Graft Compatibility in Woody Plants: An Expanded Perspective[1]

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Abstract

Four thousand years of practice and research in grafting woody plants have not provided significant answers to questions about the causes of graft incompatibility nor allowed valid predictions to be made regarding potential incompatibilities between individual plants of most species of landscape trees. In this paper, the author briefly reviews some of the more recent research findings dealing with graft success and failure and discusses three areas of research that have heretofore not been adequately studied. These are (a) wound compartmentalization, (b) girdling, and (c) lignification.

Index words: wound compartmentalization, girdling, lignification, peroxidase enzymes

Introduction

If it is true that grafting of woody plants using detached scions began before 2000 B.C. (12), we have learned precious little in the last 4000 years. To be sure, there have been hundreds, perhaps thousands, of scientific investigations and ''success'' in grafting is attested to by the annual bounty of fruit and nut crops around the world. It is, however, reasonable to conclude that this 'success' has resulted more from 'trial and error' experimentation than from an understanding of the biological-biochemical-physiological processes involved in graft compatibility.

The 'trial and error' approach is, of course, quite scientific, and is favored by the protocols of orchard crop production, which are concerned with the propagation of relatively few plant genera and species that are planted in large, uniform blocks that facilitate, and indeed demand, continual observation and evaluation. In addition, a large body of knowledge has been acquired not only on the scion cultivars, but also on the rootstocks that have been chosen (and sometimes clonally propagated) for their site adaptability or effect on scion growth and development.

On the other hand, the grafting propagation of landscape trees could involve hundreds of genera and thousands of species. The reasons that few cultivars of landscape tree species are propagated by grafting (or budding) are both economic and biological. First, the only products of most landscape trees are leaves, and each tree has a low unit value (or at least a low, measurable financial value) to the grower.

Second, landscape trees are seldom so unique that the grower is restricted to a single genus, species, or cultivar. If a silver maple (*Acer saccharinom* L.) of seedling origin can perform a landscape function as well as a selected male cultivar of Kentucky coffee-tree (*Gymnocladus dioicus* (L.) K. Koch), there is little incentive to attempt, let alone experiment with, grafting propagation in *Gymnocladus*.

Third, there is little opportunity to profit by trial and error research since the grafted products of the nursery are sold to many different growers in different parts of the country. The trees are then planted, singly or in small groupings, on many different, and sometimes difficult, sites and the reasons for success or failure cannot be determined.

Lastly, there is no standardization of rootstocks for landscape trees, in contrast to fruit crops. Rootstocks for landscape tree species are almost always of seedling origin, and the geographic origin of these rootstocks varies from year to year and from nursery to nursery. Often, the rootstock of choice, or necessity, is not even the same species as the scion.

For the above reasons, commercial propagation by grafting of landscape trees has been limited to only a few species and cultivars. And, even with these few trees, there are unresolved problems of graft incompatibility.

There is some economic advantage to propagating landscape trees by grafting and budding in that the time required to produce a tree of a given height and caliper may be reduced by 1 to 3 years. I am fairly certain, however, that if oaks (*Quercus*) or ashes (*Fraxinus*) were as easy to propagate by the rooting of stem cuttings as most poplars (*Populus*) and willows (*Sallix*), grafting propagation would practically cease. It is also possible the ''new biotechnology'' of clonal propagation by tissue or meristem culture will obviate the need for grafting. Still, I am convinced that biotechnology will not solve all of our propagation problems, and that the ability to *predict* graft compatibility will allow us to 'build' superior composite grafted trees with better scions on better rootstocks (27).

Graft Incompatibility Defined

Many of the problems in understanding 'graft incompatibility' have arisen from our failure to define the term pre-

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cisely and to have that definition accepted by all investigators. Mosse (23) has written that 'the only certain criterion of incompatibility is the characteristic interruption in cambial and vascular continuity which leads to the spectacular smooth breaks at the point of union,' and further that 'at the point of union no normal vascular tissue develops. The gap thus formed is filled in by proliferating ray tissue which does not lignify normally.' Whether or not the above quotes are correct, the failure to reconstitute a structually sound and physiologically functional continuity of vascular tissues (both xylem and phloem) has to be the cornerstone of incompatibility in woody plants.

In the light of some past and some more recent findings, it should be added that any vascular discontinuity that is, in the narrow sense, 'graft incompatibility', should not include those cases where such discontinuity is caused or influenced by microorganisms present at the time of grafting or introduced subsequently. This addition is probably unrealistic, shince we know that bark and wood may contain indigenous internal bacteria and other microorganisms and that the grafting process allows access of external or airborne microorganisms into areas where they would not normally occur. However, certain cases of 'delayed incompatibility' have been shown to be associated with viruses.

