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Graft compatibility-incompatibility in fruit crops: Mechanism and determination techniques

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ABSTRACT : Commercial fruit trees are usually formed by the combination of a rootstock and a scion to broaden the adaptability of scion cultivars to soil and climatic conditions, facilitate agricultural management, and/or increase productivity. In general, closely related cultivars and species tend to be compatible, but taxonomically distant plants often manifest incompatibility. The physiological, metabolic and molecular mechanisms that cause incompatibility remain unclear and several hypotheses have been proposed to explain it, mostly based on herbaceous species. We sum up different reasons that may have an influence on graft success: inherent system of cellular incompatibility, formation of plasmodesmata, vascular tissue connections, and the presence of growth regulators and peroxidases. Understanding the spatial organization of the graft interface is important to the evaluation of new rootstock genotypes and to the development of new grafting technologies. An early and accurate prediction of graft incompatibility has great importance because incompatible combinations could be avoided while compatible ones could be selected. The complexity of incompatibility and the mechanism behind the reactions have been investigated in several ways. More research is needed to fully understand the mechanism of graft incompatibility, particularly in woody plants. This knowledge is essential to develop molecular markers useful in rootstock breeding programmes.

KEY WORDS : Graft compatibility/incompatibility, Callus, Plasmodesmata, Electrophorosis, X-ray tomography, Phenol

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Modern fruit growing makes extensive use of selected rootstocks for a wide variety of purposes, including vigour control/imparts, which enables high density planting, disease and pest tolerance/resistance, resistance/tolerance to abiotic stresses like drought/salt, reduces time to fruit, increase profit returns, improves fruit quality and yield, improves cold hardiness, cope with the chilling requirement of the scion, and/or to nematode problems. In addition, modern cultural methods are evolving towards the use of clonal rootstocks as opposed to seeding rootstocks that were commonly used in the past. The role of rootstocks is the result of active rootstock/scion interactions, most of which are the result of complex processes occurring at the rootstock/scion union.

The most important interactions are compatibility or incompatibility between rootstocks and scion. There is rootstock/scion compatibility when a given combination is able to form a solid and durable graft union. Compatibility is difficult to predict, but there is a general consensus that a degree of taxonomic relatedness should exist in order for a particular stock/scion combination to be compatible. The greater the taxonomic distance between stock and scion the smaller the chances of forming a successful graft union. This means that the theoretical success of a particular graft union combination is intraclonal > interclonal > intraspecific > interspecific > intrageneric > intergeneric > intrafamilial (Andrews and Marquez, 1993). Also, different taxa may differ in the degree of relatedness required for the formation of successful graft unions (Rom and Carlson, 1987). Therefore, compatibility is very specific, meaning that a particular rootstock is generally not compatible with all commercial varieties of a given species.

In modern horticulture this is a limiting factor, particularly in peach and cherry where there is a lack of commercial rootstocks having broad compatibility (Zarrouk *et al*., 2006). Rootstock/scion graft compatibility is, therefore, a critical issue for orchard performance and longevity. To remain functional, the stock/scion union should unify intimately, providing a viable system for the uptake and translocation of minerals, water, assimilates and hormones throughout the entire lifespan of the plant (Martinez-Ballesta *et al*., 2010; Gregory *et al*., 2013 and Koepke and Dhingra, 2013). In contrast, graft "incompatibility" leads to unhealthy trees, breakage at the graft union, premature death or failure of the graft combination and incapacity to form a strong and lasting functional union (Zarrouk *et al*., 2006).

