GRAFT INCOMPATIBILITY

The ability of two different plants, grafted together, to produce a successful union and to develop satisfactorily into one composite plant is termed **graft compatibility** (142). **Graft failure** can be caused by anatomical mismatching, poor craftsmanship, adverse environmental conditions, disease, and graft incompatibility.

Graft incompatibility occurs because of (a) adverse physiological responses between the grafting partners, (b) virus or phytoplasma transmission, and (c) anatomical abnormalities of vascular tissue in the callus bridge (Figs. 11–31 and 11–32).

Graft incompatibility is an interruption in cambial and vascular continuity leading to a smooth break at the point of the graft union. Normal vascular tissue does not develop in the graft union (Figs. 11–31 and 11–32). Consequently, the gap formed is filled

graft compatibility

The ability of two different plants, grafted together, to produce a successful union and to develop satisfactorily into one composite or compound plant.

graft failure An unsuccessful graft caused by anatomical mismatching, poor craftsmanship, adverse environmental conditions, disease, or graft incompatibility.

graft incompatibility

An interruption in cambial and vascular continuity leading to a smooth break at the point of the graft union, causing graft failure. It is caused by adverse physiological responses between the grafting partners, disease, or anatomical abnormalities.

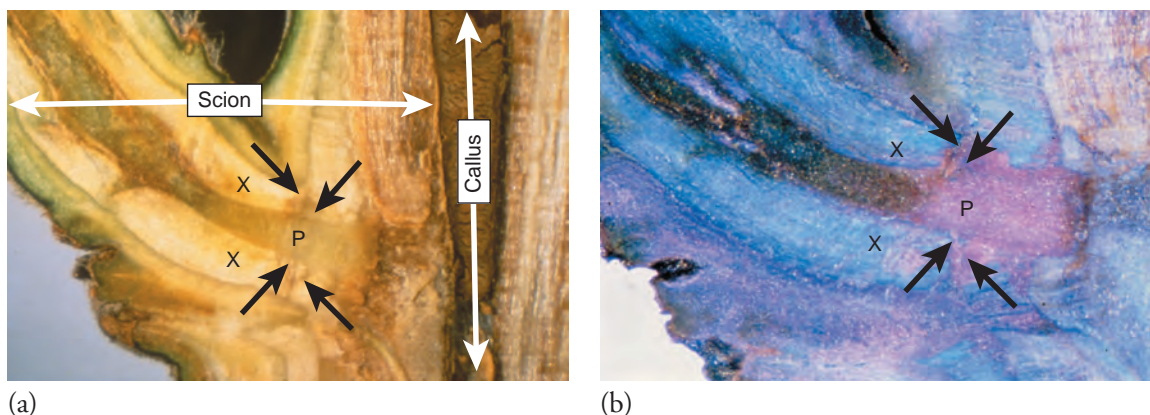
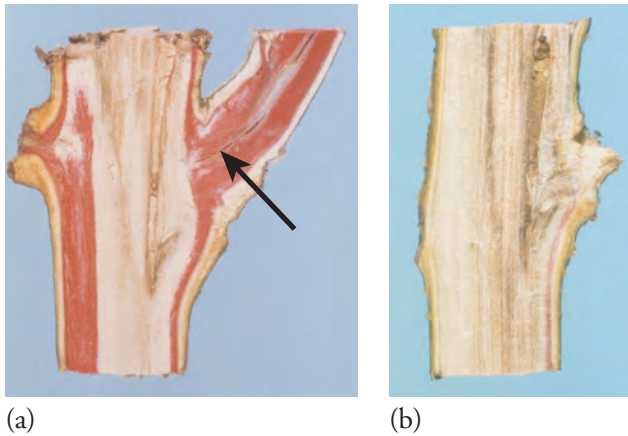


Figure 11-31

Graft incompatibility in 'Jonagold' apple scions budded to dwarfing 'Mark' rootstock. (a) Unstained section, with callus tissue between the rootstock and scion. (b) Section stained with toluidine blue O. The xylem (x) in the graft union is interrupted by parenchyma tissue (arrows) which limits water flow and survival of the scion. Courtesy of M. R. Warmund (176).

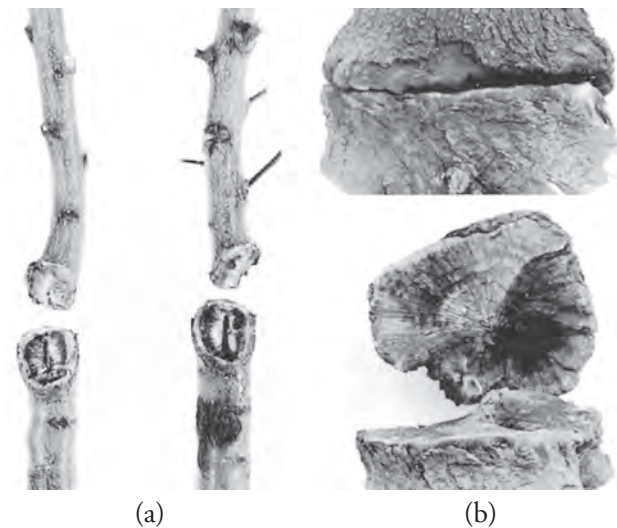
**Figure 11-32**

(a) Compatible apple chip bud with vascular continuity indicated by red dye, azosulfonate. (b) Unsuccessful chip bud with vascular discontinuity, as indicated by no visible dye. Courtesy M. R. Warmund.

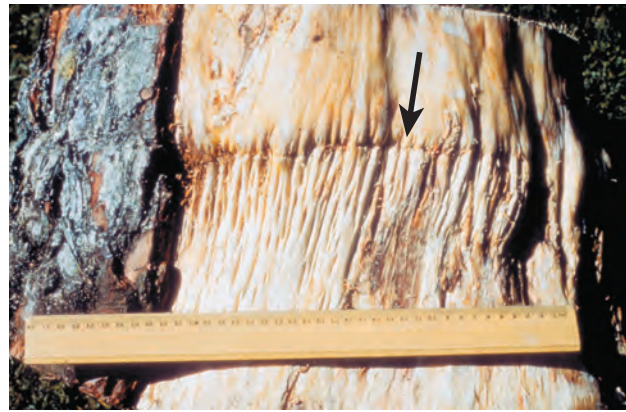
in by proliferating ray tissue that does not lignify normally (109).

Incompatibility can occur within a period of days or years (Figs. 11-33 and 11-34). Delayed incompatibility can take as long as 20 years to occur with conifers and oaks. Some apricot cultivars grafted onto myrobalan plum rootstock will not break at the graft union until the trees are fully grown and bearing crops (46).

The distinction between a compatible and an incompatible graft union is not always clear-cut. Incompatible rootstock-scion combinations can completely fail to unite. Frequently they unite initially

**Figure 11-33**

Breakage at the graft union resulting from incompatibility. (a) One-year-old nursery trees of apricot on almond seedling rootstock. (b) Fifteen-year-old 'Texas' almond tree on seedling apricot rootstock, which broke off cleanly at the graft union—a case of "delayed incompatibility" symptoms.

**Figure 11-34**

Graft incompatibility occurring some 15-plus years after the Monterey pine (*Pinus radiata*) was grafted.

with apparent success (Figs. 11-33 and 11-34) (35) but gradually develop distress symptoms with time, due either to failure at the union or to the development of abnormal growth patterns. Incompatibility of citrus and Monterey pine (*Pinus radiata*) may occur 15 or more years after grafting (Fig. 11-34). Nelson (113) has developed an extensive survey of incompatibility in horticultural plants which should be consulted before attempting graft combinations between species whose graft reactions are unknown to the grafter. Other summaries of graft compatibility have been published (2).

External Symptoms of Incompatibility

Graft union malformations resulting from incompatibility can usually be correlated with certain external symptoms. The following symptoms have been associated with incompatible graft combinations:

- Failure to form a successful graft or bud union in a high percentage of cases.
- Yellowing foliage in the latter part of the growing season, followed by early defoliation. Decline in vegetative growth, appearance of shoot die-back, and general ill health of the tree, including drought stress (Fig. 11-35).
- Premature death of the trees, which may live for only a year or two in the nursery.
- Marked differences in growth rate or vigor of scion and rootstock.
- Differences between scion and rootstock in the time at which vegetative growth for the season begins or ends.
- Overgrowths at, above, or below the graft union (Fig. 11-36).

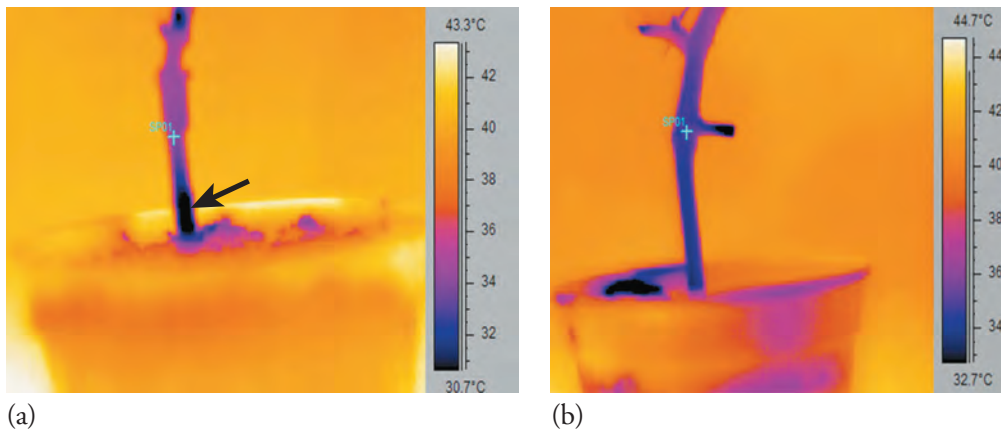


Figure 11-35 Graft compatibility affects water uptake. (a) Arava melon showing hotter scion and cooler temperature in *Cucurbita* rootstock (arrow) with noncompatible grafting combination. (b) Compatible graft showing uniform temperature between scion and rootstock. Differences in temperature gradients determined with a thermal camera. Courtesy M. Edelstein.

- Suckering of rootstock (Fig. 11-37).
- Graft components breaking apart cleanly at the graft union.

An isolated case of one or more of the preceding symptoms (except for the last) does not necessarily mean the combination is incompatible. Incompatibility is clearly indicated by trees breaking off at the point of union, particularly when they have been growing for some years and the break is clean and smooth, rather than rough or jagged. This break may occur within a year or two of the union, for instance, in the apricot on almond

roots (see Fig. 11-33), or much later with conifers and oaks (Fig. 11-34). While the scion overgrowing the rootstock (or rootstock outgrowing the scion) at the graft union is not a reliable indicator, it is sometimes associated with incompatibility (Figs. 11-38 and 11-39) (2, 26).

Anatomical Flaws Leading to Incompatibility

With incompatible cherry (*Prunus*) grafts, the number of well-differentiated phloem sieve tubes is much lower at and below the union. There is a greater autolysis of cells, and generally a very low degree of phloem differentiation (149). Poor differentiation of the phloem below the union may be due to a lack of hormones, carbohydrates, and other factors—the size of the sieve tubes depends on auxin, cytokinin, and sucrose levels (149). With incompatible apricot/plum (*Prunus*) grafts, some callus differentiation into cambium and vascular tissue does occur; however, a large portion of the callus never differentiates (Fig. 11-40) (48). The union that occurs is mechanically weak.

With incompatible apple grafts, vascular discontinuity occurs with xylem interrupted by parenchyma tissue (Figs. 11-31 and 11-32) (176), which disrupts normal xylem function leading to death of the budded scion.

Nontranslocatable (Localized) Incompatibility

For lack of better terminology, physiological factors of graft incompatibility has been traditionally classified as **nontranslocatable (localized)** or **translocatable** (109). It is difficult to distinguish differences between the symptoms of nontranslocatable and translocatable incompatibility. Anatomical symptoms of incompatibility can include phloem degeneration or phloem compression, and cambial or vascular discontinuity in



Figure 11-36 Physiological incompatibility between scion and rootstock. Scion overgrowth caused by blockage of assimilates translocating from the scion to the rootstock, causing a weak root system. The melon scion grafted on *Cucurbita* rootstock later died as a result of insufficient support from the rootstock. Photo courtesy M. Edelstein.



(a)



(b)

Figure 11-37

Undesirable suckering of rootstocks. (a) *Hamamelis vernalis* 'Sandra' grafted on *Hamamelis vernalis* rootstock, and (b) rootstock suckers on recently grafted *Ulmus alata* 'Lace Parasol' grafted onto seedling *Ulmus alata*. The suckers will need to be removed. Photo courtesy B. Upchurch.



(a)



(b)

Figure 11-38

While rootstock outgrowth is not desirable, a large, strong tree can still develop. (a) Sweet orange rootstock used for dwarfing, overgrowing the grapefruit scion. (b) Rootstock overgrowing scion on *Morus alba* 'Platanifolia.' Photo b courtesy B. Upchurch.



