>> Compatibility / Incompatibility

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Compatibility is one of the four essential criteria for successful grafting, as described in the section on the requirements for successful grafting

A. Compatibility is defined as a sufficiently close genetic (taxonomic) relationship between stock and scion for a successful graft union to form, assuming that all other factors (technique, temperature, etc.) are satisfactory.

B. Incompatibility

1. Emphasizing the taxonomic limits, I define incompatibility as *failure (immediate or delayed) of a graft union to form due to insufficiently close genetic relationship between the stock and scion. It does not include failure of the graft due to poor technique, non-optimal environment, or disease introduced as a result of grafting.*

2. Emphasizing the physiological basis, Andrews and Marquez (1993) define incompatibility as *graft union failure due to "cellular physiological intolerance" caused by "metabolic, developmental and/or anatomical differences between stock and scion".*

3. Emphasizing the anatomical consequences, Mosse (1962) defines incompatibility as *"failure to form functional vascular connections between stock and scion"*

C. The Timing of Incompatibility

A distinction is often made between immediate and delayed incompatibility (Macdonald, 1986; Hartman, Kester, Davies, and Geneveve, 1998)

1. Immediate incompatibility - rapid death of the scion characterized anatomically by total lack of even the earliest events in union formation.

2. Delayed incompatibility - survival and more or less normal growth of the scion for months or even years.

a. Incomplete progression of normal graft union formation.

Early events in normal graft union formation may occur, up to and including callus formation, as described in the sequence of graft union formation presented in the section on Anatomy and Physiology of grafting union formation, without progression to the later stages. Sufficient translocation of water and nutrients across a callus bridge may keep the scion alive for some time, but the union is mechanically weak (lacking wood fibers).

b. Delayed decline of an originally normal graft union

Graft union formation may progress through the entire sequence of the graft union formation process -more or less normal formation of xylem, phloem and periderm (outer bark), before degeneration of the graft union occurs as much as years later. For example:

- Ornamental cherry - in this case a high worked pendulous cultivar of *Prunus subhirtella* grafted onto an arborescent stock gradually developed a swollen, cracked trunk at the stock/scion junction over several years.

c. The "delay" may be only in the appearance of incompatibility symptoms that have been progressing, unobserved, since shortly after the graft was performed.

- Red maple - This picture shows an extreme example of a long "delayed" incompatibility of a red maple cultivar, grafted onto (probably) a seedling of red maple. The tree performed normally in the landscape for 12 years before the trunk broke off at the stock/scion junction during a windstorm. Note that xylem formation across the graft union was apparently normal for the first few years since the center 1 inch diameter of the trunk is splintered (uneven), indicating that the xylem formed a continuous bridge between the stock and scion. From the perimeter of this narrow cylinder of wood, outwards, the stock scion junction is smooth, indicating that after the first few years xylem no longer formed across the stock/scion junction. Remarkably, this narrow central cylinder of interconnecting wood and the continuous bridge of bark (phloem, periderm) between stock and scion, was enough to hold the tree upright, and sustain active growth of the scion, for approximately the next 9 years. Equally remarkably, water and mineral nutrients flowed from stock to scion sufficiently well, during that period, to support the needs of the growing scion. Delayed compatibility is common in red maple, but rarely does it take more than 4 or 5 years to become apparent.

d. Virus associated delayed "incompatibility"

In a recent review on graft incompatibility, Andrews and Marquez (1993) point out that most reports of long delayed incompatibility have proven to be due to (virus) diseases such as black line of walnut, in which a virus present in a disease resistant scion may take years to migrate to a virus susceptible stock.

- Virus-associated incompatibility may play a role in incompatibility, due to differential susceptibly of the stock and scion genotypes to a particular virus (or phytoplasma).
- Although this is not a true genetic incompatibility, it is sometimes regarded as a type of incompatibility since it indicates genetic differences in virus susceptibility.
- Some examples of virus-associated graft incompatibility
    1. Black line of walnut
    2. Tristeza virus of citrus
    3. Apple Union Necrosis and Decline - Image and Description

D. Historical Perspective

- ### Understanding of compatibility / incompatibility

1. The genetic basis for incompatibility has been understood by some for nearly as long as grafting has been practiced, as suggested by the writings of the ancient Greek philosopher, Theophrastus (ca. 300 B.C.), "Like always coalesces readily with like, and the bud is, as it were, of the same variety."