Furthermore, some research on grafting of non-woody plants has largely discounted the restoration of vascular continuity as a major factor in narrow-sense graft compatibility.

Grafting in Non-Woody Plants

Over the past several years, there appears to have been a resurgence of interest in basic research to determine the causes of vegetative compatibilities and incompatibilities in plants. Practically all of this work has been done on herbaceous (non-woody) plants. The rationale for the avoidance of woody plants in this 'basic' work can be summed up in the statement of McCully (18) that 'If there are specific structural features resulting from inherent tissue incompatibility, these must be looked for at early stages, particularly in grafts of herbaceous plants.'

The major causes implicated in tissue or graft incompatibility differ among the leading researchers. Yeoman and his co-workers (42) at the University of Edinburgh have emphasized the involvement of a mutual cellular 'recognition' system. Moore (21, 22) has considered cellular necrosis at the graft interface as the most characteristic response of graft incompatibility, but has amended his ideas to suggest that the non-specific toxins produced by one graft partner need not cause cellular mortality in the other partner, but need only to make the callus cells of that partner unresponsive to biochemical stimuli that would promote the formation of a successful graft union. McCully (37) has sought to determine the sequence and importance of events that take place in compatible and incompatible grafts in *Coleus*. Although the other two researchers have largely downplayed Yeoman's 'recognition' phenomena as an essential component of the grafting process, Yeoman (42) did believe that vasular continuity was essential for a successful graft. Both McCully and Moore have, at one time or another, cited references of successful grafts having occurred in the absence of vascular continuity and suggested that such continuity is not necessary for 'compatibility'. The separation of grafting 'success' and grafting 'compatibility' is a moot point. There is obviously not the space here to review all of the nuances of grafting research with herbaceous plants, but it is certain that such work will produce significant changes in how the grafting process is viewed.

McCully (18) listed 7 structural events that occur in sequence in compatible grafts:

- Formation of a necrotic zone at the interface of cut cells;
- Extension of living cells from both stock and scion into this necrotic zone;
- Cell division to form callus;
- Cohesion (physical) of stock and scion;
- Differention of "wound"-type vascular elements;
- Differentiation of a vascular cambium from callus cells; and
- Production of secondary xylem and phloem by the reconstituted cambium.

Most of these events occurred independently, but none were considered unique to graft formation (37).

There may be no all-encompassing definition of graft incompatibility. There may be different types of incompatibility. Perhaps, different types of incompatibility could be correlated with different botanical groups of plants. However, the production of a successful, long-term, vegetative union between two different woody plants must involve the development of a functional system of water (and solute) movement in xylem and phloem.

'Delayed' Incompatibility

Some delayed incompatibilities have now been explained. The classic case of "blackline" in English walnut (*Juglans regia* L.) grafted on rootstocks of *J. hindsii* (Jeps.) Jeps. or the Paradox walnut (*J. hindsii* x *J. regia*) has been shown to be caused by a virus. Mircetich *et al.* (20) demonstrated that inoculation of a walnut isolate of cherry leafroll virus above graft unions produced typical blackline symptoms and postulated that the virus was spread from infected (but symptomless) English walnuts to healthy trees through pollination.

Somewhat similar situations have been described as apple union necrosis and decline (AUND) (6,38,39) and brownline of prune (19). In both cases, the virus proved to be a strain of tomato ringspot virus and it was transmitted by soil-borne nematodes. Graft unions appear to be sound until the virus has moved, either from the roots or the fruiting branches, to the zone of union. Then, apparently because of hypersensitivity and death of the scion cells (in apples and prunes) or stock cells (in walnut), no union can be maintained. This kind of delayed incompatibility is probably more common than we suspect at this time.

Cyanogenesis

The work of Gur (13,14) has shown a relationship between the graft incompatibilities of pear-quince and peach-almond combinations and the cyanide-caused death of cells of the non-cyanogenic (or lesser cyanogenic) species at the graft interface. However, the presence of cyanogenic glycosides in woody plants is restricted to relatively few genera, and this reaction cannot be considered as a universal cause of graft failure.

Some New Ideas

To say that anything is truly new, especially an idea, is probably a confession of ignorance of the past. However, under the above heading, I would like to present and discuss three sets of factors that may influence grafting 'success' or 'compatibility' and that, to my knowledge, have not been given the consideration they deserve.