(a)



(b)

Figure 11-39

Scion or rootstock outgrowth can still lead to a large, strong tree. Such outgrowth (arrows) is more related to the genetic tendency for growth, than to incompatibility. (a) Scion overgrowing rootstock: *Acer pentaphyllum* on *A. pseudoplatanus* rootstock, and (b) grapefruit scion on sour orange rootstock, which tolerates alkaline, heavy soils, but can be susceptible to Trestiza. Photo a courtesy B. Upchurch.



BOX 11.6 GETTING MORE IN DEPTH ON THE SUBJECT TYPES OF GRAFT INCOMPATIBILITY



Anatomical Flaws

- Incompatible cherry (*Prunus*) grafts with poor phloem development and/or weak unions
- Incompatible apricot/plum (*Prunus*) grafts—mechanically weak unions
- Some budded apple (*Malus*) combinations—vascular discontinuity

Nontranslocatable (Localized) Incompatibility

- ‘Bartlett’ pear on quince roots; incompatibility overcome with ‘Old Home’ interstock

Translocatable Incompatibility

- ‘Hale’s Early’ peach on ‘Myrobalan B’ plum roots
- ‘Nonpareil’ almond on ‘Marianna 2624’ plum roots
- Peach cultivars on ‘Marianna 2624’ plum roots

Pathogen-Induced Incompatibility (Virus, Phytoplasma)

- Citrus quick decline or Tristeza
- Pear decline
- Walnut blackline
- Apple union necrosis and decline (AUND)
- Prune brownline

the union area, causing mechanical weakness and subsequent breakdown of the union. Nontranslocatable incompatibility includes graft combinations in which a **mutually compatible interstock** overcomes the incompatibility of the scion and rootstock. The interstock prevents physical contact of the rootstock and scion and affects the physiology of the normally incompatible scion and rootstock. In some innovative research, membrane filters placed between graft partners demonstrated that physical contact is not necessary to develop compatible grafts (104, 106). A good

example of nontranslocatable incompatibility is ‘Bartlett’ (‘Williams’) pear grafted directly onto dwarfing quince rootstock. When mutually compatible ‘Old Home’ or (‘Beurré Hardy’) is used as an interstock, the three-graft combination is completely compatible, and satisfactory tree growth takes place (107, 122, 132).

Translocatable Incompatibility

Translocatable incompatibility includes certain graft/rootstock combinations in which the insertion of a mutually compatible interstock does not overcome

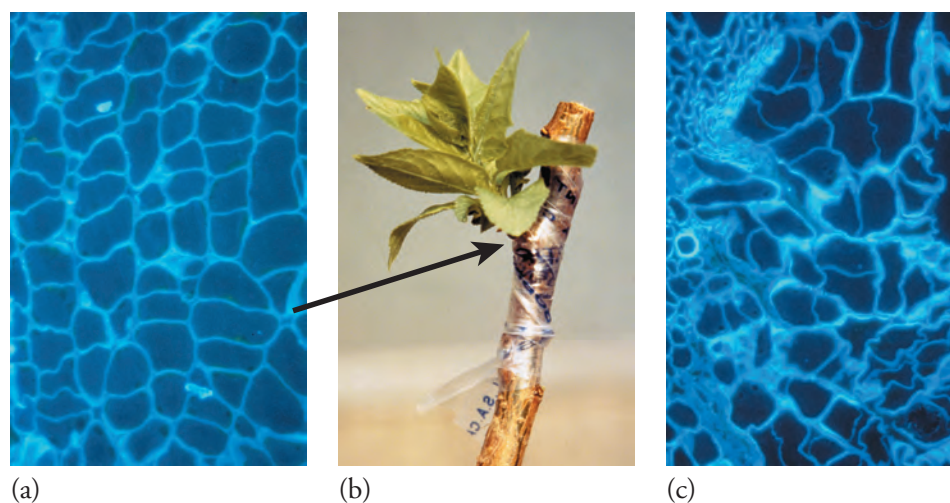


Figure 11-40

Callus bridge formation in graft union of compatible and incompatible *Prunus* spp. (a and b) Compatible ‘Luizet’ apricot grafted on ‘Myrobalan’ standard plum rootstock. (a) Callus in graft union from a compatible graft 21 days after grafting. The cells show an orderly disposition and are uniformly stained (160x magnification). (c) Callus from incompatible graft of ‘Monique’ apricot on ‘Myrobalan’ standard plum rootstock ten days after grafting. The cells show an irregular disposition and the cell walls are thick and irregular. Courtesy P. Errea (48).

incompatibility. Apparently, some biochemical influence moves across the interstock and causes phloem degeneration. This type of incompatibility can be recognized by the development of a brownline or necrotic area in the bark at the rootstock interface. Consequently, carbohydrate movement from the scion to the rootstock is restricted at the graft union.

‘Hale’s Early’ peach grafted onto ‘Myrobalan B’ plum rootstock is an example of translocatable incompatibility. The tissues are distorted and a weak union forms. Abnormal quantities of starch accumulate at the base of the peach scion. If the mutually compatible ‘Brompton’ plum is used as an interstock between the ‘Hale’s Early’ peach and the ‘Myrobalan B’ rootstock the incompatibility symptoms persist, with an accumulation of starch in the ‘Brompton’ interstock. ‘Nonpareil’ almond on ‘Marianna 2624’ plum rootstock shows complete phloem breakdown, although the xylem tissue connections are quite satisfactory. In contrast, ‘Texas’ almond, on ‘Marianna 2624’ plum rootstock produces a compatible combination. Inserting a 15-cm (6-in) piece of ‘Texas’ almond as an interstock between the ‘Nonpareil’ almond and the ‘Marianna’ plum rootstock fails to overcome the incompatibility between these two components. Bark disintegration occurs at the normally compatible ‘Texas’ almond/‘Marianna’ plum graft union (79).

Pathogen-Induced Incompatibility

Viruses and phytoplasmas (mycoplasma-like organisms) cause pathogen-induced incompatibility. Cases of

phytoplasmas (mycoplasma-like organisms) Organisms that can cause pathogen-induced incompatibility in grafted plants.

this incompatibility are widespread, and more are continually being found. In certain cases abnormalities first attributed to rootstock-scion incompatibility were later found to be

due to latent virus or phytoplasma introduced by grafting from a resistant, symptomless partner to a susceptible partner (32, 41, 95). Figure 11–41 shows such an occurrence in apple.

Tristeza, which comes from the Spanish and Portuguese word *triste*, meaning “sad” or “wretched,” is an important example of virus-induced incompatibility in citrus. Failure of sweet orange (*Citrus sinensis*) budded onto sour orange (*C. aurantium*) rootstock in South Africa (1910) and in Java (1928) was at one time blamed on incompatibility, even though this combination was a commercial success in other parts of the

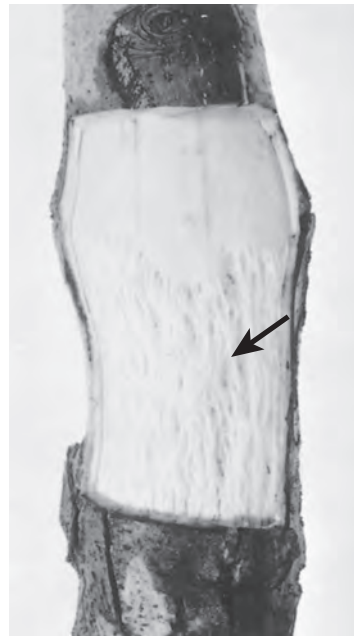


Figure 11–41

Latent viruses in the scion portion of graft combination may cause symptoms to appear in a susceptible rootstock following grafting. Here “stem pitting” virus symptoms (arrow) have developed in the sensitive ‘Virginia Crab’ apple rootstock. The wood of the scion cultivar—above the graft union—is unaffected. Courtesy H. F. Winter.

world. Incompatibility was believed due to production of a substance by the scion that was toxic to the rootstock (167). Subsequent studies involving *Tristeza* or “quick decline” of orange in Brazil and California made clear that the toxic substance from the sweet orange scions was instead a virus tolerated by the sweet orange, but lethal to sour orange rootstock (22, 177).

Other examples of virus-induced incompatibility include blackline in English walnut (*Juglans regia*), which infects susceptible walnut rootstock; apple union necrosis and decline (AUND) (37); and brownline of prune (99), which is caused by tomato mosaic virus that is transmitted by soil-borne nematodes to the rootstock, and then to the graft union. Pear decline is due to a phytoplasma, rather than a virus.

The major causes for graft incompatibility include (a) physiological and biochemical factors; (b) modification of cells and tissues at the graft union; and (c) cell recognition between grafting partners.

Causes and Mechanisms of Incompatibility

Physiological and Biochemical Mechanisms Tissue compatibility or incompatibility in plants can be regarded as a physiological tolerance or intolerance,



respectively, between different cells (103, 105, 106). Although incompatibility is clearly related to genetic differences between rootstock and scion, the mechanisms by which incompatibility is expressed are not clear. The large number of different genotypes that can be combined by grafting produces a wide range of different physiological, biochemical, and anatomical interactions when grafted. Several hypotheses have been advanced in attempts to explain incompatibility.

One proposed physiological and biochemical mechanism concerns incompatible combinations of certain pear cultivars on quince rootstock (61). The incompatibility is caused by a **cyanogenic glucoside, prunasin**, normally found in quince but not in pear tissues. Prunasin is translocated from the quince into the phloem of the pear. The pear tissues break down the prunasin in the region of the graft union, with hydrocyanic acid (cyanide) as one of the decomposition products (Fig. 11–42). The presence of the hydrocyanic acid leads to a lack of cambial activity at the graft union, with pronounced anatomical disturbances in the phloem and xylem at the resulting union. The phloem tissues are gradually destroyed at and above the graft union. Conduction of water and materials is seriously reduced in both xylem and phloem. *The presence of cyanogenic glycosides in woody plants is restricted to a relatively few genera.* Hence, this

reaction cannot be considered a universal cause of graft incompatibility.

Phenolic compounds have also been implicated in graft incompatibility (49). Phenolic compounds are widespread in plants and present in the biochemical responses to stress and wounding. They play a role in lignification (27), which occurs in graft union formation.

Modification of Cells and Tissue The **lignification** processes of cell walls are important in the formation of strong unions in pear-quince grafts. Inhibition of lignin formation and the establishment of a mutual middle lamella results in weak graft unions. In compatible pear-quince graft combinations, the lignin in cell walls at the graft union is comparable to adjacent cells outside the union (27). Conversely, adjoining cell walls in the graft union of incompatible combinations contain no lignin, and are interlocked only by cellulose fibers.

With incompatible apricot-plum (*Prunus*) grafts, some callus differentiation into cambium and vascular tissue does occur; however, a large portion of the callus never differentiates (Fig. 11–40) (48). The union that occurs is mechanically weak.

Cell Recognition of the Grafting Partners It has been postulated that the critical event deciding compatible and incompatible grafts may occur when the callus cells first

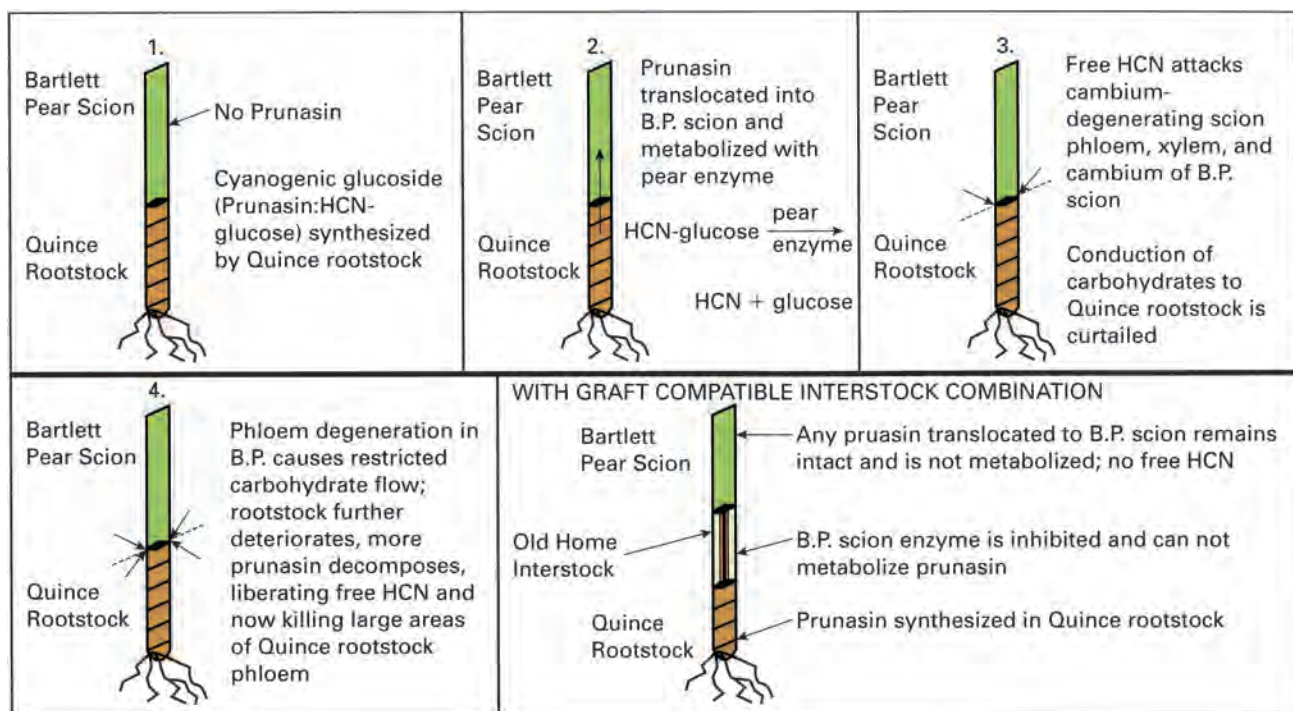


Figure 11–42

Nontranslocatable incompatibility of Bartlett pear scion overcome with 'old Home' interstock on quince rootstock (61).

cellular recognition

The union of specific cellular groups on the surfaces of the interacting cells that results in a specific defined response [e.g., pollen-stigma compatibility-incompatibility recognition responses with glycoprotein surface receptors in flowering plants (30)].

touch (189). There may be **cellular recognition** that must occur in successful graft union formation. Alternatively, the failure of procambial differentiation in incompatible grafts may be the result of a direct form of cellular communication between the graft partners (101).