Two types of incompatibility are recognized: so called translocated graft incompatibility and localized graft incompatibility. The former is usually expressed during the first year after grafting as growth cessation, defoliation, and leaf discoloration (Herrero, 1951 and Mosse, 1962). In peach/plum combinations, this form of incompatibility has been associated with both biochemical and functional alterations at the graft interface, inducing a carbohydrate blockage at the scion, above the graft union (Moing *et al*., 1990). In the latter case, incompatibility symptoms occur where the presence of some biochemical alterations across the graft union may lead to a slight and delayed incompatibility, it has been described in cherry and peach/plum combinations (Treutter and Feucht, 1991; Salesses and Bonnet, 1992). This type of incompatibility is characterized by anatomical irregularities at the stock/scion union interface, with breaks in vascular and cambial continuity patterns and poor vascular connections that induce mechanical weakness in the union (Koepke and Dhingra, 2013) that may break out after years of orchard establishment, leading to major economic losses.

Callus formation: a common response to wounding:

The formation of callus tissue at the graft interface is the first response to grafting. Whereas, it has been found that grafting failure can be characterized by a lack of callus formation at the graft interface, the new callus formed is a passive event that occurs in compatible and incompatible grafts and is also supported by the fact that callus formation is independent event in graft development. Once the callus has formed, the events that follow this initial formation seem to be essential for the critical event deciding the development of future vascular connections. Yeoman was the first to document structural events correlated with the changes in cell walls occurring during graft formation in Solanacea describing a cell recognition mechanism in which opposing cells of graft partners touch (Yeoman, 1984). The basis of this recognition system is that protein molecules released from the plasmalemmas combine to form a complex with catalytic activity that subsequently initiates a developmental sequence resulting in the formation of a successful graft union. Neither the nature of these proteins nor their roles have been describes up to date. When this complex is not formed, due to differences between the cells in contact, a special kind of protein called lectin, produces a mutual rejection of the opposing graft cells leading to the formation of incompatible grafts (Yeoman and Brown, 1976).

The formation of callus tissue implies some of the compounds in the mechanism of adhesion of the graft partners. Wart-like projections on the cell wall surface have been reported in callus cells at the graft union (Jefree and Yeoman, 1983; Barnett and Weatherhead, 1988). The beadlike projections from the callus that consist of a homogeneous matrix made up of a mixture of pectin, carbohydrate, protein and fatty acids, and a fibril/vesicular component comprised mainly by carbohydrate and pectins (Miller and Barnett, 1993). These beadlike projections, besides acting as binding or cementing cells, may serve a more active role in cell recognition and in successful merging of tissues of the graft partners.

In incompatible grafts, the failure of procambial development may be the result of the absence of an additional and more direct form of cellular communication between the graft partners. The cell wall polymers proposed for cellular recognition reaction are abundant in the graft union. These would be pectic fragments considered as chemical messengers in the determination of graft compatibility (Jefree and Yeoman, 1983). The cell wall derived oligosaccharides are capable of modulating plant growth and development (Ridley *et al*., 2001 and Creelman and Mullet, 1997).

Plasmodesmata and its role in cellular communication :

Plasmodesmata are diverse and highly dynamic structures that offer a unique pathway for symplastic cell communication and constitute a potential pathway among cells in the graft bridge. Studies on the mechanism of plasmodesmata have shown their important role in the mechanism of cellular communications (Lucas *et al*., 1993 and Schulz, 1999) being subject to discussion the occurrence of symplastic connections in grafts for a long time. As Jefree and Yeoman (1983) defined, when callus cells come into contact, the cell walls undergo dissolution, holes in the cell walls appear, plasmalemma contact and plasmodesmata form. The mechanism of plasmodesmata formation has shown prominent differences in the development of interspecific plasmodesmata between graft partners suggesting that cell recognition and functional co-ordination may be involved in graft formation (Kollmann and Glockmann, 1985 and Kollmann *et al*., 1985).

If the insufficient co-ordination between adjacent cells leads to the formation of mismatching, half plasmodesmata through the cell wall only in one cell partner. In graft interfaces of incompatible heterografts, discontinuous and half plasmodesmata have been observed in the graft unions between different types of cells, using species-specific cell markers in order to identify the graft interface (Kollmann *et al*., 1985). It indicate that plasmodesmata may contribute to graft failure due to a misalignment of the graft partners, although they may not be unique to graft compatibility.