Wound Compartmentalization

All grafting involves wounding of both stock and scion, ranging from complete sevarence of both members, to severance of the scion only (in budding), to mere removal of tissue in both members (in approach grafting). Even when one or both members is not severed in making the graft, the stock plant must be severed later in order to allow optimum growth of the scion. Woody plants respond to wounds that include exposing xylem tissue by the production of chemical compounds that are inhibitory to the growth or spread of microorganisms, thus 'walling off' the injury and preventing wood discoloration and decay. This process has been termed 'compartmentalization', and a model system, CODIT (Compartmentalization of Decay in Trees) has been developed (35). The potential for any given tree to successfully compartmentalize or wall off the cells killed by the initial injury is under moderate to strong genetic control (26,36).

Here I must interject that I have some problems with the CODIT model. In the first (35) and later papers (34), it is implied or stated that Walls 1,2, and 3 are present in the tree before wounding and that only Wall 4, the Wall formed by cambial activity to restrict decay development to wood present at the time of wounding, is a functional response of the wounded tree. Certainly, there are boundaries present in the tree. Boundary 1 can be visualized as the tops and bottoms of cells in a vertical sense, Boundary 2 as the annual rings, and Boundary 3 as the radial ray parenchyma. The fact is that a real Wall 2 containing altered cells with increased contents of inhibitory chemicals can be formed even in the middle of an annual ring. Because of the abundance of rays and the impossibility of having half a cell, it might be more difficult to demonstrate that new Walls 1 and Walls 3 are also not necessarily coincidental with the performed boundaries.

At any rate, trees do differ in their ability to produce new Walls and, using Wall 2 production as a basis for comparison, I have distinguished between strong and weak compartmentalizers. It is likely that genetically strong and weak compartmentalizers occur in every woody species possessing a complete cambium.

In studying the wound compartmentalization response of cultivars of many genera and species of trees, we found that all the cultivars were genetically strong compartmentalizers (30,31,32). It was hypothesisized that the cultivar propagation techniques of budding and grafting constituted an inadvertent selection screening for strong compartmentalization.

Furthermore, it is possible that weak compartmentalizing trees could not even be successfully grafted to themselves. Some cultivars of tree genera normally propagated from stem cuttings (e.g. *Populus*, rather than grafting, were weak compartmentalizers and some were strong.

Why is there an apparent correlation between strong Wall 2 compartmentalization response and grafting success? It may be that Wall 2 formation, *per se* is not a major factor in graftability. However, there is good evidence that the building of a strong Wall 2 is dependent on the availability of stored carbohydrates (usually starch) in xylem parenchyma cells. Perhaps, then, the correlation is based on the genetically controlled capacity of some trees to be more efficient in the storage or utilization of carbohydrates. There are, indeed, many localized biochemical, physiological, and anatomical differences between normal tissues and those formed after wounding (17). It might be that further study of these differences would provide data for a more complete understanding of graft compatibility.

Girdling

The stem of a woody plant is girdled when there is a disruption in the vertical continuity of phloem cells around the total circumference of the stem. Girdling can be accomplished by the removal of a ring of bark, including phellem, phloem, and cambial initials, from the tree. In partial girdles, a small area of intact and vertically continuous bark and phloem is not removed. Girdling or ringing are old techniques that have been used to promote flowering in fruit trees and to kill landscape trees, the result usually depending on the width of the girdled zone.

In any method of grafting that involves severance of both stock and scion, the resulting composite plant is, at least temporarily, totally girdled. The scion used in budding is also totally girdled. Other methods of grafting involve, at least, partial girdling of both graft members.

Noel (1970) has pointed out that various terms such as peeling, banding, ringing, barking, and girdling have been applied to various techniques that have been used to describe various practical or experimental techniques of phloem interruption. It is likely that the effects of such interruption will vary according to the width of phloem removed, the time of removal, and the degree to which xylem is injured in the girdling process. In this paper, I would consider girdling to apply to any event or process that breaks the continuity of phloem transport of materials down the stem.

The disruption of phloem continuity may have a profound effect on cell activity near the graft junction. Unfortunately, there have been no experiments that have dealt precisely with the problem of girdling in relation to grafting. Therefore, we must consider some of the more general effects of phloem disruption.

The following quote is taken from Evert *et al.* (9): ''Normal cambial activity in woody plants requires a continuous supply during the growing season of phloem-translocated products from the shoots (Kozlowski, 1971) (16). Thus, severing the phloem so as to prevent transport of carbohydrates and hormonal growth regulators to the lower stem greatly modifies production and maturation of xylem and phloem cells below the wound. The effects of phloem blockage on cambial growth vary with species and particularly with the time of treatment.''