In a compatible graft, the wound response is followed by a dissolution of the necrotic layer, perhaps as a prerequisite to the formation of secondary plasmodesmata between cells of the graft partners (165). *There is direct cellular contact* of plasmodesmata (minute cytoplasmic threads that extend through openings in cell walls and connect the protoplasts of connecting cells) in the callus bridge that symplastically connects the grafting partners (Fig. 11–19) (81). This forms a potential communication pathway among cells in the graft bridge, which may be important in cell recognition and compatibility/incompatibility responses.

Conversely, cellular recognition may not be a factor in grafting compatibility/incompatibility. Partners of compatible and incompatible grafts adhere during the early stages of graft union formation; this passive event does not require mutual cell recognition [grafted *Sedum* will even adhere to inert wooden objects (101, 103)], nor is it related to compatibility (106). Adhesion of graft partners results from the deposition and subsequent polymerization of cell wall materials that occur in

response to wounding. Callus proliferation is not related to graft compatibility-incompatibility systems, since it does not require a recognition event to occur; that is, callus proliferation occurs in wounded cuttings, as well as in incompatible and compatible graft systems (101, 103).

Vascular differentiation in the callus bridge, which typically occurs from the severed vascular strands of the scion and rootstock, can occur even when the scion and rootstock are physically separated by a porous membrane filter (inserted in order to prevent direct cellular contact without impeding the flow of diffusible substances between the graft partners) (102, 104); this was done with **autografts** of *Sedum* (a herbaceous species), which may not be representative

autograft The scion and rootstock are from the same plant or species.

of graftage in woody perennial plants. Nonetheless, it is evidence that successful graft union formation can occur in the absence of direct cellular contact, and does not require a positive recognition system.

Tissue alignment [e.g., vascular cambium of woody plants, vascular bundles of cacti (152)] determines what cell types and tissue will be differentiated in the callus bridge. It has been proposed that phytohormones are released from wounded vascular bundles into the surrounding tissue where they function as morphogenic substances inducing and controlling the regeneration of cambium and vascular tissue (3). This hypothesis can be applied to graft union formation, with phytohormones such as auxin as potential morphogens needed for graft union formation. Auxin should not be considered as a specific recognition molecule per se because of its common occurrence and involvement in numerous other developmental processes (104, 106). Phytohormones (and carbohydrates, etc.), predominantly released from

BOX 11.7 GETTING MORE IN DEPTH ON THE SUBJECT CELLULAR RECOGNITION



It is currently not known if some kind of cell-to-cell recognition in grafting must occur as part of adhesion and the events that follow in successful graft union formation. Possibly, the formation of superimposed sieve areas and sieve plates (in sieve elements), pits and perforation plates (in xylem elements), and the plasmodesmata (in vascular parenchyma) require some sort of cellular recognition or cellular communication (101). Evidence suggests that in the graftage of *Cucumis* and *Cucurbita*, changes in protein banding may be due to polypeptides migrating symplastically across the graft union via the connecting phloem (165). Translocation of signaling molecules, such

as polypeptides in the phloem, could be significant in cell recognition and compatibility between the graft partners. (In graft incompatibility, phloem degeneration frequently takes place at the graft union.)

Pectin fragments formed during the adhesion process of grafting may act as signaling molecules—and influence cell recognition. In Sitka spruce, the beadlike projections from callus formed during graftage are in part composed of pectins, proteins, carbohydrates, and fatty acids. These beadlike projections, besides binding or cementing cells, may serve a more active role in cell recognition and the successful merging of tissues of the grafting partners (96).



the scion, enable vascular connections to develop and join as a functional unit in the graft union, without any cellular recognition required.

A model for graft compatibility-incompatibility is presented that suggests grafts will be incompatible only if naturally occurring morphogens that promote the formation of a successful graft (e.g., auxin) are overridden by toxins [e.g., hydrocyanic acid, benzaldehyde (62, 63)] that elicit graft incompatibility (Fig. 11–43) (106).

There is probably no universal cause of graft incompatibility in plants (145). Most likely, graft compatibility-incompatibility is a combination of the auxin-toxin interactions of Figure 11–43 and/or some chemical recognition response. To date, we have little understanding of the molecular chain of events that occurs during wounding (180) and graft union formation, or how those chains of events vary between compatible-incompatible graft partners. In Douglas-fir, graft incompatibility is apparently controlled by multiple genes with additive effects (36).

Predicting Incompatible Combinations

Accurately predicting whether or not the components of the proposed scion-stock combination are compatible would be tremendously valuable. An *electrophoresis test* was used for testing *cambial peroxidase* banding patterns of the scion and rootstock of chestnut, oak, and maple (138, 140–145). Peroxidases mediate lignin production. Increased peroxidase activity occurs in incompatible

heterografts, compared with compatible auto-grafts, and adjacent rootstock and scion cells must produce similar lignins and have identical peroxidase enzyme patterns to ensure the development of a functional vascular system across the graft union (40). With electrophoresis, if the peroxidase bands match, the combination may be compatible; if they do not, incompatibility may be predicted. Using electrophoresis is an important step in developing diagnostic tests for graft compatibility. Perhaps serological tests for graft compatibility may be developed in the future, to complement those currently used in disease diagnostic kits of plant pathogens.

The introduction of new *Prunus* rootstock can be difficult (and very costly!) because incompatibility can occur some years after grafting. The composite tree can grow “normally” for years, and then a breakdown occurs at the graft union area. It is now known that with incompatible apricot-plum (*Prunus*) grafts, some callus differentiation into cambium and vascular tissue does occur; however, a large portion of the callus never differentiates (Fig. 11–40) (48). Early detection of graft incompatibility in fruit trees is greatly facilitated since this process can be detected histologically within weeks after grafting (48).

Magnetic resonance imaging (MRI) can be used to

heterograft The scion and rootstock are from a different cultivar or species.

Magnetic Resonance Imaging (MRI)

A diagnostic imaging technique that can be used for detecting vascular continuity in the callus bridge.

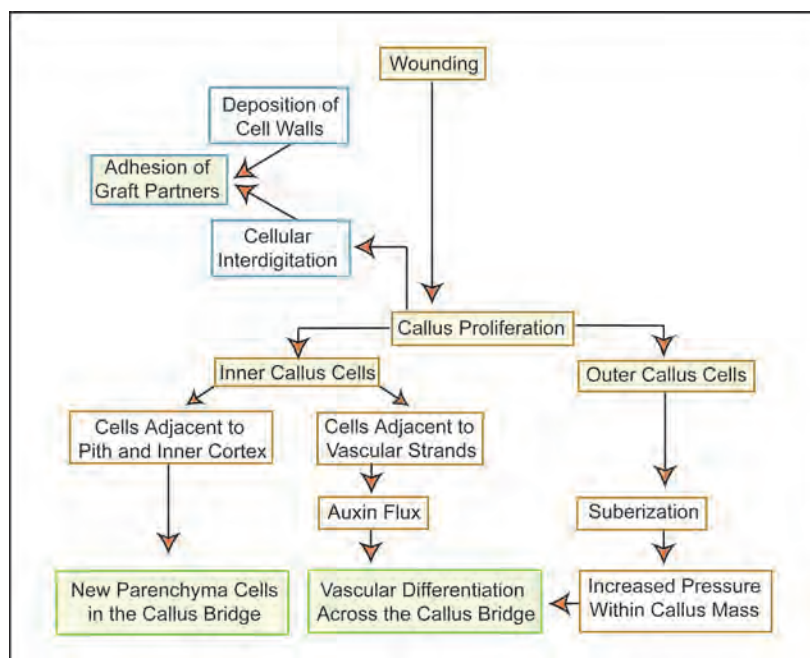


Figure 11–43

A model to explain the development of a compatible graft union. The stages are adhesion of the scion and rootstock, proliferation of callus cells to form the callus bridge, and vascular differentiation across the graft interface. The outer callus cells are from the periderm and outer cortex. The pressure exerted on the graft is from the physical contact of the scion to the rootstock—and the development of a suberized periderm. Auxin is a potential morphogen, enhancing vascular dedifferentiation. In this model, incompatibility is not caused by specific cellular recognition events between the graft partners. Rather, incompatibility may occur when a toxin, such as hydrocyanic acid (HCN) or benzaldehyde, counteracts naturally occurring morphogens (e.g., auxin), thus inhibiting or degenerating vascular tissues in the graft union (106).

BOX 11.8 GETTING MORE IN DEPTH ON THE SUBJECT

CELLULAR RESPONSES OF COMPATIBLE AND INCOMPATIBLE GRAFTS



At the cellular level, the initial stages of graft union formation were similar between the incompatible combination (heterografts) of *Sedum telephoides* (Crassulaceae) on *Solanum pennellii* (Solanaceae) and those occurring in a compatible autograft of *Sedum* on *Sedum*. However, after 48 hours, *Sedum* cells in the incompatible graft deposited an insulating layer of suberin along the cell wall. The cell walls later underwent lethal senescence and collapse and

formed a necrotic layer of increasing thickness (Fig. 11–44) (101, 103). Associated with this cellular senescence in *Sedum* cells was a dramatic increase in a hydrolytic enzyme, acid phosphatase (102). Rather than callus cells interlocking, the thick necrotic layer prevented cellular connections, which led to scion desiccation and eventual death. Interestingly, the *Solanum* rootstock did not show the rejection response that the *Sedum* scion did.

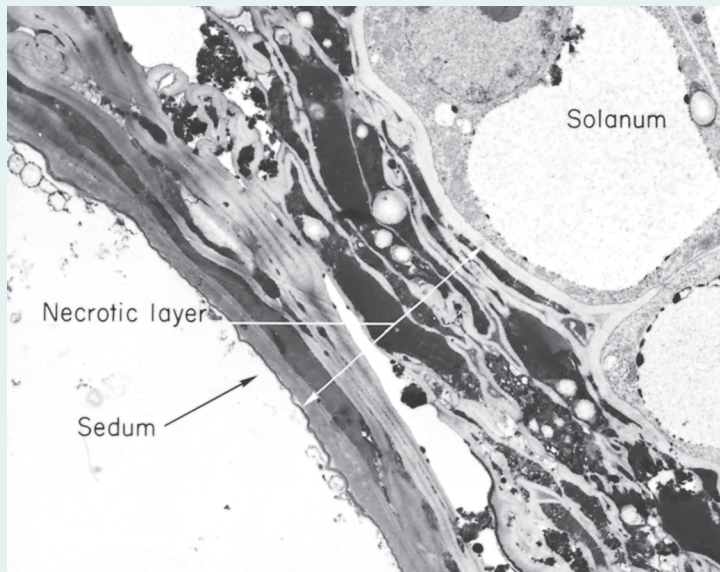


Figure 11–44

The graft interface of an incompatible graft between *Sedum telephoides* and *Solanum pennellii* at eight days after grafting. Lethal cellular senescence in *Sedum* has resulted in the formation of a necrotic layer of collapsed cells that separates the two graft partners. $\times 5,000$. Courtesy R. Moore and D. B. Walker (101).

detect vascular discontinuity in bud unions of apple (176). A high MRI signal intensity is associated with bound water in live tissue and the establishment of vascular continuity between the rootstock and scion. MRI may be useful for detecting graft incompatibilities caused by poor vascular connections.