In apricot (*Prunus armeniaca*) on plum grafts, the formation of new vascular connections occurs in both compatible and incompatible combinations (Errea *et al*., 1994b). The transport of disodium fluorescein across the graft union confirms the communication and functionality of these connections since fluorescence can be seen in both the partners of graft. In these combinations, the difference between compatible and incompatible grafts lies in the presence of a portion of the callus tissue in incompatible grafts that cannot differentiate into cambium and vascular tissue, resulting in the existence of wide areas at the union similar to undifferentiated callus cells. This lack of cambial activity in some areas of the graft union could affect the activity of the new xylem and phloem formed, causing discontinuities in the cambiumGraft compatibility-incompatibility in fruit crops: Mechanism and determination techniques and the formation of a parenchymatous line interrupting the vascular connection (Hartmann *et al*., 2002), producing a mechanically weak union.

Effect of growth regulators in compatibility and incompatibility :

In addition, the relationships between scion and stock are affected by growth regulators, and it has been postulated that graft incompatibility may also exist. For example, an important substance involved in the development of compatible unions is auxin, which is released from vascular strands of the stock and the scion and induces the differentiation of vascular tissues, functioning as morphogenic substances (Aloni, 1987 and Mattsson *et al*., 2003). Its translocation from the root system has been studied in apples and has been related to graft incompatibility, since a supra and basipetal movement of auxin can organize the morphogenetic pattern of the entire plant body (Zajaczowski *et al*., 1983), even accelerating the formation of a successful graft (Shimomura and Fujihara, 1977). Additionally, other compounds, like polyphenols also play a prominent role in graft union formation by influencing lignification processes and by their protein-precipitating feature. It has been proposed that stress situations can lead to both the accumulation of flavanols and their degradation by oxidases (Van Sumere *et al*., 1985), which can bring about marked effects on the growth and metabolism of tissues such as an inhibition of the lignin pathway (Buchloh, 1960). Some papers also report that observation on the characterization of monomeric and oligomeric flavan-3-ols in apricot cultivars and rootstocks (Errea *et al*., 1994a) and their accumulation in apricot combinations with a different degree of compatibility (Errea *et al*., 1992 and 2000). Synthesis of flavanones can determine incompatibility in *Prunus*, such as prunasin and can be stimulated by ABA and GA (Treutter and Feucht, 1988).

Endogenous plant hormones are thought to be involved in regulating the complex relationships between rootstock and scion (Aloni *et al*., 2010 and Koepke and Dhingra, 2013). In vascular regeneration experiments, when auxins were applied exogenously to stem segments, low concentrations (0.1% w/w) of indole-3-acetic acid

(IAA) stimulated phloem differentiation, whereas higher levels (1.0% w/w) induced xylem differentiation (Aloni, 2010). Auxin translocation from the scion to the stock was found to accelerate the development of a successful graft union in Cactus (Shimomura and Fujihara, 1977).

The involvement of auxin in the incompatibility mechanism emerged from three additional observations: (i) endogenous IAA analysis revealed that the roots and stems of incompatible combinations contained higher IAA concentrations than the same tissues of compatible ones; (ii) application of the auxin transport inhibitor, 2,3,5-tri-iodobenzoic acid, to the stems of grafted plants negated root degradation in incompatible combinations, whereas it had only slight effect on compatible graft combinations; and (iii) root and shoot development of incompatible grafts was normal after blocking basipetal IAA transport by partial stem girdling (Aloni *et al*., 2008). These results support the hypothesis that auxin produced in the scion is translocated downwards to the root after the graft connection is established, where, after reaching a threshold concentration, auxin triggers degradative processes causing root decay (Aloni, 2010 and Aloni *et al*., 2010).

