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Graft incompatibility in fruit crops: Causes, detection techniques and remedial measures

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ABSTRACT

Graft incompatibility is a major constraint in fruit tree propagation, especially among temperate species such as apple, pear, plum, apricot, and cherry. Graft incompatibility comprises inability of scion and stock to form a strong, functional, and lasting union, leading to weak growth, vascular discontinuity, nutritional imbalances, or eventual tree death. The causes are diverse, including anatomical mismatches, physiological and biochemical disturbances, nutrient deficiencies, viral infections, and genetic factors influencing secondary metabolism and lignification. Various techniques—such as electrophoresis, phenol profiling, X-ray tomography, molecular marker analysis, and histological studies—facilitate early detection of graft incompatibility. Recent advances in genomics and proteomics have provided molecular insights into compatibility mechanisms, offering new tools for rootstock breeding and selection to ensure long-term graft success in temperate fruit crops. Remedial measures include using compatible rootstock-scion or interstock combinations, hormonal and antioxidant treatments, optimized grafting conditions, and molecular breeding for compatibility traits. Understanding incompatibility mechanisms helps in producing healthy, long-lived fruit trees and supports efficient propagation and rootstock improvement programs in commercial horticulture.

Keywords: *Graft, stock, scion, genetic, propagation, horticulture.*

A. Introduction

Usually commercial fruit trees are composite plants comprising of a scion and a rootstock (graft/bud) to improve environmental adaptability so as to withstand various climatic and soil conditions, modify growth & vigour, control size and canopy architecture, improve yield and fruit quality, facilitate agricultural management, facilitates hybridization and breeding programs etc[1]. Graft incompatibility refers that two different plants joined by grafting/budding cannot form a proper, successful union. In horticulture, graft is used for a bud or shoot of plant positioned on the stem of another plant in such a way that composite plant grows successfully for its entire life span [2]. In real world, compatibility in grafting is hard to predict, however it is generally agreed that some sort of taxonomic closeness between the stock and scion is essential for a successful union [3]. As the taxonomic distance between the scion and stock increases, the likelihood of forming a successful graft union decreases [4]. Successful grafting depends on the natural biological relationship between the two plants. Closely related species usually graft easily and grow together as a single composite plant, whereas unrelated plants rarely form lasting unions. In fruit crops, probability of graft success follows this order: intraclonal > interclonal > intraspecific > interspecific > intrageneric > intergeneric > intrafamilial [5]. However, different plant groups vary in how closely related the stock and scion must be to achieve successful grafting [6]. As a result, graft compatibility is highly specific, and a single rootstock is not necessarily compatible with all commercial varieties of the same species. In some cases, stock and scion from unrelated species may initially unite, but symptoms of incompatibility can appear later, ultimately leading to plant death.

Graft incompatibility can result in weak or unhealthy plants, breakage at the graft union, early decline, failure of the graft combination, and the inability to form a strong, durable, and functional union [7].

B: Symptoms of graft incompatibility:

Graft incompatibility can be expressed through a range of symptoms that vary in nature, largely depending on the genotypes of the graft components involved [8]. Various findings have reported several symptoms associated with graft incompatibility across different fruit crops [2].

1. Failure to establish a successful graft or bud union in certain species, varieties, or clones.
2. Very poor or low graft success rates.
3. Graft union and growth may occur initially, but the plant dies later on in the nursery or in field.
4. Tissue degeneration at the graft union, leading to reduced vegetative growth and early leaf drop.
5. Noticeable imbalance in growth between the rootstock and scion.
6. Expression of nutrient deficiencies or physiological disorders.
7. Overall stunted growth and poor health of the grafted plant.
8. Progressive yellowing of foliage during the later stages of the growing season.
9. Development of abnormal swellings or outgrowths at, above, or below the graft union.
10. Excessive thickening at the graft union.
11. Clean and smooth breakage of graft components at the graft union.