Correcting Incompatible Combinations

There is not a practical, cost-effective way to correct large-scale plantings of incompatible graft partners. Plants are normally rogued and discarded. With some isolated specimen trees of value, if the incompatibility were discovered before the tree died or broke off at the union, a bridge graft could be done with a mutually compatible rootstock. Another costly alternative is to inarch with seedlings of a compatible rootstock. The inarched seedlings would eventually become the main root system (see Chapter 12).

SCION-ROOTSTOCK (SHOOT-ROOT) RELATIONSHIPS

Combining two (or more, in the case of interstocks) different plants (genotypes) into one plant by grafting—one part producing the top and the other part the root system—can produce growth patterns that are different from those that would have occurred if each component part had been grown separately. Some of these effects are of major importance in horticulture and forestry, while others are detrimental and should be avoided. These altered characteristics may result from (a) specific characteristics of the graft partners not found in the other; for example, resistance to certain diseases, insects, or nematodes, or tolerance of certain adverse environmental or soil conditions; (b) interactions between the rootstock and the scion that alter size, growth, productivity, fruit quality, or other horticultural attributes; and (c) incompatibility

reactions. In practice, it may be difficult to separate which influencing factor is dominant in any given graft combination growing in a particular environment.

Long-term results depend on the rootstock-scion combination, environment (climate, edaphic factors such as soil), propagation, and production management, which affects yield, quality, plant form, and ornamental characteristics (if applicable), and by extension, the economics of production.

Effects of the Rootstock on the Scion Cultivar

Size and Growth Habit Size control, sometimes accompanied by change in tree shape, is one of the most significant rootstock effects. Rootstock selection in apple has produced a complete range of tree sizes—from dwarfing to very vigorous—by grafting the same scion cultivar to different rootstocks (Fig. 11–10).

That specific rootstocks can be used to influence the size of trees has been known since ancient times. Theophrastus—and later the Roman horticulturists—used dwarfing apple rootstocks that could be easily propagated. The name “Paradise,” which refers to a Persian (Iranian) park or garden—*pairidaeza*—was applied to dwarfing apple rootstocks about the end of the 15th Century.

A wide assortment of size-controlling rootstocks has now been developed for certain of the major tree fruit crops. Most notable is the series of clonally propagated apple rootstocks collected and developed at the East Malling Research Station in England, beginning in 1912. These apple rootstocks were classified into four groups, according primarily to the degree of vigor imparted to the scion cultivar: **dwarfing**, **semi-dwarfing**, **vigorous**, and **very vigorous**—same size as seedling rootstock (Fig. 11–10). Similarly, the size-controlling effects of the rootstock on sweet cherry (*Prunus avium*) scion cultivars has been known since the early part of the 18th Century. Mazzard (*P. avium*) seedling rootstocks produce large, vigorous, long-lived trees, whereas *P. mahaleb* seedlings, as a rootstock, tend to produce smaller trees that do not live as long. However, individual seedlings of these species, when propagated asexually and maintained as clones, can produce different, distinct rootstock effects. Rootstock effects on tree size and vigor are recognized also in citrus, pear, peach, olive and other species. A discussion of specific rootstocks for the various fruit and nut crops is given in Chapter 19.

Fruiting *Fruiting precocity, fruit bud formation, fruit set, and yield* of a tree can be influenced by the rootstock used. In general, fruiting precocity is associated

with dwarfing rootstocks, and delay in fruiting with vigorous rootstocks. Apple rootstocks are used primarily for reducing tree size and for increasing precocity and yield efficiency.

Besides being more precocious, intensive plantings of small trees resulting from dwarfing rootstock intercept more light and have less internal shading, which is related to greater dry matter production and fruit yield. The higher ratio of fruit weight to trunk and branch weight (partitioning of photosynthate to fruit rather than wood formation) may also contribute to higher *yield efficiencies* for trees growing on dwarfing rootstock than more vigorous clonal and seedling rootstock (121, 160).

Vigorous, strongly growing rootstocks, in some cases, result in a larger plant that produces a bigger crop (per individual tree) over many years. On the other hand, trees on dwarfing rootstocks are more fruitful, and if closely planted, produce higher yields per hectare (acre). The producer’s cash flow and return on investment are much improved because an apple crop on dwarfing rootstock produces more fruit earlier. Furthermore, the management costs of harvesting, pruning, spraying, and general maintenance are much greater on large trees.

Size, Quality, and Maturity of Fruit There is considerable variation among plant species in regard to the effect of the rootstock on fruit characteristics of the scion cultivar. However, *in a grafted tree there is no transmission of fruit traits characteristic of the rootstock to the fruit produced by the grafted scion*. For example, quince, commonly used as a dwarfing pear rootstock, has fruits with a pronounced tart and astringent flavor, yet this flavor does not appear in the pear fruits. The peach is often used as a rootstock for apricot, yet apricot fruits do not have any characteristics of peach fruits.

Although there is no transfer of fruit characteristics between the rootstock and the scion, certain rootstocks can affect fruit quality of the scion cultivar. A good example of this is the “black-end” defect of pears. ‘Bartlett,’ ‘Anjou,’ and some other pear cultivars on several different rootstocks often produce fruits that are abnormal at the calyx end. While the fruit quality and yield of tomatoes and cucurbits is generally enhanced with the correct stock-scion combination, sometimes melon fruit quality is impaired when grafted on disease resistant *Cucurbita* rootstock (39). Rootstocks of chili peppers (*Capsicum annuum*) can increase the level of capsaicin, which influences the “hotness” of peppers (185).

In citrus, striking effects of the rootstock appear in fruit characteristics of the scion cultivar (23). If sour



Figure 11-45

Stock-scion relations. (a) Seedless 'Marsh White' grapefruit scion on rough lemon rootstock (left top & bottom), compared to (b) 'Marsh White' on sour orange rootstock (right top & bottom), which has a thinner peel (arrows)—and is also sweeter and juicier.

orange (*Citrus aurantium*) is used as the rootstock, fruits of sweet orange, tangerine, and grapefruit are smooth, thin-skinned, and juicy, with excellent quality, and they store well without deterioration (Fig. 11-45). Sweet orange (*C. sinensis*) rootstocks also result in thin-skinned, juicy, high-quality fruits. The larger fruit size of 'Valencia' oranges is associated with the dwarfing trifoliolate orange rootstock, whereas sweet orange rootstocks produce smaller fruits. Semi-dwarfing clonal rootstock will enhance the fruit size of 'Red Delicious' and 'Granny Smith' apples, compared with seedling rootstock, while 'Gala' is unaffected by rootstocks (69).

Miscellaneous Effects of the Rootstock on the Scion Cultivar Rootstocks can also increase cold-hardiness, nitrogen efficiency, enhance tolerance of adverse edaphic conditions, and increase disease and insect resistance of the grafted scion.

Cold-Hardiness. In citrus, which rootstock is used can affect the winter-hardiness of the scion cultivar. Grapefruit cultivars on 'Rangpur' lime rootstock survive cold better than those on sour orange or rough lemon rootstock. The rootstock can affect the rate of

own-rooted The propagation of a plant by rooted cutting, as opposed to propagating the cultivar on a grafted rootstock.

maturity of the scion wood as it hardens-off in the fall (54). Greater low-root temperature resistance can occur in grafted, herbaceous vegetable crops. When

cucumber (*Cucumis sativus*) scions are grafted onto figleaf gourd rootstocks (*Cucurbita ficifolia*), there is greater low-root temperature resistance compared to **own-rooted** cucumber plants, a phenomenon is attributed to greater water absorption capacity of the figleaf gourd rootstock exposed to root temperatures of less than 20°C (68°F), which causes own-rooted cucumber plants to wilt, as the result of reduced water absorption (1).

Increased Nitrogen Efficiency. Grafted vegetable crops with very vigorous root systems can absorb more inorganic nutrients than own-rooted plants (82, 85). The organic nitrogen and fruit yield increased with grafted melon cultivars (*Cucumis melo*) on *Cucurbita maxima xmoschata* rootstock, compared with own-rooted plants (137). There was greater nitrogen utilization and assimilation in the grafted than own-rooted plants. Mini-watermelon plants (*Citrullus lanatus*) grafted on *Cucurbita* rootstock had a higher marketable yield, higher nutritional status (including nitrogen, potassium, and phosphorus), photosynthesis, and water uptake than non-grafted plants under limited-water supply (136).

Extending Scion Tolerance of Adverse Edaphic Conditions. For many kinds of plants, rootstocks are available that tolerate unfavorable conditions, such as heavy, wet soils (124–126, 129), or high soil pH (Fig. 11-2). In the southeastern United States, where high temperatures and periodic flooding of soils (low soil oxygen) are the norm, cultivars of birch (*Betula*), fir (*Abies*), and oak (*Quercus*) are grafted onto rootstock that tolerate these atmospheric and edaphic environments (Fig. 11-1) (125, 126, 129). 'Whitespire' Japanese birch (*Betula populifolia*) is an excellent landscape tree for the southeastern United States. It tolerates heat and drought but will not tolerate poorly drained soils. The ecological niche of 'Whitespire' may be expanded by grafting it onto flood-tolerant rootstock of river birch (*B. nigra*) (125). Compared with many other genera of temperate woody plants, trees in the genus *Prunus* are often intolerant of poor drainage conditions. Ornamental *Prunus* cultivars can be adapted to poorly drained landscape sites by grafting onto more flood-tolerant 'Newport' plum (*Prunus hybrida*) and 'F-12/1' Mazzard cherry (*P. avium*) (124). Japanese Momi fir (*Abies firma*) is one of the few firs that will tolerate the heavy clay, wet soil conditions, and heat of the southeastern United States. Consequently, it is being recommended as the rootstock for more desirable fir cultivars (129).



Disease and Pest Resistance. Some rootstocks are more tolerant to adverse soil pests, such as nematodes (*Meloidogyne* spp.), than others; for example, ‘Nemaguard’ peach rootstock. The growth of the scion cultivar is subsequently enhanced by the rootstock’s ability to withstand these soil pests. Grape cultivars susceptible to the insect pest, phylloxera (*Dactylosphaera vitifoliae*), are grafted onto resistant rootstocks. Many cucurbits and solonaceous crops are grafted for enhanced disease resistance and tolerance of abiotic stress (Figs. 11–3 and 11–4) (34, 39, 82, 86, 131). Grafting with disease-resistant rootstock also offers new IPM management strategies for organic vegetable production (131).

Effect of the Scion Cultivar on the Rootstock

Although there is a tendency to attribute all cases of dwarfing or invigoration of a grafted plant to the rootstock, the effect of the scion on the behavior of the composite plant may be as important as that of the rootstock.

Effect of the Scion on the Vigor and Development of the Rootstock Scion vigor can have a major effect on rootstock growth, just as rootstocks can affect scion growth. If a strongly growing scion cultivar is grafted on a weak rootstock, the growth of the rootstock will be stimulated so as to become larger than it would have been if left ungrafted. Conversely, if a weakly growing scion cultivar is grafted onto a vigorous rootstock, the growth of the rootstock will be lessened from what it might have been if left ungrafted. In citrus when the scion cultivar is less vigorous than the rootstock cultivar, it is the scion cultivar rather than the rootstock that determines the rate of growth and ultimate size of the tree (66).

Effect of Interstock on Scion and Rootstock

The ability of certain dwarfing rootstock clones, inserted as an interstock between a vigorous top and vigorous root, to produce dwarfed and early bearing fruit trees has been used for centuries to propagate dwarfed trees. The degree of size control induced in apples by various dwarfing rootstock is shown in Figure 11–10. Dwarfing of apple trees by the use of a ‘Malling 9’ as an interstock was a common commercial practice for many years (Fig. 11–11). This dwarfing method had the advantage of allowing the use of well-anchored, vigorous rootstock rather than a brittle, poorly anchored dwarfing clone. Sometimes excessive suckering from the roots occurred due to the dwarfing

interstock, even in rootstock types that normally do not sucker freely. Today, apple interstocks are rarely used except in China (G. Fazio, personal communication).

Possible Mechanisms for the Effects of Rootstock on Scion and Scion on Rootstock

While many of the effects of rootstock-scion relations are known, the fundamental mechanisms of control, particularly on the molecular basis, are not well understood. A better understanding of the mechanisms controlling growth and development in grafted plants would speed up the design, development, and commercialization of new composite plant systems. By understanding these mechanisms, breeders could better predict the growth responses of new potential graft partners (while they are still on the “drawing board”) and develop more efficient screening tests—rather than relying on cumbersome trial and error processes that may take up to 10 years or more in evaluating grafted, woody perennial plants.