Studies on trembling aspen (*Populus tremuloides* Michx.) and sugar maple (*Acer saccharum* Marsh.), both species that produce diffuse-porous wood, indicated that bark isolations made during the growing season (as might be typical in budding) led to the production of atypically short vessel and sieve-tube members, the curtailment of secondary wall formation, and the septation and maturation of cambial initials, and thus the elimination of a true cambium (8,9).

Initiation of cambial activity the following spring was prevented in about 50% of the treated trees. The effects of girdling on ring-porous trees could be quite similar, and Wareing (41) reported cessation of cambial activity in May as a result of "ringing" European ash (*Fraxinus excelsior* L.) in March.

The only point I want to make here is that, in grafting, the interruption of normal phloem activity can result in sometimes drastic alterations in cambial physiology (most pronounced below the interruption) and the subsequent continuity of the vascular system. The timing and size of such interruptions, the species of tree (especially with regard to xylem vessel type), the duration of the interruption, and undoubtedly many other factors will influence these effects.

Lignification and Enzymes

The statement by Buchloh (1) that a strongly lignified graft union was essential for graft compatibility and the proof (15) that peroxidase was the only enzyme involved in the polymerization of p-coumaryl alcohols to lignin provided the bases for our research, over the past decade, into the relation between cambial isoperoxidases and graft compatibility. Along the way, we have examined the isoperoxidase patterns of thousands of trees to provide baseline data. Some interesting sidelights (28, 29, 33) showed that isoperoxidase banding patterns were correlated with infrageneric taxonomic classes in *Acer* and *Quercus* and that no infrageneric classes were justified, from a genetics viewpoint, in *Castanea*. We also used isoperoxidase patterns to distinguish cultivars and verify interspecific hybrids. One of the major findings of a broad survey of cambial isoperoxidases in woody plants was that there was little or no variation among cultivars and populations in species which do not engender grafting problems for commercial nurserymen (e.g. honeylocust, Norway maple, sugar maple). On the other hand, when nurserymen did observe problems of graft compatibility in certain species, those species showed considerable intraspecifc variability in peroxidase isozyme banding patterns (e.g. red maple, Chinese chestnut, pin oak).

The following discussion provides the theoretical basis for a series of reports on graft compatibility in various genera that will appear in this Journal. To begin, we have to start with lignin. No one can write a complete chemical structure for lignin—any lignin. The lignin of spruce is different than the lignin of birch, and, if definitive analyses could be made, the lignins of two birches of the same parentage might be different. And we shall see that the lignins may vary within the same tree.

Lignin is the second most common organic compound in the world. It is the pesky stuff that has to be removed in order to obtain the relatively pure cellulose (the most common organic compound) that made the paper on which this article is printed. Cellulose absorbs water, swells and shrinks, and makes a reasonably good cell wall in annual plants. Linked and impregnated with lignin, the cell walls of woody plants are much more stable, and lignification allowed the development of large, perennial plants called trees.

Chemically, lignin is a polymer derived from dehydrogenation of three relatively simple alcohols: coniferyl alcohol, sinapyl alcohol, and p-coumaric alcohol. Lignins made primarily from coniferyl alcohol are termed guaiacyl lignins, those containing predominantly sinapyl alcohol are called syringyl lignins, and, when appreciable amounts of these two alcohols are involved, the product is syringyl-guiacyl lignin. The ratio of syringyl to guiacyl residues in lignin of this latter type may range from 1:4 to 2:1. There are probably always some p-hydroxyphenyl residues from p-coumaric alcohol in most lignins but they are only abundant in conifer compression wood.

Our thinking at the inception of the isozyme studies was, as inferred by Buchloh, that the "strength" of the graft union was somehow related to the deposition of lignin in secondary cell walls. This kind of reasoning required more of a quantum leap than we could justify. However, while it is true that the bulk of the lignin in wood does occur in secondary cell walls of fiber and vessel members in hardwoods and of tracheids in conifers, appreciable and important levels are also found in the middle lamella and in the cell corners.

The data in Table 1 illustrate several points. First, spruce (and most other conifers) produces only lignins of the guaiacyl type, whereas birch (and most other hardwoods) produce three types of lignin. Second, different types of lignin occur in different parts of the same cell in hardwoods. Third, the middle lamella (including primary wall and probably cell corners) of different cells in the same tree may contain different lignins.