C: Types of graft incompatibility: In temperate fruit crops, it can be categorized into five types;

1. Localized graft incompatibility: It refers to incompatibility reactions that are confined to the graft union and arise due to direct contact between the stock and scion. In this type of incompatibility, the graft union remains weak, resulting in discontinuity of the cambial and vascular tissues between the stock and scion [9]. Localized incompatibility can often be overcome by inserting a compatible interstock between the scion and stock, thereby separating the incompatible graft partners [3]. Because of the discontinuity in vascular tissues, the movement of water and metabolites across union is limited. Consequently, external symptoms develop gradually and their expression depends on the extent of anatomical mismatch at the graft junction [4]. Typically, masses of undifferentiated tissue are observed at the graft union, and in some cases, inclusion of bark tissue may occur. These abnormalities hinders normal establishment of vascular connections between the stock and scion [10]. This type of graft incompatibility is commonly observed in apple grafted onto pear and in plum grafted onto cherry. A well-known example is Bartlett pear grafted onto quince rootstock, which exhibits incompatibility [11]. However, Lal *et al* [12] reported that when a compatible interstock such as 'Old Home' pear is inserted, the graft combination becomes compatible, resulting in satisfactory tree growth.

2.Translocated graft incompatibility:
In translocated graft incompatibility, the incompatibility is due to some mobile or labile factor that can move across the graft union. In this type of incompatibility, degeneration of the phloem occurs, leading to the formation of a brown line and necrotic areas in the bark. These deformities limit the translocation of carbohydrates across the graft junction [9]. Due to this restricted movement of photosynthates, region above graft union accumulates these compounds whereas, drastic reduction below graft union is observed in terms of concentration of these compounds [3]. This form of incompatibility is distinguished by anatomical contortion at the graft-union interface, poor vascular connections, mechanical flaw, and eventual breakdown of the graft union at later stages of plant development [13]. A classic example is Hale's Early peach grafted onto Myrobalan B plum rootstock forms a weak union, noticeable by tissue distortion and starch build up at the base of the peach scion. When a compatible interstock such as Brompton plum is inserted between these two components, incompatibility still persists, with starch accumulating at the base of the Brompton interstock. However, when the same graft combinations are made at the cotyledonary stage, they displayed high compatibility, stipulating that the factors accountable for incompatibility are lacking during the juvenile or formative plant growth stages [3]. Similarly, the grafting Non Pareil almond on Mariana 2624 plum rootstock reveal complete phloem breakdown despite normal xylem development. In contrast, the Texas almond cultivar shows high compatibility when grafted onto Mariana 2624. Interestingly, when Texas almond is used as an interstock between Non Pareil almond and Mariana 2624 rootstock, bark disintegration occurs, resulting in an incompatible graft [2].

3. Pathogen induced graft incompatibility: A third category of graft incompatibility is pathogen-induced incompatibility, which is widespread and continues to be increasingly reported. In such reports, failure of a graft union is caused by pathogenic organisms, particularly viruses [14]. For instance, sweet orange budded onto sour orange was found to be incompatible in few regions, while the same combination was successful elsewhere. Detailed investigations revealed that this incompatibility was predominately due to viral infections. Compatibility reactions may also change over time. For example, the pear cultivar *Bristol Cross* grafted onto quince showed good growth in 1932; however, after about 30 years, the use of an interstock such as *Beurre Hardy* became necessary to maintain an acceptable graft union. Such changes in compatibility may result from genetic mutations or the presence of latent viruses. A well-known example of delayed, pathogen-induced incompatibility is black line disease in walnut.

4. Anatomical flaws: Apart from above mentioned types of graft incompatibility, sometimes failure to form successful graft can be due to anatomical differences between scion and stock. For example, a detailed reports on incompatible cherry grafts have shown reduced phloem differentiation and a lower number of well-developed phloem sieve tubes below the graft union, which has been attributed to insufficient levels of auxin, cytokinin, and carbohydrates thereby resulting in incompatibility [15]. Similarly, grafting apricot on plum rootstock results in callus formation but fails to differentiate into functional cambium and vascular tissues, ultimately resulting in a weak graft union [16].

5. Delayed incompatibility: Delayed incompatibility can develop between certain graft partners many years after grafting [17]. In such cases, the graft union may appear functional for a decade or more before ultimately failing. In maple grafting only part of the graft union forms properly. Over time, the increasing weight of the canopy combined with a strong wind causes the mature tree to break at the graft point. Delayed graft incompatibility has been documented in red maple, pear, several oak species, ash, and some conifers [2].