Without question, the nature of the rootstock-scion relationship is very complex and differs among genetically different combinations. Furthermore, in a composite plant system, size control, plant form, flowering, fruiting, disease resistance, flood tolerance, etc. are not controlled by the same genes or physiological/morphological mechanisms. Theories advanced as possible explanations for the interaction between the rootstock and scion include: (a) **anatomical factors**, (b) **nutritional and carbohydrate levels**, (c) **absorption and translocation of nutrients and water**, (d) **phytohormones and correlative effects**, and (e) **other physiological factors**.

Anatomical Factors The roots and stems of dwarfing apple rootstocks, which can reduce vegetative growth and increase flowering, are characterized by several anatomical features. These include: (a) a high ratio of bark (periderm, cortex, and phloem tissue) to wood (xylem tissue); (b) a large proportionate volume occupied by living cells (axial parenchyma and ray parenchyma cells) relative to functionally dead xylem cells (vessels and fibers); and (c) fewer and smaller xylem vessels (13, 14, 92, 153).

Much of the functional wood tissue of roots of dwarfing apple stocks is composed of living cells, whereas in nondwarfing, vigorous rootstocks, the wood consists of a relatively large amount of lignified tissue without living cell contents (i.e., a larger vessel/tracheid system for more efficient water transport). At the graft interface between the scion bud and dwarfing apple rootstock, xylem vessels with smaller than normal diameter are formed, whereas semi-dwarfing rootstock produces normal xylem after a

brief interruption (157). It has been proposed that failure of auxin to cross the bud-union interface in the case of the dwarfing rootstock leads to reduced rootstock xylem formation, and hence a reduced supply of water and minerals to the scion, thus causing the dwarfing effect (87). Defects in the graft union that cause a partial discontinuity of the vascular tissues may in part explain the marked depletion of solutes, nutrients, and cytokinins (produced from root apices) in the sap contents of dwarfing interstocks and rootstocks (73).

Conversely, with kiwifruit, the roots of flower-promoting rootstock tend to have more and larger xylem vessels, more crystalline idioblasts, and more starch grains (173, 174). Most likely the greater water supply from the rootstock to the scion in early spring determines the abundance of flower production of the kiwifruit scions.

Morphologically, dwarfing rootstock have fewer coarse roots (diameter greater than 2 mm) and fewer fine roots (diameter less than 2 mm) than more vigorous apple rootstocks (5, 6). There is not always a clear relationship between root length growth and size control characteristics of dwarfing versus vigorous rootstock. However, there are fewer active root tips in dwarfing than vigorous apple rootstock (51). The roots and shoots of vigorous apple rootstocks also have a longer growing season than dwarfing rootstock (78).

Nutritional and Carbohydrate Levels Dwarfing rootstock of apple tends to partition a greater proportion of carbon to reproductive areas (**spurs**, spur leaves, fruit) and less to the tree branch and frame dry weight, compared with nondwarfing rootstocks (160). The greater water and nutrient uptake of the vigorous rootstock contributes

spurs The principal fruiting unit in apple, which may be classified as *short shoots*. The *terminal bud* of a spur may be either vegetative, containing only leaves, or reproductive. *Reproductive buds* of apple are *mixed buds* that produce both flowers and leaves.

competing sink The competition of two independent growth processes (such as flowering and adventitious root formation) for the same limited metabolic resources (e.g., carbohydrates, proteins).

to the production of new vegetative growth, which is a **competing sink** with reproductive growth.

The rootstock affects the partitioning of the dry matter between above- and below-ground tree components. Vigorous rootstocks accumulate more dry matter in the shoot and root system than dwarfing stock (6, 161). At the time apples are being

harvested, the insoluble root starch supply is greater, but soluble sucrose and sorbitol are less in vigorous rootstock compared with dwarfing rootstock.

It appears that apple rootstock does not influence mineral nutrition at the site of flower formation (65). Most likely, rootstock effects on flowering are due to internal control mechanisms that affect the proportion of spurs that become floral (64).

To summarize, dwarf apple rootstocks do affect precocity and flowering, in part, because of differences in carbohydrate metabolism and the greater carbon partitioning to the reproductive areas. The contributing influence of hormones, which also affects carbon partitioning and flowering, is discussed below.

Absorption and Translocation of Nutrients and Water

Apple rootstocks affect Ca, Mg, Mn, and B uptake, but there is no apparent direct relationship of mineral status with rootstock vigor, productivity, or spur characteristics (65).

Rootstocks do differ in their ability to absorb and translocate P (74), but a direct role of phosphorus at the site of flower formation induced by rootstock seems unlikely (65). In a study of the translocation of radioactive phosphorus (^{32}P) and calcium (^{45}Ca) from the roots to the tops of 1-year 'McIntosh' apple trees grown in solution culture, it was shown that more than three times as much of both elements was found in the scion top when vigorous rootstock was used in comparison with the dwarfing rootstock (29). This may indicate a superior ability of the vigorous rootstock to absorb and translocate mineral nutrients to the scion in comparison with the dwarfing rootstock. Or it may only mean that roots of the dwarfing rootstock, with their higher percentage of living tissue, formed a greater "sink" for these materials, retaining them in the roots.

Interstocks of such dwarfing apple clones as 'Malling 9' will cause a certain amount of dwarfing, suggesting reduced translocation due to partial blockage at the graft unions or to a reduction in movement of water or nutrient materials (or both) through the interstock piece. Differences among rootstocks in water translocation have been demonstrated with a steady-state, heat-balance technique that accurately measures xylem sap flow rate and sap flow accumulation over time. Under nonstress conditions, sap flow was greater in 'Granny Smith' apple scions grafted to very vigorous seedling (standard) rootstock, while sap flow was similar between the dwarfing and semi-dwarfing rootstock (70). Moisture stress affects the sap flow of the vigorous seedling rootstock the least and reduced sap flow on the dwarfing rootstock the most.

Sweet cherries grafted on dwarfing rootstock have smaller and fewer xylem vessels in the scion and graft union, and irregular vessel orientations in the vascular tissue compared to non-dwarfing rootstock; this difference could contribute to greater hydraulic resistance in the graft union, resulting in reduced scion growth (dwarfing) (116). With peach trees grafted on rootstocks with differing size-controlling potentials, the higher root resistance (reduced sap flow) plays a central role in the dwarfing mechanism induced by size-controlling rootstock (semi-dwarfing). Interestingly, the root system accounted for the *majority* of resistance of water flow through the tree and had *no effect* on hydraulic conductance through the scion or graft union (12).

Conversely, with olive trees (*Olea europaea* L.), while there was lower hydraulic conductance in dwarfing than vigorous rootstock during the first several months, but after 1 year hydraulic conductivity was the same between dwarfing or vigorous rootstocks (55).

In summary, as long as mineral elements are not limiting, the greater uptake of P and Ca by the more vigorous rootstock does not adequately account for dwarfing effects (29). While rootstocks can influence leaf mineral nutrition, results have been inconsistent (65). In general, sap flow is greatest in vigorous and least in dwarfing rootstock. While differences in sap flow may be attributed to differences in root characteristics, xylem anatomy or other features of the hydraulic architecture from the roots to the graft union, or the union itself, the primary influence probably lies more in the nature of the growth characteristics of such rootstocks.

Phytohormones and Correlative Effects Plants maintain a constant root/shoot ratio, and any attempt to alter this ratio results in the plant redirecting its growth pattern until the ratio is reestablished. This also applies to

correlative effects

The influence of one organ over another, due to phytohormones (e.g., high ABA produced in the root tips of dwarfing apple rootstock reduces the vegetative growth of the scion).

grafted plants and plants transplanted into a landscape site or orchard. Producing a composite plant by grafting onto a dwarfing rootstock is an alteration in the normal growth pattern (87). Growth in the composite plant will be redirected until equilibrium is reached between the rootstock-scion system. Intimately involved in redirecting plant growth are the **correlative effects** of root (rootstock)/shoot (scion) systems, mediated by phytohormones. Auxins, which are produced predominantly in the shoot system, are basipetally translocated through the phloem and

into the root system, where they affect root growth. Cytokinins are produced predominantly from root apices, and are translocated primarily through the xylem, where they can influence physiological responses and growth in the scion.

Of the phytohormones, auxin plays one of the most important roles in dwarfing rootstock control of apple scion growth (75). The dwarfing effect may be explained by reduced auxin transport into the graft union of the dwarf rootstock (87); this could alter the hormonal balance between shoots and roots, and account for the reduced vegetative growth and vigor of the scion. Auxin affects vascular differentiation, and is important for stimulating cambial activity and xylem development (1) in the graft union area and the vascular system of the grafting partners. Dwarfing yields greater reduction in cambial activity and xylem formation in the graft union than vigorous rootstock (158) because of the dwarfing's reduced capacity to support polar auxin transport (not auxin uptake into cells), and a reduced capacity for auxin efflux from transporting cells (158). Since auxin is known to stimulate its own transport (58), lower endogenous auxin levels in the dwarfing rootstock may limit its capacity to support polar auxin transport. A chain of events is set off with less auxin being transported, which leads to reduced cambial activity and subsequently reduced xylem formation. Reduced xylem formation limits conduction in the dwarf rootstock, which concurs with the reports on lower xylem sap flow (70).

There is evidence for greater auxin accumulation in the scion of dwarfing apple understock. With apple, hydraulic conductivity of the graft tissue was lower for grafted trees on dwarfing rootstocks, compared to semi-vigorous rootstocks. The amount of functional xylem tissue in the graft union and scion initially increased with rootstock vigor (7). However, as the grafted *tree aged*, any differences in sap flow become *marginal*. The dwarfing tree compensated for hydraulic limitations imposed by the graft tissue and abnormal xylem anatomy (compared to more vigorous rootstock) by initially reducing its transpiring leaf area, and producing a smaller canopy (smaller tree). As the dwarfed tree aged, the cross-sectional area of the graft union increased (7), brought about by greater auxin accumulation (reduced transport) in the graft tissue of the dwarfing rootstock, which led to *increased xylem development later, as the dwarf tree aged*.

Auxin can indirectly affect cytokinin production. Reduced auxin transport leads to a smaller root system in the dwarf rootstock that produces less cytokinin, and/or the root metabolism is sufficiently altered to affect cytokinin synthesis. Subsequently, there is less

cytokinin translocated upward from the roots to the shoots and reduced top growth occurs; hence, the dwarfing effect. This correlative effect is mediated by auxin and cytokinin as growth in the composite plant is redirected and equilibrium is reached between the dwarf rootstock/scion system.

Abscisic acid (ABA) and gibberellic acid (GA) may also play a role in the correlative effects of dwarfing rootstock. Root apices are an important site of ABA synthesis. The dwarfing ‘Malling 9’ apple rootstock contains lower amounts of growth-promoting materials—but more growth inhibitors—than does the very vigorous ‘Malling 16’ rootstock (88). ABA levels are also reported to be higher in dwarfing rootstock (184), and in the stems of dwarfed apple trees, than in more vigorous ones (135).

There are higher ratios of ABA:IAA (auxin) in dwarfing than vigorous apple rootstock, a finding confirmed using gas chromatography-mass spectropho-

marker A morphological, biochemical, genetic indication of a trait (e.g., higher ABA in shoot bark of dwarfing compared with a vigorous apple rootstock).

tometer selective ion monitoring techniques (78). Higher ABA:IAA ratios may lead to greater differentiation of phloem and related tissues in dwarfing rootstocks, which could explain why dwarfing rootstocks have higher

bark (periderm, cortex, phloem, vascular cambium) to wood (xylem) ratios than vigorous rootstocks. The higher concentration of ABA in shoot bark of dwarfing compared with vigorous rootstock is a potentially useful **marker** in selecting for dwarfing apple rootstock (78).

There are conflicting reports that higher GA is found in more vigorous rootstock. Earlier reports

concluded there was little evidence to support a role for gibberellin in vigorous, compared to dwarfing rootstock (87, 134, 135). However, in other studies, dwarfing (M9) interstock labeled GA₃ was lower, and glycosyl conjugated GA₃ (inactive GA₃ form) was higher compared to nondwarfing (MM115) interstocks (130). However, a problem with hormonal studies is that the composition of the xylem sap often has very little resemblance to that flowing through the intact, transpiring trees. Hormone and ion concentrations in osmotically exuding sap do not always reflect the condition of the intact plant (5). For instance, slow-flowing sap concentrates solutes faster than fast-flowing sap diluted solutes. Apparently, xylem-borne substances are not delivered in proportion to sap flow, suggesting that differences in tree transpiration or leaf area have considerable influence on signal molecule concentration and delivery (5).

In summary, with apple, auxin is directly involved in dwarfing rootstock effects, and cytokinins (which are affected by auxin-mediated root growth and subsequent cytokinin biosynthesis) are either directly or indirectly involved in plant size control. There is a strong case for ABA-mediated dwarfing effects, while there are conflicting reports on the role of GA. Most likely, there is an interaction of factors affecting dwarfing phenomena such as phytohormones, anatomical factors, nutrition and carbohydrate levels, sap flow, and translocation of carbohydrates across the graft union.