2. Although Theophrastus had it right in ca. 300 BC, there has been considerable misunderstanding of the taxonomic limits of graft compatibility throughout history. This quotation from the Georgics (epic poem on agriculture) by the Roman poet Virgil, suggests that although he was quite knowledgeable about other aspects of grafting he must have been under the mistaken assumption that essentially any two taxa could be successfully grafted together. Ironically, not a single one of the combinations he lists here will form a successful graft union.

> "But the rough arbutus with walnut-fruit Is grafted; so have barren planes ere now Stout apples borne, with chestnut-flower the beech, The mountain ash with pear-bloom whitened o'er. And swine crunched acorns 'neath the boughs of elms." -- from the Georgics by Virgil, 29A.D.BIB)

3. Historical considerations are further discussed in the section on **Natural and Human history of grafting and budding**

E. Taxonomic Limits of Compatibility

1. A comprehensive survey of the taxonomic limits of graft compatibility has been published by Nelson (1968). A more recent compilation is presented in Andrews and Marquez (1993).

2. The hierarchy of plant taxa (degree of relatedness) of relevance to this discussion is as follows

Taxa	Example
Family	Rosaceae (Rose family)
Genus	*Malus* (the apple genus within the rose family)
species	*domestica* (the species of the domestic apple within the apple genus)
clone	Macintosh (clonal variety of apples)

3. The necessary degree-of-relatedness that constitutes a "sufficiently close genetic relationship…" for a particular stock / scion combination to be compatible varies among different taxa, as is can be seen in the Limits of Compatibility table.

a. As the degree of "unrelatedness" between stock and scion increases (intraclonal > interclonal / intraspecific > interspecific / intrageneric > intergeneric / intrafamilial), the probability of a given stock scion combination forming a successful graft union declines overall (across all genotypes), but it may be higher for some taxa than for others.

b. For each degree-of-relatedness there is at least one compatible and one incompatible example given in the table, although there are fewer and fewer cases of compatibility along the progression from left (more closely related) to right (less closely related).

4. Likelihood of graft compatibility at each taxonomic level

a. Intraclonal (within a clone)
In all cases a stock and scion from the same clone (intraclonal) will be compatible, since individuals of a clone are genetically identical, but there are few useful applications of intraclonal grafting except for repair of a girdled stem, as in the case of the use of a twig from the canopy of a tree for bridge grafting.

b. Interclonal (between clones) / intraspecific

Interclonal / intraspecific compatibility is the rule rather than the exception. An excellent example is the nearly universal intercompatibility among apple fruiting varieties (Macintosh, Red Delicious, etc.) and nearly all clonal apple rootstocks (East Malling series, Malling Merton series, etc.)

c. Interspecific / intrageneric

- Compatibility among species within a genus varies considerably with different types of plants. For example, nearly all interspecific grafts of different citrus species are compatible (e.g. sweet orange, *Citrus sinensis* on rough lemon, *C. jambhiri*), whereas only some, but by no means all, stone fruit species (genus *Prunus*) are compatible (e.g. almond (*Prunus amygdalus*) on peach, (*P. persica*) is compatible, whereas almond on apricot (*P. armeniaca*) is not.
- Interspecific compatibility may or may not exhibit reciprocity; i.e. the union is compatible regardless of which member is used as stock and which is used as scion. This is true for most compatible stock /scion combinations, but in a few cases the compatibility is not reciprocal. For example 'Myrobalan B' plum (*Prunus cersifera*) [scion] / 'Hales Early' peach *(P. persica*) [stock] is compatible, but the reciprocal combination, 'Hales Early' peach [scion] / 'Myrobalan' plum [stock] is not.