D: Causes of graft incompatibility
The mechanisms underlying specific types of graft failure are not fully understood. Till date numerous hypotheses have been proposed to explain this phenomenon however, the supporting evidence is often limited and sometimes contradictory [3]. Among the potential causes, structural, physiological, and biochemical factors, as well as the presence of diseases or insect pests—or a combination of these factors—may contribute to incompatible graft union (Table 1).

1. Structural or anatomical reasons
Histological investigations have revealed that certain abnormalities can develop at the graft union, although the stock and scion may appear structurally similar [4]. Excessive proliferation of parenchymatous cells at the union can obstruct the establishment of vascular continuity between the stock and scion, preventing proper connections of xylem and phloem tissues [10]. Sometimes formation of bark or necrotic layer at graft junction acts as a barrier and ultimately leading to graft incompatibility. Distortions in vascular tissues between the stock and scion have been reported in few grafts, sometimes due to the formation of whorls or loops and these abnormalities restrict the movement of water and various nutrients across the graft union, resulting in poor plant growth or graft failure [3]. In various temperate fruit species such as plum, pear, and peach,

graft incompatibility is primarily attributed to structural abnormalities. The development of undifferentiated tissues at the graft junction creates mechanical weakness, leading to phloem disintegration and uneven or poor growth of the grafted plant [11].

2. Biochemical and physiological reasons

Insufficient supply of the necessary components either by stock or scion may lead to incompatibility. An inadequate supply of essential components from either the stock or the scion can lead to failure of graft formation. Several studies have reported impaired water transport in incompatible graft combinations [3]. When proper phloem or xylem connections fail to develop at the graft union, the roots may become starved, ultimately causing wilting and death of the scion [2]. Gautier et al. [19] reported that in compatible unions, translocation of sugars from scion to stock is normal while as accumulation of assimilates in the scions of incompatible combinations. Santos-Pereira et al. [20] reported that when certain *Pyrus* cultivars are grafted onto *Cydonia oblonga* rootstocks, a cyanogenic compound commonly referred as prunasin which is present in quince but absent in pear—is translocated into the pear phloem. Pear tissues subsequently break down prunasin, producing hydrocyanic acid as a by-product. This toxic compound accumulates near the graft union, leading to tissue degradation, reduced cambial activity, and significant anatomical disruptions in the phloem and xylem. Consequently, the transport of water and other essential materials is severely restricted. Thus, the presence of toxic compounds can inhibit growth or even cause death of one of the graft partners. Similarly, Hayat et al [21] found that dwarfing effect of certain rootstocks on scion cultivars of various fruit crops is largely attributed to a limited supply of water and nutrients to the scion. Additionally, the formation of outgrowths at or above the graft union in dwarfing rootstocks further restricts the movement of water and nutrients to the canopy, resulting in reduced plant stature [22].

3. Nutritional reasons

Deficiencies of specific nutrients can also lead to graft incompatibility. Kumar et al [3] reported that grafting of 'Jonathan' apple cultivar onto EM-IX rootstock suffers from molybdenum deficiency thereby resulting in appearance of incompatibility symptoms. This is likely due to the limited ability of the EM-IX rootstock to absorb and supply sufficient molybdenum to the scion. In contrast, 'Jonathan' grafted onto other rootstocks does not exhibit these deficiency symptoms. Similarly, deficiencies of phosphorus, potassium, and magnesium have been reported in peach when grafted onto Myrobalan B plum rootstock, leading to the development of incompatibility symptoms [3].

4. Presence of viruses

The presence of latent viruses and mycoplasma-like pathogens can also lead to graft union failure. For instance, pear decline disease commonly occurs in 'Bartlett' pear trees grafted onto *Pyrus pyrifolia* rootstock due to viral infections at the graft union; however, this problem does not arise when *Pyrus communis* is used as the rootstock. In citrus, graft incompatibility reactions are largely associated with viral diseases such as tristeza, psorosis, and xyloporosis. In Punjab, the failure of rough lemon rootstock with many sweet orange cultivars has been attributed to viral bud-union disease. Similarly, black line disease of walnut, which represents a form of delayed graft incompatibility, is believed to result from viral infection rather than inherent rootstock failure.