Determination techniques:

An early and accurate prediction of graft incompatibility has great importance because incompatible combinations could be avoided while compatible ones could be selected (Petkou *et al*., 2004). The involvement of certain enzymes in the cellular behavior during the first steps of graft formation has been studied in different species; although the specific role and effects on incompatibility is still not clear (Pina and Errea, 2005). The complexity of incompatibility and the mechanism behind the reactions have been investigated in several ways: *in vitro* pear and quince combinations (Moore, 1984), or between callus cultures of many different Prunus species, peroxidase activity and the production of phenolic compounds in Prunus (Rodrigues *et al*., 2001) and in pear-quince graftings (Musacchi *et al*., 2000) and the analysis of cyanogenic glycosides in some incompatible combinations. Different methods for an early detection of graft incompatibility have already been used, like *in vitro* techniques (Errea *et al*., 2001), histological studies (Ermel *et al*., 1995 and 1999), isozyme analyses (Fernandez-Garcia *et al*., 2004 and Gulen *et al*., 2002) and phenol analyses (Musacchi *et al*., 2000).

Electrophorosis method:

Isoforms of enzymes separated by electrophoresis were one of the earliest *in vitro* methods used for the prediction of graft incompatibility. Santamour *et al*. (1986) reported that isoenzyme analysis of scions and rootstocks could be used to predict incompatibility before grafting in different cultivars. They stated that when stock and 'scions' phenotype of peroxidase isoenzyme, the enzyme responsible for the polymerization of p-coumaryl alcohols to lignin (Quiroga *et al*., 2000), matched, grafting resulted in a compatible union. In contrast, if isoenzyme phenotypes of graft partners were different, callus formation was impaired at the graft union (Santamour, 1988 a and b). Past research with other plant species showed that analysis of isoenzymes, especially peroxidases, and protein spectra between rootstock and scion before grafting could be used to predict intraspecific compatibility or incompatibility (Gulen *et al*., 2002; Fernandez-Garcia *et al*., 2004 and Pedersen, 2006).

Lachaund (1975) suggested that incompatibility could be avoided, to a certain extent, where similarity of protein composition between the partners would increase the probability of graft success. The comparison of protein profiles of graft combinations to predict graft incompatibility using SDS-PAGE was studied in Prunus species (Huang *et al*., 1984; Schmid and Feucht, 1985) and in *V. vinifera* (Masa, 1985, 1986 and 1989). Poessel *et al*. (2006) showed by using proteome analysis of 2D-PAGE analysis that some constituent proteins of leaves could be good candidates as compatibility markers. Researchers should keep in mind that grapes do not show immediate incompatibility, a situation more encountered between any other woody fruit crops such as pear and quince, and that grafting incompatibility between grapevine rootstock and scions may have resulted from virus at the graft union or even *Agrobacterium* infected material (May, 1994 and Creasap *et al*., 2004) or from a viral agent in the scion (Uyemoto and Rowhani, 2003).

Phenol analysis:

The grafted partners often belong to the same species or genus but the use of genetically divergent genotypes is also common. In apricot (*Prunus armeniaca*) when is grafted on other *Prunus species* (especially in inter-specific combinations), like peach (Lapins, 1959), plum and peach x almond (Cambra, 1986) graft incompatibility frequently occurs (Errea *et al*., 2001). The presence of phenols was generally associated with small cells in incompatible combinations, which did not form successful unions (Errea *et al*., 2001). The activity of IAA oxidase (Aloni, 1997) and transport of IAA transport (Stenlid, 1976) can be altered by naturally occuring substances such as phenols. Quantitative and qualitative differences in the phenol pattern between two graft partners can imply metabolic disfunctions at the graft union (Errea, 1998). Higher concentrations of catechin and epicatechin were found in the quince-incompatible cultivars before the appearance of visible incompatibility symptoms (Musacchi *et al*., 2000). In less compatible apricot combination higher level of flavanols, catechin and epicatechin, was characteristics (Errea *et al*., 1992 and 2000). The theory that an accumulation of catechin above the graft union can be used as a biochemical marker of graft incompatibility (Musacchi *et al*., 2000). Phenol analysis is an applicable early sign for the prediction of graft incompatibility especially when new cultivars were used for different new cultivar/ rootstock combinations.