d. Intergeneric / intrafamilial

1. Broadly speaking, across all plant taxa, most intergeneric combinations within a given family are incompatible.
2. For example the major genera of conifers in the Pinaceae family including pine (*Pinus*) spruce (*Picea*), fir (*Abies*), and Douglas fir (*Pseudotsuga*) are all incompatible with each other.
3. In his discussion of graft compatibility among 15 genera of pome fruits in the Rosaceae family, Westwood (1993) lists only 5 incompatible combinations out of the 64 combinations tested. Twenty-nine intergeneric stock were classified as completely compatible, while the remained were classified as partially compatible.
4. Many cases of intergeneric graft incompatibility in the Rosaceae and in other families, are only "partial" in the sense that they may hold for only certain combinations of clones, or depend on the polar arrangement of the combination, or may exhibit compatibility for a limited period only.
    - Intergeneric compatibility may depend on which clones are involved. For example:

      Pyrus communis (pear) / *Cydonia oblonga* (quince)
      Quince is sometimes used as a dwarfing rootstock for pear, but only certain pear cultivars are directly compatible with quince. For example the pear cultivars Old Home, Anjou, Comice, Hardy, Gorham, Flemish Beauty and others are all compatible with quince, but the cultivars Bartlett, Bosc, Seckel, Winter Nelis, and others are not (Westwood, 1993).

      The incompatibility between Bartlett and other pear scions listed above, and quince stock, depends on direct contact between the two. Hence the insertion of a mutually compatible interstock between the two can result in a functional tree. For example, insertion of an Old Home interstock between the Bartlett scion and the quince rootstock is used to overcome the otherwise incompatible Bartlett / quince combination. Research on this system (Gur, et.al. 1968) has resulted in one of the better-understood examples of (one of) the physiological mechanisms of graft incompatibility, as will be discussed below.

- **Apparent intergeneric compatibility may decline over time (delayed incompatibility) or reduce the productive life of the grafted tree.**

1. *Syringa vulgaris* and French hybrids (Lilac) / *Ligustrum ovalifolium* (Privet)
Although the grafting of French hybrid lilacs (*Syringa*) onto privet (*Ligustrum*) understocks was common in the industry until fairly recently (before the increasing popularity of lilac micropropagation), it would be somewhat misleading to refer to *Syringa / Ligustrum* as a compatible combination. It is more accurate to describe it as a delayed incompatibility, which is taken advantage of to facilitate self rooting of lilac in a process called nurse root grafting. (Explained in more detail in the section on Reasons for Grafting and Budding.)

2. Apple / Pear
This combination is listed by Westwood (1993) as partially compatible, since it grows normally and productively for a number of years, but the combination does not remain productive as long as an apple variety grafted onto an apple rootstock.

e. Interfamilial

- Although there are a few reports of short-term graft union formation between distantly related (interfamilial) herbaceous species, there are no confirmed reports of interfamilial grafts between woody perennials.
- One extremely curious report of natural interfamilial graft compatibility which must be considered unconfirmed, and even unlikely, was the observation of La Rue (1934) that,

> **"Roots of *Betula lutea* [yellow birch, in the family Betulaceae] were found which were firmly united to roots of *Ulmus americana* [American elm in the family Ulmaceae]. There could be no question that a strong union was formed, for the roots could not be pulled apart. Some roots of *Betula lutea* appeared to be grafted with those of *Acer saccharinum* [sugar maple in the family Aceraceae], but since the roots were large, they could not be bent so as to determine whether the roots were merely grown around each other or really fused."**

F. Symptoms of incompatibility

1. Low % take

2. Clean break at the graft union.

- As described above, the 12 year old, extremely delayed, incompatible graft union between a red maple cultivar and a seedling of the same species exhibited a smooth surface at the point of separation between stock and scion, except the approx. 1 inch diameter central cylinder, which splintered. Apparently, stock and scion were compatible for the first few years after the graft was made, so that xylem (wood) bridged the gap only during that period. Later, after the delayed incompatibility set in, no further bridging xylem formed, so that smooth stock and scion surfaces were in contact but not anatomically joined, resulting in a "clean break" at the graft union
- This splintered, not smooth, break just below the graft union between an apple fruiting variety grafted onto an M9 rootstock, snapped off due to an excessively heavy fruit load. This was a result not of incompatibility but rather the short wood fiber cells typical of this dwarfing stock, which tend to make it "brittle".