5. Molecular and genetic reasons:

Graft incompatibility is also strongly influenced by the genetic relationship between the stock and scion. Genome-wide quantitative trait loci (QTL) mapping has been employed to explain the genetic basis of incompatibility among different genotypes. However, graft incompatibility phenotyping remains burdensome because large populations are required to achieve sufficient statistical power for meaningful analysis [23]. Alterations in the expression of genes involved in production of secondary metabolites play a significant role in graft incompatibility. In *Prunus* species, two phenylalanine ammonia-lyase (PAL) genes, *ParPAL1* and *ParPAL2*, have been shown to exhibit differential expression in incompatible graft combinations. Specifically, *ParPAL1* is more highly expressed at 10 and 21 days after grafting, while *ParPAL2* shows increased expression at 21 days after grafting compared with compatible combinations, leading to higher polyphenol accumulation in incompatible grafts [24]. Differences in PAL gene expression have also been observed in compatible and incompatible peach–plum grafts, providing a set of transcripts that signal the onset of graft incompatibility [25].Proteomic analyses have identified UDP-glucose pyrophosphorylase as a potential marker of graft compatibility in *Prunus* species. Molecular studies of new apricot cultivars grafted onto different *Prunus* rootstocks further suggest that *PAL1* expression can serve as an indicator of graft incompatibility [27]. Moreover, QTL mapping associated with graft incompatibility between widely used *Prunus* rootstocks and apricot cultivars has demonstrated that genetic mapping and QTL identification are valuable tools for understanding the genetic control of this trait. These QTLs represent important genomic resources for apricot breeding programs and support future efforts aimed at identifying candidate genes involved in graft incompatibility in apricot and other *Prunus* species [28].

Table 1: Type of graft incompatibility in various fruit species

Fruit plant	Type of incompatibility	Causes	Reference
Apple	Structural anomalies	Discontinuity in vascular tissue	Warmund *et al.* [29]
Apricot/plum	Structural anomalies	Feeble graft union formation	Errea*et al.* [30]
Cherries	Structural anomalies	Poor phloem development	Errea*et al.* [30]
Apricot/plum	Structural anomalies	Bark and wood discontinuity at union	Reig *et al* [31]
Apricot	Localized	Differential phenol content between tissues above and below union	Usenik *et al* [32]
Pear/quince	Localized	Limited lignification, disruption of vascular continuity, and interruption vascular cambium	Ciobotari *et al* [33]
Grapevine	Localized	Build up of phenolic compounds at union	Assuncao, *et al* [34]
Kiwifruit	Localized	Contrast in genetic affinity coefficients	Li *et al* [35]
Litchi	Localized	Lower superoxide dismutase, peroxidase, and polyphenol oxidase activities	Chen *et al* [36]
Olive	Localized	Problem in differentiation of cambium and vascular systems at graft interface	Azimi *et al* [37]
European and Japanese plums on peach-almond hybrids	Localized	Prune brown line disease symptoms	Reig *et al* [31]
Sweet cherry	Translocated	Peroxidase activity	Guclu and Koyuncu [15]
Peach/plum	Translocated	Phloem degeneration and carbohydrate remobilization limitation	Moing *et al* [38]
Pear	Pathogen-induced	Disruption of graft union by phytoplasma	Amri *et al* [25]
Citrus	Pathogen-induced	production of viral protein	Moreno *et al* [39]
Walnut	Pathogen-induced	Blackline and death of scion	Mircetich and Rowhani [40]
Apple	Pathogen-induced	Apple union necrosis and decline (AUND)	Stouffer and Uyemoto [41]

E: Techniques for determination of graft incompatibility

Early and reliable detection of graft incompatibility is very important, as it allows inappropriate graft combinations to be avoided while ensuring the selection of compatible stock–scion pairs [42]. Having prior knowledge of compatibility is especially necessary before the release and large-scale adoption of grafted fruit trees for commercial orchards, particularly when new cultivars or rootstocks are involved and their compatibility has not been thoroughly evaluated. In many cases, incompatibility symptoms may not become evident until several years after grafting, highlighting the need for predictive tools that can identify compatibility issues at an early stage. Studies have shown that certain enzymes participate in cellular processes during the initial stages of graft union formation in various species; however, their precise roles in the development of incompatibility are not yet fully understood [43]. Due to the complex nature of graft incompatibility, multiple approaches have been used to investigate its underlying mechanisms. These include *in vitro* studies of pear–quince grafts and callus cultures of different *Prunus* species, analyses of peroxidase activity and phenolic compound production in *Prunus* and pear–quince combinations, as well as the examination of cyanogenic glycosides in incompatible grafts [44, 45]. Several techniques have already been applied for the early diagnosis of graft incompatibility, such as *in vitro* screening methods [46], histological examinations [47], isozyme profiling [48], and phenolic compound analyses [45].