Other Physiological Factors A wide range of physiological characteristics have been found to affect rootstocks, scions, and their resulting interactions (87, 127, 162). For example, rootstocks have been found to influence transpiration rate and crop water-use efficiency in peach; leaf conductance and osmotic potential in apple; and midday leaf water potential in citrus, peach, and

BOX 11.9 GETTING MORE IN DEPTH ON THE SUBJECT MOLECULAR APPROACHES TO STOCK-SCION RELATIONS



There has been recent progress with homografts and heterografts of *Arabidopsis thaliana* as a model system for graft union development. Using mutants of *A. thaliana* could lead to a greater understanding of the fundamental genetic and molecular aspects of graft union formation and plants' stock-scion relations (52). In other developments, the phloem sap transports carbohydrates, amino acids, other nutrients, and specific RNA molecules [small regulatory RNA (183)]. In heterografts of potato (scion) and tomato (understock) graft, transmittable RNA from the leafless tomato rootstock caused changes in the leaf morphology of the

potato scion (83). In grafting of transgenic tobacco, **gene silencing** was transmitted by a diffusible messenger that mediated the *de novo*, post-transcriptional silencing from silenced rootstock to non-silenced scions (117). Hence, grafting enables signaling in plants via RNA and protein movement. While plant yield, desirable dwarfing characteristics, and disease resistance are complex, multi-gene traits, there is future potential for genetic engineering to manipulate desirable RNA that could enhance or suppress scion phenotype characteristics (110). See Box 2.2, pages 35–6 for discussion of micro RNA and gene silencing.

apple trees. Rootstock-scion combinations can also influence net photosynthesis and growth characteristics of grafted *Prunus* species under droughted conditions (127). The greater tolerance to flooding found in selected rootstock of *Prunus* (124) and fir (*Abies*) is probably due to physiological and/or morphological mechanisms (45) that allow selected rootstock to handle anaerobic conditions better than other rootstock.

Net photosynthesis of leaves tends to be higher with apple scions on vigorous rootstock than on dwarfing rootstock (148). But photosynthetic rates cannot be used to explain differences in yield and yield efficiencies induced by the rootstock. Part of this complexity is because the presence of fruit increases leaf net photosynthesis by some unknown mechanism (148).

Cytokinins are known to promote photosynthesis, and root-produced ABA—translocated in xylem sap—can reduce stomatal conductance and photosynthetic rates in the shoot system.

More needs to be done with the molecular basis of rootstock-scion relations. It is possible that certain genes are being turned on and off and/or that genetic information may be transmitted between the graft partners of the composite plant (115). Epigenetic changes occur in grafting with the speeding up of maturation on grafted versus seedling-grown plants (see discussion on epigenetic changes in Chapter 16). Conversely, micropropagated dwarfing apple rootstocks that are grafted can have more juvenile-like characteristics, which delays bearing and fruit cropping of trees (76).

DISCUSSION ITEMS

1. What have been some historical reasons for grafting compared to other propagation methods?
2. Compare budding and grafting.
3. What are the differences between seedlings and clonal rootstock? What are the advantages of each system?
4. Using an interstock (double working) is expensive. Why is it still used as a propagation technique?
5. What are some of the ecological advantages of natural root grafting? How can it be a disadvantage in the dissemination of diseases, such as oak wilt and Dutch elm disease?
6. What are the stages of graft union formation?
7. Does cellular recognition take place in grafting, and, if so, how might that be important to graft compatibility/incompatibility?
8. Why is there potentially more rapid graft union development and frequently a higher percentage of “takes” in chip budding compared to T-budding?
9. What environmental conditions are desirable during and following grafting?
10. What are the genetic limits of grafting, (i.e., when is grafting most likely to be successful)?
11. What are the different types of graft incompatibility, and what causes them?
12. What are some techniques to help predict graft incompatibility?
13. What are some possible mechanisms for size control (dwarfing) in stock-scion relations?

REFERENCES

1. Ahn, S. J., Y. J. Im, G. C. Chung, B. H. Cho, and S. R. Suh. 1999. Physiological response of grafted-cucumber leaves and rootstock roots affected by low root temperature. *Scientia Hort.* 81:397–408.
2. Alexander, J. H. 1998. A summary of graft compatibility from the records of the Arnold Arboretum. *Comb. Proc. Intl. Plant Prop. Soc.* 48:371–83.
3. Aloni, R. 1987. Differentiation of vascular tissues. *Annu. Rev. Plant Physiol.* 38:179–204.
4. Asante, A. K., and J. R. Barnett. 1998. Effect of temperature on graft union formation in mango (*Mangifera indica* L.) *Trop. Agric. (Trinidad)* 75:401–4.
5. Atkinson, C. J., and M. Else. 2001. Understanding how rootstocks dwarf fruit trees. *Compact Fruit Tree* 34:46–9.
6. Atkinson, C. J., M. Policarpo, A. D. Webster, and A. M. Kuden. 1999. Drought tolerance of apple rootstocks: Production and partitioning of dry matter. *Plant Soil* 206:223–25.
7. Atkinson, C. J., M. A. Else, L. Taylor, and C. J. Dover. 2003. Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (*Malus pumila* Mill.). *J. Exp. Bot.* 54:1221–29.
8. Bailey, L. H. 1891. *The nursery book*. New York: Rural Publishing Company.

9. Barnett, J. R., and I. Weatherhead. 1988. Graft formation in Sitka spruce: A scanning electron microscope study. *Ann. Bot.* 61:581–87.
10. Barnett, J. R., and I. Weatherhead. 1989. The effect of scion water potential on graft success in Sitka spruce (*Picea sitchensis*). *Ann. Bot.* 64:9–12.
11. Barnett, J. R., and H. Miller. 1994. The effect of applied heat on graft union formation in dormant *Picea sitchensis* (Bong.). *Carr. J. Exp. Bot.* 45:135–43.
12. Basile, B., J. Marsal, L. I. Solari, M. T. Tyree, D. R. Brylan, and T. M. Dejong. 2003. Hydraulic conductance of peach trees grafted on rootstocks with differing size control potentials. *J. Hort. Sci. Biotech.* 78:768–74.
13. Beakbane, A. B. 1953. Anatomical structure in relation to rootstock behavior. *Rpt. 13th Inter. Hort. Cong.* Vol. I. pp. 152–58.
14. Beakbane, A. B., and W. S. Rogers. 1956. The relative importance of stem and root in determining rootstock influence in apples. *J. Hort. Sci.* 31:99–110.
15. Beeson, R. C., Jr., and W. M. Proebsting. 1988. Scion water relations during union development in Colorado blue spruce grafts. *J. Amer. Soc. Hort. Sci.* 113:427–31.
16. Beeson, R. C., Jr., and W. M. Proebsting. 1988. Relationship between transpiration and water potential in grafted scions of *Picea*. *Physiol. Plant.* 74:481–86.
17. Beeson, R. C., Jr., and W. M. Proebsting. 1989. *Picea* graft success: Effects of environment, rootstock disbudding, growth regulators, and antitranspirants. *HortScience* 24:253–54.
18. Beeson, R. C., Jr., and W. M. Proebsting. 1988. Photosynthate translocation during union development in *Picea* grafts. *Can. J. For. Res.* 18:986–90.
19. Beeson, R. C., Jr. 1991. Scheduling woody plants for production and harvest. *HortTechnology* 1:30–6.
20. Beveridge, C. A., J. J. Ross, and I. C. Murfet. 1994. Branching mutant rms-2 in *Pisum sativum*: Grafting studies and indole-3-acetic acid levels. *Plant Physiol.* 104:953–59.
21. Biggs, F., and T. Biggs. 1990. Tomato grafting. *Comb. Proc. Intl. Plant Prop. Soc.* 40:97–101.
22. Bitters, W. P., and E. R. Parker. 1953. Quick decline of citrus as influenced by top-root relationships. *Calif. Agr. Exp. Sta. Bul.* 733.
23. Bitters, W. P. 1961. Physical characters and chemical composition as affected by scions and rootstocks. In W. B. Sinclair, ed. *The orange: Its biochemistry and physiology*. Berkeley: Univ. Calif. Div. Agr. Sci.
24. Bloch, R. 1943. Polarity in plants. *Bot. Rev.* 9:261–310.
25. Bloch, R. 1952. Wound healing in higher plants. *Bot. Rev.* 18:655–79.
26. Bradford, F. C., and B. G. Sitton. 1929. Defective graft unions in the apple and pear. *Mich. Agr. Exp. Sta. Tech. Bul.* 99.
27. Buchloh, G. 1960. The lignification in stock-scion junctions and its relation to compatibility. In J. B. Pridham, ed. *Phenolics in plants in health and disease*. Long Island City, NY: Pergamon Press.
28. Buck, G. J. 1953. The histological development of the bud graft union in roses. *Proc. Amer. Soc. Hort. Sci.* 63:497–502.
29. Bukovac, M. J., S. H. Wittwer, and H. B. Tukey. 1958. Effect of stock-scion interrelationships on the transport of ³²P and ⁴⁵Ca in the apple. *J. Amer. Soc. Hort. Sci.* 33:145–52.
30. Burnet, F. M. 1971. Self-recognition in colonial marine forms and flowering plants in relation to the evolution of immunity. *Nature (London)* 232:230–35.
31. Carlson, R. F. 1967. The incidence of scion-rooting of apple cultivars planted at different soil depths. *Hort. Res.* 7:113–15.
32. Cation, D., and R. F. Carlson. 1962. Determination of virus entities in an apple scion/rootstock test orchard. *Quart. Bul. Mich. Agr. Exp. Sta. Rpt. I*, 45(2):435–43, 1960. *Rpt. II*, 45(17):159–66.
33. Cline, M. N., and D. Neely. 1983. The histology and histochemistry of the wound healing process in geranium cuttings. *J. Amer. Soc. Hort. Sci.* 108:452–96.
34. Cohen, R., Y. Burger, C. Horev, A. Porat, and M. Edelstein. 2005. Performance of Galia type melons grafted onto Cucurbita rootstock in *Monosporascus cannonballus*-infested and non-infested soils. *Ann. Appl. Biol.* 146:381–87.
35. Copes, D. L. 1969. Graft union formation in Douglas-fir. *Amer. J. Bot.* 56:285–89.
36. Copes, D. L. 1974. Genetics of graft rejection in Douglas-fir. *Can. J. For. Res.* 4:186–92.
37. Cummins, J. N., and D. Gonsalves. 1982. Recovery of tomato ring-spot virus from inoculated apple trees. *J. Amer. Soc. Hort. Sci.* 107:798–800.
38. Davies, F. T., Jr., Y. Fann, and J. E. Lazarte. 1980. Bench chip budding of field roses. *HortScience* 15:817–18.
39. Davis, A. R., P. Perkins-Veazie, R. Hassell, S. R. King, and X. Zhang. 2008. Grafting effects on vegetable quality. *HortScience* 43:1670–72.
40. Deloire, A., and C. Hebant. 1982. Peroxidase activity and lignification at the interface between stock and scion of compatible and incompatible grafts of *Capsicum* on *Lycopersicon*. *Ann. Bot.* 49:887–91.