Thus, it would follow that the middle lamellae in cells of trees that had different cambial isoperoxidase enzymes could contain structurally different lignins and perhaps different bonding between lignins and carbohydrates. If these different cells were contiguous to one another, as might be expected when derived from a cambium that arose from callus tissue at a graft union, the cells would probably still function in their genetically-proscribed biochemical mode. Then, if the lignin-producing and lignin-bonding systems of these adjacent cells interferred with the normal production of matching pits and primary pit fields, perforation plates of xylem vessel members, and sieve plates of sieve-tube members in the phloem, there could be a disruption of normal cell-to-cell connections and a breakdown in cell development. The foregoing is strictly an hypothesis to explain what we have observed: the inability of adjacent tissues of two individuals of the same species, differing only in cambial isoperoxidase patterns, to reconstitute a working vascular system. Unfortunately, there are no data on the variability of lignins in phloem cells, so we can only speculate on the vascular system in the xylem.

Aside from the work of Buchloh (1,2), there has been little attention given to the role of lignin production or lignification as a positive factor in graft success. Vance *et al.* (40) discussed lignification as a potential aspect of disease resistance and Romberger and Tabor (25) found that lignin-like substances were extruded from severed apical meristems. Deloïre and Hebant (7) reported that the deposition of lignin at the graft interface of tomato and pepper grafts was much higher in incompatible that in compatible unions. The techniques used to identify lignin in the above studies were not specific and precise localization of lignin deposition was not investigated. It is possible that what is being identified is 'garbage lignin' formed extracellularly as a result of wounding.

Deloire and Hebant (7) also noted increased peroxidase activity in incompatible grafts as compared to autografts and Lipetz (17) cited several references to increased peroxidase

Table 1. Distribution of Lignin in Black Spruce (*Picea mariana* (Mill.) B.S.P.) and Paper Birch (*Betula papyrifera* Marsh.) xylem.[z]

Cell	Region[y]	Lignin[x]	Tissue Vol.	Lignin	Lignin Conc.
			(%)	(%)	(%)
Picea					
Tracheid[w]	S	Gu	90	77	23
	ML	Gu	7	13	55
	CC	Gu	3	10	93
Betula					
Fiber	S	Sy	73	60	19
	ML	SyGu	5	9	85
	CC	SyGu	2	9	85
Vessel	S	Gu	8	9	27
	ML	Gu	1	2	42
Ray	CC	Sy	11	11	27

[z] From Fergus *et al.* (10) and Fergus and Goring (11).

[y] S = secondary wall, ML = middle lamella, CC = cell corner.

[x] Sy = syringyl lignin, SyGu = syringyl-guiacyl lignin, Gu = guaiacyl lignin.

[w] Data for early wood and latewood combined.

activity in tissues of herbaceous plants after wounding. We were not able to detect any significant increase in peroxidase activity in callus tissue formed after wounding in elm (*Ulmus*), maple (*Acer*), or oak (*Quercus*).

Perhaps the single study that most closely relates to our present hypothesis is that of Copes (5) on the conifer Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco. He stated that "The presence or absence of particular (isoperoxidase or isoesterase) bands had no relationship to whether a graft union would be compatible or incompatible." However, no data were provided on the quantitative or qualitative variation of these enzyme bands. Furthermore, Copes (5) used the increased activity (darker staining) of certain isoperoxidase and isoesterase bands at the graft union as indicators of graft incompatibility as deduced from anatomical studies. There was so much variability in the correlation between increased enzyme activity and anatomy, that the value of isozyme analysis appeared doubtful. For grafts made in 1974, for instance, the increased activity of one pair of isoperoxidase bands gave an 85% predictability of graft failure 5 months after grafting but "0" predictability at 7 months. Another isoperoxidase band pair gave "0" predictability at 7 months after grafting, but 100% at 10 months. One very interesting and potentially significant finding (3, 4) was that graft compatibility in Douglas-fir was apparently controlled by multiple genes with additive effects.

Significance to the Nursery Industry

Grafting and budding are not old-fashioned propagation practices that must yield to the 'brave new world' of biotechnology. Once the causes of graft incompatibilities and other graft failures are understood, it will not only be possible to achieve greater propagation success with woody plants that have long been grafted, but nurserymen will be able to expand their range of graft-propagated and selected cultivars into genera and species currently not grown. Being able to predict graft success will allow rootstocks and scions selected for different desirable characteristics to be joined into trees with superiorities that might not be possible by conventional breeding and selection procedures.

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