1. Electrophoresis

This approach offers a useful technique for the early assessment of graft compatibility between rootstock and scion. Santamour [49] demonstrated that isoenzyme profiling through electrophoresis can serve as a prognostic method for graft incompatibility in several fruit crops, even prior to grafting. His findings indicated that when the peroxidase isoenzyme patterns (enzymes involved in lignin formation through the polymerization of p-coumaryl alcohols) were similar in both stock and scion, successful and stable graft unions were formed [50]. Conversely, differences in peroxidase isoenzyme profiles between graft partners were associated with poor callus development at the graft interface, ultimately leading to graft failure.

Earlier studies in various fruit species further support the use of isoenzyme analysis, particularly of peroxidases, as well as comparisons of protein spectra between rootstock and scion, as reliable indicators for predicting intraspecific graft compatibility or incompatibility [48, 51]. Similarly, Lachaund [52] reported that evaluating the protein profiles of stock and scion can help forecast graft success, with greater similarity in protein patterns corresponding to a higher likelihood of successful graft union formation.

2. Phenol analysis

In several fruit crops, analysis of phenolic compounds has proven to be an effective tool for anticipating graft success or failure between rootstock and scion at an early stage. Both qualitative and quantitative variations in phenolic profiles between graft partners may indicate metabolic disturbances developing at the graft interface [30]. Studies have shown that elevated levels of catechin and epicatechin were present in quince cultivars known to be incompatible, even before visible symptoms of incompatibility became apparent [45]. Similarly, less compatible apricot graft combinations have been characterized by increased concentrations of flavanols, particularly catechin and epicatechin [30]. The buildup of catechin above the graft union has been suggested as a reliable biochemical indicator of graft incompatibility [45]. In general, higher phenolic content has been associated with the presence of smaller, poorly differentiated cells in incompatible graft combinations, which fail to establish a stable union [31]. Phenolic compounds can also influence plant hormone dynamics by modifying indole-3-acetic acid (IAA) oxidase activity [53] and disrupting IAA transport [54]. Consequently, phenolic profiling represents a practical and early diagnostic approach for predicting graft incompatibility, especially when evaluating newly developed cultivars and novel rootstock–scion combinations.

3. X-ray tomography

Beyond assessing xylem continuity at the graft junction, X-ray tomography approach has broad potential for evaluating graft success or failure well in advance. The technique enables detailed visualization of the three-dimensional structure of the graft union between the rootstock and scion.

To the best of current knowledge, the first report of 3D imaging of the graft interface and associated vascular connections was presented by Milien *et al* [55]. Such advanced imaging methods offer promising opportunities for improving graft quality assessment in woody plant species including fruit crops. Although graft incompatibility is relatively uncommon in grapevine, the success of grafting can vary considerably [56]. Following extensive testing and optimization of scanning conditions, this technique was applied to young grapevines exhibiting different levels of graft success to better understand how tissues and internal structures reorganize during graft formation. The three-dimensional characterization of the grapevine graft interface provides valuable insights and represents a novel tool for evaluating graft quality in woody plants. In addition, histological approaches combined with X-ray tomography can be employed to visualize the earliest stages of graft development, including the formation of plasmodesmata, organization of callus tissue, and programmed cell death (PCD) processes [27].