41. Dimalla, G. G., and J. A. Milbrath. 1965. The prevalence of latent viruses in Oregon apple trees. *Plant Dis. Rpt.* 49:15–7.
42. Dole, J. M., and H. F. Wilkins. 1991. Vegetative and reproductive characteristics of poinsettia altered by a graft-transmissible agent. *J. Amer. Soc. Hort. Sci.* 116:307–11.
43. Doley, D., and L. Leyton. 1970. Effects of growth regulating substances and water potential on the development of wound callus in *Fraxinus*. *New Phytol.* 69:87–102.
44. Dorsman, C. 1966. Grafting of woody plants in the glasshouse. *Proc. 17th Inter. Hort. Cong.* 1:366.
45. Drew, M. C., and L. H. Stolzy. 1996. Growth under oxygen stress. In Y. Waisel, E. Amram, and U. Katkafi, eds. *Plant roots: The hidden half*. New York: Marcel Dekker, pp. 397–414.
46. Eames, A. J., and L. G. Cox. 1945. A remarkable tree-fall and an unusual type of graft union failure. *Amer. J. Bot.* 32:331–35.
47. Edelstein, M., M. Ben-Hur, R. Cohen, Y. Burger, and I. Ravina. 2004. Boron and salinity effects on grafted and non-grafted melon plant. *Plant Soil* 269:273–84.
48. Errea, P., A. Felipe, and H. Herrero. 1994. Graft establishment between compatible and incompatible *Prunus* spp. *J. Exp. Bot.* 45:393–401.
49. Evans, G. E., and H. P. Rasmussen. 1972. Anatomical changes in developing graft unions of *Juniperus*. *J. Amer. Soc. Hort. Sci.* 97:228–32.
50. Fann, Y. S., J. F. T. Davies, and D. R. Paterson. 1983. Correlative effects of bench chip budded 'Mirandy' roses. *J. Amer. Soc. Hort. Sci.* 108:180–83.
51. Fernandez, R. T., R. L. Perry, and D. C. Ferree. 1995. Root distribution patterns of nine apple rootstocks in two contrasting soil types. *J. Amer. Soc. Hort. Sci.* 120:6–13.
52. Flaishman, M. A., K. Loginovsky, S. Golobowich, and S. Lev-Yadun. 2008. *Arabidopsis thaliana* as a model system for graft union development in homografts and heterografts. *J. Plant Growth Regul.* 27:231–39.
53. Flemer, W., III. 1989. Why we must still bud and graft. *Comb. Proc. Intl. Plant Prop. Soc.* 39: 516–22.
54. Gardner, F. E., and G. H. Horanic. 1963. Cold tolerance and vigor of young citrus trees on various rootstocks. *Proc. Fla. State Hort. Soc.* 76:105–10.
55. Gascó, A., A. Nardini, F. Raimondo, E. Gortan, A. Motisi, M. A. Lo Gullo, and S. Salleo. 2007. Hydraulic kinetics of the graft union in different *Olea europaea* L. scion/rootstock combinations. *Environ. Exp. Bot.* 60:245–50.
56. Gebhardt, K., and H. Goldbach. 1988. Establishment, graft union characteristics and growth of *Prunus* micrografts. *Physiol. Plant.* 72:153–59.
57. Geneve, R. L., M. Mokhtari, and W. P. Hackett. 1991. Adventitious root initiation in reciprocally grafted leaf cuttings from the juvenile and mature phase of *Hedera helix* L. *J. Exp. Bot.* 42:65–9.
58. Goldsmith, M. H. A. 1982. A site responsible for polar transport of indole-3-acetic acid in sections of maize coleoptiles. *Planta* 155:68–75.
59. Graham, B. F., Jr., and F. H. Bornmann. 1966. Natural root grafts. *Bot. Rev.* 32:255–92.
60. Guengerich, H. W., and D. F. Milliken. 1965. Root grafting, a potential source of error in apple indexing. *Plant Dis. Rpt.* 49:39–41.
61. Gur, A., R. M. Samish, and E. Lifshitz. 1968. The role of the cyanogenic glycoside of the quince in the incompatibility between pear cultivars and quince rootstocks. *Hort. Res.* 8:113–34.
62. Heuser, C. W. 1984. Graft incompatibility in woody plants. *Comb. Proc. Intl. Plant Prop. Soc.* 34:407–12.
63. Heuser, C. W. 1987. Graft incompatibility: Effect of cyanogenic glycoside on almond and plum callus growth. *Comb. Proc. Intl. Plant Prop. Soc.* 37:91–7.
64. Hirst, P. M., and D. C. Ferree. 1995a. Rootstock effects on the flowering of 'Delicious' apple. I. Bud development. *J. Amer. Soc. Hort. Sci.* 120:1010–17.
65. Hirst, P. M., and D. C. Ferree. 1995b. Rootstock effects on the flowering of 'Delicious' apple. II. Nutritional effects with specific reference to phosphorus. *J. Amer. Soc. Hort. Sci.* 120:1018–24.
66. Hodgson, R. W. 1943. Some instances of scion domination in citrus. *Proc. Amer. Soc. Hort. Sci.* 43:131–38.
67. Honma, S. 1977. Grafting eggplants. *Scientia Hort.* 7:207–11.
68. Howard, B. H. 1993. Understanding vegetative propagation. *Comb. Proc. Intl. Plant Prop. Soc.* 43:157–62.
69. Hussein, I. A., and D. C. Slack. 1994. Fruit diameter and daily fruit growth rate of three apple cultivars on rootstock-scion combinations. *HortScience* 29:79–81.
70. Hussein, I. A., and M. J. McFarland. 1994. Rootstock-induced differences in sap flow of 'Granny Smith' apple. *HortScience* 29:1120–23.
71. Jayawickrama, K. J., J. B. Brett, and S. E. McKeand. 1991. Rootstock effects in grafted conifers: A review. *New Forests* 5:157–73.
72. Jeffree, C. E., and M. M. Yeoman. 1983. Development of intercellular connections between

opposing cells in a graft union. *New Phytol.* 93:491–509.

73. Jones, O. P. 1974. Xylem sap composition in apple trees: Effect of the graft union. *Ann. Bot.* 38:463–67.

74. Jones, O. P. 1976. Effect of dwarfing interstocks on xylem sap composition in apple trees: Effect on nitrogen, potassium, phosphorus, calcium and magnesium content. *Ann. Bot.* 40:1231–35.

75. Jones, O. P. 1986. Endogenous growth regulators and rootstock/scion interaction in apple and cherry trees. *Acta Hort.* 179:177–83.

76. Jones, O. P. 1989. Juvenile-like character of apple trees produced by grafting scions and rootstock produced by micropropagation. *J. Hort. Sci.* 64:395–401.

77. Jones, O. P., and C.A. Webster. 1993. Nursery performance of ‘Cox’ apple trees with rootstocks of M.9 from either micropagation or improved conventional propagation from micro-propagated plants. *J. Hort. Sci.* 68:763–66.

78. Kamboj, J. S., G. Browning, P. S. Blake, J. D. Quinlan, and D. A. Baker. 1999. GC-MS-SIM analysis of abscisic acid and indole-3-acetic acid in shoot bark of apple rootstocks. *Plant Growth Regul.* 28:21–7.

79. Kester, D. E., C. J. Hansen, and C. Panetsos. 1965. Effect of scion and interstock variety on incompatibility of almond on Marianna 2624 rootstock. *Proc. Amer. Soc. Hort. Sci.* 86:169–77.

80. Kollman, R., and C. Glockmann. 1991. Studies on graft unions. III. On the mechanism of secondary formation of plasmodesmata at the graft interface. *Protoplasma* 165:71–85.

81. Kollmann, R., S. Yang, and C. Glockmann. 1985. Studies on graft unions. II. Continuous and half plasmodesmata in different regions of the graft interface. *Protoplasma* 126:19–29.

82. Kubota, C., M. A. McClure, N. Kokalis-Burelle, M. G. Bausher, and E. N. Roskopf. 2008. Vegetable grafting: History, use, and current technology status in North America *HortScience* 43:1664–69.

83. Kudo, H., and T. Harada. 2007. A graft-transmissible RNA from tomato rootstock changes leaf morphology of potato scion. *HortScience* 42:225–26.

84. Langford, M. H., and J. C. H. T. Townsend, Jr.. 1954. Control of South American leaf blight of *Hevea* rubber trees. *Plant Dis. Rpt. Suppl.* p. 225.

85. Lee, J. M. 1994. Cultivation of grafted vegetables. I. Current status, grafting methods, and benefits. *HortScience* 29:235–39.

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

87. Lockard, R. G., and G. W. Schneider. 1981. Stock and scion growth relationships and the dwarfing mechanism in apple. *Hort. Rev.* 3:315–75.

88. Martin, G. C., and E. A. Stahly. 1967. Endogenous growth regulating factors in bark of EM IX and XVI apple trees. *Proc. Amer. Soc. Hort. Sci.* 91:31–8.

89. Maynard, B. K., and N. L. Bassuk. 1990. Comparisons of stock plant etiolation with traditional propagation methods. *Comb. Proc. Intl. Plant Prop. Soc.* 40:517–23.

90. McClintock, J. A. 1948. A study of uncongeniality between peaches as scions and the Marianna plum as a stock. *J. Agr. Res.* 77:253–60.

91. McCully, M. E. 1983. Structural aspects of graft development. In R. Moore, ed. *Vegetative compatibility responses in plants*. Waco, TX: Baylor Univ. Press.

92. McKenzie, D. W. 1961. Rootstock-scion interaction in apples with special reference to root anatomy. *J. Hort. Sci.* 36:40–7.

93. McQuilkin, W. E. 1950. Effects of some growth regulators and dressings on the healing of tree wounds. *J. Forest* 48:423–28.

94. Mendel, K. 1936. The anatomy and histology of the bud-union in citrus. *Palest. J. Bot.* 1:13–46.

95. Milbrath, J. A., and S. M. Zeller. 1945. Latent viruses in stone fruits. *Science* 101:114–15.

96. Miller, H., and J. R. Barnett. 1993. The structure and composition of beadlike projections on Sitka spruce callus cells formed during grafting and in culture. *Ann. Bot.* 72:441–48.

97. Miller, L., and F. W. Woods. 1965. Root grafting in loblolly pine. *Bot. Gaz.* 126:252–55.

98. Millner, M. E. 1932. Natural grafting in *Hedera helix*. *New Phytol.* 31:2–25.

99. Mircetich, S. M., and J. W. Hoy. 1981. Brownline of prune trees, a disease associated with tomato ringspot virus infection of myrobalan and peach rootstocks. *Phytopathology* 71:31–5.

100. Monzer, J., and R. Kollmann. 1986. Vascular connections in the heterograft *Lophophora williamsii* Coult. on *Trichocereus spachianus* Ricc. *J. Plant Physiol.* 123:359–72.

101. Moore, R., and D. B. Walker. 1981. Studies of vegetative compatibility-incompatibility in higher plants. I. A structural study of a compatible autograft in *Sedum telephoides* (Crassulaceae). II. A structural study of an incompatible heterograft between *Sedum telephoides* (Crassulaceae) and *Solanum penellii* (Solanaceae). *Amer. J. Bot.* 68:820–42.

102. Moore, R., and D. B. Walker. 1981. Studies of vegetative compatibility-incompatibility in higher

- plants. III. The involvement of acid phosphatase in the lethal cellular senescence associated with an incompatible heterograft. *Protoplasma* 109:317–34.
103. Moore, R., and D. B. Walker. 1981. Graft compatibility-incompatibility in plants. *BioScience* 31:389–91.
104. Moore, R. 1982. Studies of vegetative compatibility-incompatibility in higher plants. V. A morphometric analysis of the development of a compatible and an incompatible graft. *Can. J. Bot.* 60:2780–87.
105. Moore, R. 1982. Graft formation in *Kalanchoe blossfeldiana*. *J. Exp. Bot.* 33:533–40.
106. Moore, R. 1984. A model for graft compatibility-incompatibility in higher plants. *Amer. J. Bot.* 71:752–58.
107. Mosse, B. 1958. Further observations on growth and union structure of double-grafted pear on quince. *J. Hort. Sci.* 33:186–93.
108. Mosse, B., and M. V. Labern. 1960. The structure and development of vascular nodules in apple bud unions. *Ann. Bot.* 24:500–7.
109. Mosse, B. 1962. *Graft-incompatibility in fruit trees*. Tech. Comm. 28. East Malling, England: Comm. Bur. Hort. and Plant. Crops.
110. Mudge, K., J. Janick, S. Scofield, and E. E. Goldschmidt. 2009. A History of Grafting. *Hort. Rev.* 35:437–93.
111. Muzik, T. J. 1958. Role of parenchyma cells in graft union in vanilla orchid. *Science* 127:82.
112. Navarro, L., C. N. Roistacher, and T. Murashige. 1975. Improvement of shoot tip grafting in vitro for virus-free Citrus. *J. Amer. Soc. Hort. Sci.* 100:471–79.
113. Nelson, S.H. 1968. Incompatibility survey among horticultural plants. *Comb. Proc. Intl. Plant Prop. Soc.* 18:343–407.
114. Nickell, L. G. 1946. Heteroplastic grafts. *Science* 108:389.
115. Ohta, Y. 1991. Graft-transformation, the mechanism for graft-induced genetic changes in higher plants. *Euphytica* 55:91–9.
116. Olmstead, M. A., N. S. Lang, F. W. Ewers, and S. A. Owens. 2006. Xylem vessel anatomy of sweet cherries grafted onto dwarfing and nondwarfing and nondwarfing rootstocks. *J. Amer. Soc. Hort. Sci.* 131:577–85.
117. Palauqui, J. C., T. Elmayan, J. M. Pollien, and H. Vaucheret. 1997. Systemic acquired silencing: transgene-specific post-transcriptional silencing is transmitted by grafting from silenced stocks to non-silenced scions. *EMBO Journal* 6:4738–45.
118. Parkinson, M., and M. M. Yeoman. 1982. Graft formation in cultured explanted internodes. *New Phytol.* 91:711–19.
119. Pliego-Alfaro, E., and T. Murashige. 1987. Possible rejuvenation of adult avocado by graftage onto juvenile rootstocks in vitro. *HortScience* 22: 1231–24.
120. Porada, H. 1993. Timber species propagation. *Comb. Proc. Intl. Plant Prop. Soc.* 43: 80–5.
121. Preston, A. P. 1967. Apple rootstock studies: Fifteen years' results with some M.IX crosses. *J. Hort. Sci.* 42:41–50.
122. Proebsting, E. L. 1928. Further observations on structural defects of the graft union. *Bot. Gaz.* 86:82–92.
123. Rachow-Brandt, G., and R. Kollmann. 1992. Studies on graft unions. IV. Assimilate transport and sieve element restitution in homo- and heterografts. *J. Plant Physiol.* 139:579–83.
124. Ranney, T. G. 1994. Differential tolerance of eleven *Prunus* Taxa to root zone flooding. *J. Environ. Hort.* 12:138–41.
125. Ranney, T. G., and E. P. Whitman II. 1995. Growth and survival of 'Whitespire' Japanese birch grafted on rootstocks of five species of birch. *HortScience* 30:521–22.
126. Ranney, T. G., and R. E. Birr. 1994. Comparative flood tolerance of birch rootstocks. *J. Amer. Soc. Hort. Sci.* 119:43–8.
127. Ranney, T. G., N. L. Bassuk, and T. H. Whitlow. 1991. Influence of rootstock, scion, and water deficits on growth of 'Colt' and 'Meteor' cherry trees. *HortScience* 26:1204–7.
128. Rao, A. N. 1966. Developmental anatomy of natural grafts in *Ficus globosa*. *Aust. J. Bot.* 14:269–76.
129. Raulston, J. C. 1995. New concepts in improving ornamental plant adaptability with stress tolerant rootstocks. *Comb. Proc. Intl. Plant Prop. Soc.* 45:566–69.
130. Richards, D., W. K. Thompson, and R. P. Pharis. 1986. The influence of dwarfing interstocks on the distribution and metabolism of xylem-applied [³H] Gibberellin A₄ in apple. *Plant Physiol.* 82:1090–95.
131. Rivard, C. L., and F. J. Louws. 2008. Grafting to manage soilborne diseases in heirloom tomato production. *HortScience* 43:2104–11.
132. Roberts, A. N., and L. T. Blaney. 1967. Qualitative, quantitative, and positional aspects of interstock influence on growth and flowering of the apple. *Proc. Amer. Soc. Hort. Sci.* 91:39–50.
133. Robitaille, R. H., and R. F. Carlson. 1970. Graft union behavior of certain species of *Malus* and *Prunus*. *J. Amer. Soc. Hort. Sci.* 95:131–34.