X-ray tomography: future potential application :

The main interest of X-ray tomography method is associated with the image analysis; we present a non-destructive 3D visualization of the graft interface that could provide new insights into the spatial tissue organization of the graft interface in grapevine. It was the first time, to the knowledge, that 3D imaging of the graft interface and vascular connections has been reported by Milien *et al*. (2012). This method could open new avenues to study graft quality assessment in woody plants.

The cellular events at the graft interface have been well characterized by histological studies in various woody plants, such as, *Picea* spp., apples and *Prunus* spp. (Soumelidou *et al*., 1994 and Olmstead *et al*., 2006). These histological studies (using light, confocal and electron microscopy) give beautiful and detailed images of the graft interface, but only in one plane. Understanding spatial tissue organization between the two partners of a graft union is of paramount importance to management and selection of future rootstock genotypes as well as being of scientific interest. Till date graft union morphology has been studied with magnetic resonance imaging (MRI) in pine trees (Leszczynski *et al*., 2000) and in grapevine (Bahar *et al*., 2010). Unfortunately, these MRI studies are of relatively low resolution and only present 2D virtual sections of the graft interface. Fluorescent dyes and ^{14}C-sucrose markers have been employed to characterize the functional developments of the phloem at the graft interface in tomato but the morphological characterization was also destructive and only provided 2D information (Schoning and Kollmann, 1997).

X-ray tomography is a minimally invasive structural imaging method that allows 3D reconstruction of scanned objects (Larabell and Nugent, 2010). It has since been applied to the study of animals and minerals; the use of X-ray tomography began in plants in the late 1990s (Pierret *et al*., 1999). X-ray tomography has been applied to the study of the anatomy of stem wood samples of trees (Fromm *et al*., 2001; Steppe *et al*., 2004 and Longuetaud *et al*., 2005) and recently to the study of vessel dimensions and intervessel connections in grapevine (Brodersen *et al*., 2011). Other higher resolution tomography technologies also exist; these technologies can visualize and 3D reconstruct to the single cell level, but only in small plant samples such as seeds (Cloetens *et al*., 2006). Although graft incompatibility is rare in grapevine, grafting success can be very variable (May, 1994). After different tests and optimization of the scanning parameters, the method was applied to young vines with differing degrees of grafting success in order to understand how grapevine tissues and structures organize in response to the grafting. In the 3D organization of the graft interface in grapevine, could open new avenues to assess graft quality in woody plants.

Conclusion :

When new rootstocks are bred and selected a number of traits need to be evaluated in addition to disease resistance such as their affinity and compatibility, vigour and adaptation to soils and climatic conditions. The mechanism of graft incompatibility is not fully understood. Researchers have studied how the union develops and functions over time and have confirmed that there is an incompatibility between different scion-rootstock combinations. This incompatibility can be detected a few weeks after grafting by a poor vascular connection and phloem degeneration at the graft union. Despite the fact that callus formation can be considered as a common wound healing response in plants, recent advances in studying the plasmodesmata as the highly dynamic structures that offer a pathway for symplastic cell communication, open the door to its important role in cell recognition, and compatibility and incompatibility response. As the mechanisms involved in all these processes have been related to herbaceous graft combinations, future studies should include a much wider range of similarities on woody responses to reach a better understanding of the mechanism of compatibility and incompatibility in these graft combinations. This review will focus on the knowledge currently available on the metabolic response during the formation and determination techniques of the stock/scion graft union in order to help the effort for identify future metabolic markers to be used in breeding programmes.

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