3. Bulges exhibiting cracked and abnormal bark formation.

- This incompatible graft union between weeping cherry grafted high on a seedling rootstock shows a bulge with deep cracks at the graft union which eventually killed this tree.
- On the other hand, this decades old weeping American beech clone grafted onto a seedling rootstock exhibits a dramatic overgrowth, without the cracking, and the tree shows no sign of ill health. Apparently the overgrowth was due to an inherently higher growth rate in the former.

4. Differential termination or resumption of growth (early fall color; either stock or scion resumes growth in spring before the other) - i.e. the two parts are not growing synchronously.

5. Interruption of cambial and vascular continuity characterized by abnormal lignification, phloem degradation, failure of xylem fibers to interlock, and/or formation of a cork layer.

G. Causes of incompatibility

The cellular and biochemical causes of incompatibility are not well understood. The current state of understanding is summarized in recent review by Andrews and Marquez (1993).

1.Toxin production

So called "incompatibility toxins" are substances produced by either stock (or scion) that are toxic to and cause cellular injury to the other member, either directly or as a result of being chemically altered by the other member.

a. Incompatibility toxins are thought to be a common cause of incompatibility within the Rosaceae family including pear / quince and peach / almond.

b. The best studied example (Gur et al, 1968) is the incompatibility between pear grafted on quince rootstock; caused by a cyanogenic glucoside known as prunasin which is a natural component of the quince.

- Prunasin from the stock travels a short distance into the pear scion, where an enzyme known as glucosidase in the pear tissue catalyzes the hydrolysis of the -CN portion of prunasin, resulting in release of free CN (no longer attached to the prunasin molecule) into the pear tissue. Free CN is the well-known respiratory inhibitor, cyanide, which destroys xylem and phloem cells of the pear, near the scion stock interface, resulting in eventual death of the scion. Cellular damage is restricted to the scion / stock interface because prunasin is relatively immobile and does not travel far up into the scion.

- As described above not all pear varieties are incompatible with quince. Bartlett is incompatible, for example, while Old Home is not. Old Home manages to escape the cyanide toxicity because its cells produce an enzyme that detoxifies the prunasin before it can release cyanide.
- A very practical horticultural application of this differential sensitivity to prunasin, and the fact that it is poorly translocated, is that the incompatibility can be entirely avoided by grafting Old Home or other compatible pear variety as an interstock between the Bartlett or other incompatible pear scion and the quince rootstock. This is an example of doubleworking to avoid incompatibility. Doubleworking, for this and other purposes, is described in the section on Concepts and Definitions.

2. Abnormal Lignification

The greatest contributor to the strength of any graft union is the formation of a xylem bridge between scion and stock. It is the deposition of lignin in the secondary cell walls of xylem cells that gives xylem its woodiness. One theory for graft incompatibility proposed first by Santimore (1988) is that incompatible scion / stock combinations are incapable of normal lignification because of incompatible peroxidases, which are the enzymes that catalyze the process of lignification. There is limited and inconclusive evidence to support this explanation for incompatibility.

3.Other mechanisms that have been proposed to explain graft incompatibility include abnormal cellular "recognition" between stock and scion, and hormonal anomalies, but little evidence exists for either (Andrews and Marquez, 1993).

4. Virus

The role of virus in certain types of delayed incompatibilities is discussed above. Recall from the discussion above that viral induced graft failure is not really "incompatibility" in the strictest sense.

5. Perhaps a different approach to studying the question of the causes of incompatibility would be to better understand the nature of compatibility at the genetic, cellular, and molecular levels.

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