134. Robitaille, R. H., and R. F. Carlson. 1971. Response of dwarfed apple trees to stem injections of gibberellic and abscisic acids. *HortScience* 6:539–40.
135. Robitaille, R. H., and R. F. Carlson. 1976. Gibberellic and abscisic acid-like substances in the regulation of apple shoot extension. *J. Amer. Soc. Hort. Sci.* 101:388–92.
136. Roupshael, Y., M. Cardarelli, and G. Colla. 2008. Yield, mineral composition, water relations and water-use efficiency of grafted mini-watermelon plants under drought irrigation. *HortScience* 43:730–36.
137. Ruiz, J. M., and L. Romero. 1999. Nitrogen efficiency and metabolism in grafted melon plants. *Scientia Hort.* 81:113–23.
138. Santamour, F. S., and M. V. Coggeshall. 1996. Cambial peroxidases as predictors of graft incompatibility in red oak. *J. Environ. Hort.* 14:154–57.
139. Santamour, F. S., Jr. 1979. Inheritance of wound compartmentalization in soft maples. *J. Arboricul.* 5:220–25.
140. Santamour, F. S., Jr., A. J. McArdle, and R. A. Jaynes. 1986. Cambial isoperoxidase patterns in *Castanea*. *J. Environ. Hort.* 4:14–6.
141. Santamour, F. S., Jr. 1988. Graft incompatibility related to cambial peroxidase isozymes in Chinese chestnut. *J. Environ. Hort.* 6:33–9.
142. Santamour, F. S., Jr. 1988. Graft compatibility in woody plants: An expanded perspective. *J. Environ. Hort.* 6:27–32.
143. Santamour, F. S., Jr. 1988. Cambial peroxidase enzymes related to graft incompatibility in red oak. *J. Environ. Hort.* 6:87–93.
144. Santamour, F. S., Jr. 1989. Cambial peroxidase enzymes related to graft incompatibility in red maple. *J. Environ. Hort.* 7:8–14.
145. Santamour, F. S., Jr. 1996. Potential causes of graft incompatibility. *Comb. Proc. Intl. Plant Prop. Soc.* 46:339–42.
146. Sass, J. E. 1932. Formation of callus knots on apple grafts as related to the histology of the graft union. *Bot. Gaz.* 94:365–80.
147. Sax, K., and A. Q. Dickson. 1956. Phloem polarity in bark regeneration. *J. Arn. Arb.* 37:173–79.
148. Schechter, I., D. C. Elfving, and J. T. A. Proctor. 1991. Apple tree canopy development and photosynthesis as affected by rootstock. *Can. J. Bot.* 69:295–300.
149. Schmid, P. P., and W. Feucht. 1981. Differentiation of sieve tubes in compatible and incompatible *Prunus* graftings. *Scientia Hort.* 15:349–54.
150. Shigo, L. A., and H. G. Marx. 1977. *Compartmentalization of decay in trees*, U.S.D.A.F. Ser., Editor. 1977.
151. Shigo, L. A. 1993. *100 Tree Myths*. Durham, NH: Shigo and Trees Assoc.
152. Shimomura, T., and K. Fuzihara. 1977. Physiological study of graft union formation in cactus. II. Role of auxin on vascular connection between stock and scion. *J. Japan. Soc. Hort. Sci.* 45:397–406.
153. Simmons, R. K., and M. C. Chu. 1984. Tissue development within the graft union as related to dwarfism in apple. *Acta Hort.* 146: 203–10.
154. Sitton, B. G. 1931. Vegetative propagation of the black walnut. *Mich. Agr. Exp. Sta. Tech. Bul.* 119.
155. Skene, D. S., H. R. Shepard, and B. H. Howard. 1983. Characteristic anatomy of union formation in T- and chip-budded fruit and ornamental trees. *J. Hort. Sci.* 58:295–99.
156. Soule, J. 1971. Anatomy of the bud union in mango (*Mangifera indica* L.). *J. Amer. Soc. Hort. Sci.* 96:380–83.
157. Soumelidou, K., N. H. Battey, P. John, and J. R. Barnett. 1994a. The anatomy of the developing bud union and its relationship to dwarfing in apple. *Ann. Bot.* 74:605–11.
158. Soumelidou, K., D. A. Morris, N. H. Battey, J. R. Barnett, and P. John. 1994b. Auxin transport capacity in relation to the dwarfing effect of apple rootstocks. *J. Hort. Sci.* 69:719–25.
159. Stoddard, F. L., and M. E. McCully. 1980. Effects of excision of stock and scion organs on the formation of the graft union in coleus: A histological study. *Bot. Gaz.* 141:401–2.
160. Strong, D., and A. Miller-Azarenko. 1991. Dry matter partitioning in ‘Starkspur supreme delicious’ on nine rootstocks. *Fruit Var. J.* 45:238–41.
161. Stutte, G. W., T. A. Baugher, S. P. Walter, D. W. Leach, D. M. Glenn, and T. J. Tworowski. 1994. Rootstock and training system affect dry-matter and carbohydrate distribution in ‘golden delicious’ apple trees. *J. Amer. Soc. Hort. Sci.* 119:492–97.
162. Syvertsen, J. P. 1985. Integration of water stress in fruit trees. *HortScience* 20:1039–43.
163. Thüin, A. 1821. *Monographie des greffes, ou description technique*. London.
164. Tiedemann, R. 1989. Graft union development and symplastic phloem contact in the heterograft *Cucumis sativus* on *Cucurbita ficifolia*. *J. Plant Physiol.* 134:427–40.
165. Tiedemann, R., and U. Carsens-Behrens. 1994. Influence of grafting on the phloem protein patterns in Cucurbitacea. I. additional phloem exudate

- proteins in *Cucumis sativus* grafted on two *Cucurbita* species. *J. Plant Physiol.* 143:189–94.
166. Torrey, J. G., D. E. Fosket, and P. K. Hepler. 1971. Xylem formation: A paradigm of cytodifferentiation in higher plants. *Amer. Sci.* 59:338–52.
167. Toxopeus, H. J. 1936. Stock-scion incompatibility in citrus and its cause. *J. Pom. and Hort. Sci.* 14:360–64.
168. Troncoso, A., J. Liñán, M. Cantos, M. M. Acebedo, and H. F. Rapoport. 1999. Feasibility and anatomical development of an *in vitro* olive cleft-graft. *J. Hort. Sci. Biotech.* 74:584–87.
169. Tydeman, H. M., and F. H. Alston. 1965. The influence of dwarfing rootstocks in shortening the juvenile phase of apple seedlings. *Ann. Rpt. E. Malling Res. Sta. for 1964.* pp. 97–8.
170. Vertrees, J. D. 1991. Understock for rare *Acer* species. *Comb. Proc. Intl. Plant Prop. Soc.* 41:272–75.
171. Vöchting, H. 1892. *Veber transplantation am pflanzenkörper.*
172. Wagner, D. F. 1969. *Ultrastructure of the bud graft union in Malus.* Ph.D. dissertation. 1969. Ames: Iowa State Univ.
173. Wang, Z. M., K. J. Patterson, K. S. Gould, and R. G. Lowe. 1994. Rootstock effects on budburst and flowering in kiwifruit. *Scientia Hort.* 57:187–99.
174. Wang, Z. M., K. S. Gould, and K. J. Patterson. 1994. Comparative root anatomy of five *Actinida* species in relation to rootstock effects on kiwifruit flowering. *Ann. Bot.* 73:403–14.
175. Wareing, P. F., C. E. A. Hanney, and J. Digby. 1964. The role of endogenous hormones in cambial activity and xylem differentiation. In M. H. Zimmerman, ed. *The formation of wood in forest trees.* New York: Academic Press.
176. Warmund, M. R., B. H. Barritt, J. M. Brown, K. L. Schaffer, and B. R. Jeong. 1993. Detection of vascular discontinuity in bud unions of 'Jonagold' apple on mark rootstock with magnetic resonance imaging. *J. Amer. Soc. Hort. Sci.* 118:92–6.
177. Webber, H. J. 1943. The "tristeza" disease of sour orange rootstock. *Proc. Amer. Soc. Hort. Sci.* 43:160–68.
178. Wells, R. B. 1986. A historical review of grafting techniques. *Comb. Proc. Intl. Plant Prop. Soc.* 35:96–101.
179. Westwood, M. N. 1993. *Temperate-zone pomology: Physiology and culture.* 3rd ed. Portland, OR: Timber Press.
180. Wildon, D. C., J. F. Thain, P. E. H. Minchin, I. R. Gubb, A. J. Riley, Y. D. Skipper, H. M. Doherty, P. J. O'Donnell, and D. J. Bowles. 1992. Electrical signalling and systemic proteinase inhibitor induction in the wounded plant. *Nature* 360:62–5.
181. Williamson, J. G., W. S. Castle, and K. E. Koch. 1992. Growth and ¹⁴C-photosynthate allocation in citrus nursery trees subjected to one or three bud-forcing methods. *J. Amer. Soc. Hort. Sci.* 117:37–40.
182. Williamson, J. G., and B. E. Maust. 1995. Growth of budded, containerized, citrus nursery plants when photosynthesis of rootstock shoots is limited. *HortScience* 30: 1363–5.
183. Wu, X., D. Weigel, and P.A. Wigge. 2006. Signaling in plants by intercellular RNA and protein movement. *Genes Dev.* 16:151–58.
184. Yadava, U. L., and D. F. Dayton. 1972. The relation of endogenous abscisic acid to the dwarfing capability of East Malling apple rootstocks. *J. Amer. Soc. Hort. Sci.* 97:701–5.
185. Yagishita, S., Y. Hirata, J. Okochi, K. Kimura, H. Miukami, and H. Ohashi. 1985. Characterization of graft-induced change in capsaicin contents of *Capsicum annuum* L. *Euphytica* 34:297–301.
186. Yates, I. E., and D. Sparks. 1992. Pecan cultivar conversion by grafting onto roots of 70-year-old trees. *HortScience* 27:3–7.
187. Yeager, A. F. 1944. Xylem formation from ring grafts. *Proc. Amer. Soc. Hort. Sci.* 44:221–22.
188. Yeoman, M. M., and R. Brown. 1976. Implications of the formation of the graft union for organization in the intact plant. *Ann. Bot.* 40: 1265–76.
189. Yeoman, M. M. 1984. Cellular recognition systems in grafting. *Encyclopedia of Plant Physiology.* Heidelberg: Springer-Verlag. pp. 453–72.