4.Other techniques

Additional approaches have been explored for the early identification of graft incompatibility. The development of molecular markers linked to compatibility traits would be particularly beneficial for rootstock breeding and selection programs [57]. Predictive insights into graft incompatibility can also be gained by studying metabolic and signaling pathways, including those related to the phenylpropanoid pathway, oxidative stress, and plant defense mechanisms, which reflect downstream gene expression responses [2]. Translocated incompatibility can be assessed using a SPAD chlorophyll meter, where reduced SPAD values may signal impaired carbohydrate transport resulting from an incompatible graft union [7]. Early evaluation of graft compatibility may also be achieved through the measurement of leaf chlorophyll levels and phenolic compound content [58]. Isozyme profiling represents another useful diagnostic tool; for example, in sweet cherry, variations in peroxidase isozyme activity have shown a strong correlation with graft compatibility and may help predict delayed incompatibility [15]. Advanced imaging techniques have also been applied to study graft unions. Magnetic resonance imaging (MRI) has been used to visualize internal incompatibility-related features [16], while scanning electron microscopy (SEM) can reveal anatomical and histological changes during graft union formation [11]. Chlorophyll fluorescence imaging enables detection of incompatibility at very early stages following grafting [11]. *In vitro* techniques, such as micrografting, callus grafting, and other tissue culture-based methods, are valuable for screening graft combinations for compatibility [23]. Furthermore, emerging tools including proteomic analyses, molecular marker development, and gene expression profiling linked to specific metabolites are increasingly being used to improve early prediction of graft incompatibility [4].

F: Remedial measures to overcome graft incompatibility in fruit crops

There are several remedial strategies to mitigate or minimize graft incompitability between scion and rootstock. These measures aim to ensure successful union formation, sustained vascular connection, and long-term tree performance.

1.Compatible rootstock-scion combination

Using compatible rootstock and scion during grafting/budding is one of the basic strategies to avoid graft incompatibility caused by either biochemical, physiological or genetical causes [59]. During grafting closely related species with similar genetic background should be given priority. Using anatomical and biochemical assays, preliminary compatibility testing should be conducted before going for large scale grafting [60]. In stone fruits, peach and almond hybrids like GF 677 exhibit better compatibility with peach scions.

2.Hormonal and biochemical regulation

Various findings report that application of certain growth regulators at graft union can overcome graft incompatibility by stimulating rapid callus formation and vascular connection. Auxins and cytokinin application has been reported to stimulate better vascular connection between stock and scion [43]. Certain antioxidants like polyamines, ascorbic acid reduce oxidative stress thereby preventing graft failure [61]. Pre-treatment of scion and stock with activated charcoal and thidiazuron prevent phenolic compound accumulation during grafting thereby prevent tissue necrosis at the union which is believed to be main culprit for graft incompatibility.

3. Employing compatible interstock

This method maintains dwarfing effect of rootstock apart from compatibility between the incompatible scion and stock [3]. In apple certain Malling Merton interstockslike MM.106 has been reported to overcome incompatibility between incompatible scion and stock [21]. Similarly, In pear (*Pyrus communis*) on quince (*Cydonia oblonga*), cultivars like 'Old Home' or 'Beurré Hardy' serve as compatible interstocks [62].

4. Genetic and molecular approaches

Using these advanced techniques, screening and breeding of compatible gentotypes within species and genera has become possible. Molecular markers like SSR, SNPs, RAPD, RFLP etc have been used extensively to identify compatibility linked genes in various fruit crops [63]. Certain novel non-conventional approaches like genetic engineering and gene cloning has been used to develop transgenic rootstocks and scions producing less phenolic compounds or improved hormone balance so as to overcome incompatibility by preventing phenolic oxidation, tissue necrosis and by stimulating rapid callus formation and vascular connection [64].

5. Environmental and cultural management

Temperature, humidity and grafting time has a significant effect on union success therefore optimizing grafting temperature (23-25^{0}C) and humidity (>80%) favours rapid callus bridge formation [65]. Water stress and unbalanced nutrition results in weak vascular development and connection thereby graft failure. Adequate boron and calcium is considered as a pre-requisite for strong vascular development. Avoiding mechanical stress or desiccation at the union by proper wrapping and sealing with grafting wax or paraffin has been reported to overcome incompatibility [3].

6. Nursery and post-graft management

Proper grafting procedures, use of young, healthy and disease/virusfree scion and stock results in better alignments of cambial layers which is turn produces good vascular connections [66]. Care should be taken to transplant only those plants in main field which have formed strong graft union with no swelling and cracking or any delayed incompatibility symptoms [5]. Monitoring and individual care to every plant in the nursery in the basic method to detect any symptoms of graft incompatibility [10].

7. Alterative vegetative propagation method

Apart from grafting and budding, there are other vegetative propagation techniques like layering, cutting or micropropagation which results in true to type genotypes [67]. When graft incompatibility is persistent, it is better to use these methods for clonal multiplication, especially in species like walnut or persimmon where grafting success is low.

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