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Review

An overview of grafting re-establishment in woody fruit species

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ABSTRACT

The formation of a successful graft includes a series of biological steps involving immediate responses to the wound, such as callus and functional vascular system formation between graft partners. However, grafts are not always successful when different genotypes (plant species) are grafted, resulting in tissue union and regeneration problems—popularly known as graft incompatibility. Numerous studies on graft union formation and graft compatibility between scion–rootstock plants have tested several scientific hypotheses related to the physiological and molecular mechanisms underlying scion–rootstock union at the early and late growth stages following the grafting of herbaceous plants. However, due to long juvenile periods, long generation times, and large plant sizes, few studies have focused on the different growth stages of grafts using woody fruit plants due to inherent difficulties in their study. In the present review, a scientific analysis of existing studies promotes a discussion of scion–rootstock grafts. If such grafts exhibit a certain level of success in their re-establishment immediately following grafting, they are termed "graft compatible." However, if the scion–rootstock union becomes graft incompatible immediately after grafting, this is called "incompatibility," while "late graft incompatibility" occurs when the union dies within three to five years.

1. Introduction

Grafting has been used in agriculture for over 2000 years. Historical records indicate that grafting was practiced by the ancient Chinese (1560 B.C.), the ancient Greeks, and during early Christianity (Melnyk and Meyerowitz, 2015). These cultures were the first to utilize the technique of grafting plants with different species within the genus *Citrus* (family Rutaceae) and olives (family Oleaceae) (see for review Hartmann et al., 2011; Melnyk and Meyerowitz, 2015). Currently, the use of grafted plants is commonplace in orchards, greenhouses, and gardening, and its applications extend beyond horticultural contexts.

The technique for grafting involves the union of two parts of living plants: a root system (rootstock) and a shoot system (scion). Through tissue regeneration, the assembly of these two parts from different species constitutes a new plant (Martínez-Ballesta et al., 2010; Cookson et al., 2014). Grafting is widely used in several woody plants such as the rubber tree (*Hevea brasiliensis* Muell. Arg.) (Prabpreea et al., 2018), pecan [*Carya illinoensis* (Wang.) K.] (Mo et al., 2018), orange (*Citrus* spp.) (Caballero et al., 2013; He et al., 2018), apple (*Malus* spp.) (Adams et al., 2018; Atkinson et al., 2003), pear (*Pyrus communis* L.) (Hudina et al., 2014; Yang et al., 2017), grape (*Vitis vinifera* L.) (Moreno et al., 2014), atemoya (*Annona* x *atemoya* Mabb.) (Baron et al., 2016), *Prunus* spp. (Zarrouk et al., 2010; Pina and Errea, 2008a), and olive (*Olea europaea* L.) (Fabbri et al., 2004). Although this plant propagation technique has been used for many centuries in evergreen plants—-mainly fruit, forest, and ornamental trees—it remains unclear how physiological mechanisms act in the re-establishment of tissues at the graft junction. During the 20th century, the widespread use of grafting for vegetables plants—mainly species belonging to the Cucurbitaceae and Solanaceae families—led to significant advances in knowledge related to the physiological aspects of grafted herbaceous plants (Goldschmidt, 2014).

Grafting can also be used to assist plants in the adaptation to biotic stress, such as resistance to pathogens (Ramírez-Gil et al., 2017) and abiotic stress conditions including drought (Zhou et al., 2018), salinity (Mehdi-Tounsi et al., 2017), and mineral deficiency (Jimenes et al.,

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2018). In addition, another goal of grafting is to increase precocity at the beginning of production in order to avoid the juvenile state of the scion plant. The scion grafted onto a rootstock species will maintain its current growth stage, including the capacity to immediately produce fruits, which provides the possibility of reduced spacing in commercial orchards by using dwarf rootstock species that confer a smaller size on the grafted plant.

In addition, grafting can be used as a tool for the study of different biological processes. In particular, grafting on *Arabidopsis thaliana* L.—a plant widely studied as a "model-plant"—has greatly contributed to existing knowledge on many issues related to plant physiology, including the transmission of floral stimuli, proteins, and long-distance RNAs in the phloem tissue (Notaguchi et al., 2009).

In particular, one factor believed to trigger graft mortality is the natural incompatibility reaction between scion–rootstock species known as "incompatibility between partners". However, it should be considered that additional factors can produce graft failure; for instance, pathogens active within the phloem vascular tissue, inadequate environmental conditions (temperature and/or humidity), and the inability to align the cambial tissues of both graft partners (Martínez-Ballesta et al., 2010; Goldschmidt, 2014).

However, even without the interference of abiotic factors, some scion–rootstock combinations are truly incompatible, either immediately following grafting or over time, indicating several physiological, biochemical, and molecular mechanisms being involved in scion–rootstock interaction. Thus, biochemical-molecular and/or anatomical processes (Hartmann et al., 2011) represent some of the factors collaborating in the re-establishment of plants. Nevertheless, the interrelation of these interactions remains poorly understood.

Thus, the present review provides an overview of the current state of the art for grafting woody plants based on several review articles, research articles, and book chapters, each emphasizing a specific aspect of the procedure, such as grafting techniques or the vascular alignment of cambium tissues (Pina et al., 2012; Lima et al., 2017), candidate gene expression (Chen et al., 2017), phenolic compounds (Zarrouk et al., 2010; Irisarri et al., 2016; Prabpreea et al., 2018), or phytohormones (Wang et al., 2014; Xu et al., 2015). In addition, several reports following the restoration of the vascular connection focus on scion–rootstock interaction in relation to leaf gas exchange (Xu et al., 2015; Baron et al., 2017), ion accumulation (Moreno et al., 2014; Samuolienė et al., 2016), production, and vigor, among other factors. As such, we have presented a number of botanical characteristics that may have a direct influence on the re-establishment of vascular connections. Correct anatomical tissue positioning between scion and rootstock triggers the genetic potential necessary for the regeneration of injured tissues and the production of secondary metabolites. Phenolic compounds and phytohormones induce the re-establishment and survival of the grafted plant. A compatible combination will transport and translocate nutrients, carbohydrates, promoters, and phytohormones for normal plant development (Fig. 1).

2. Taxonomic identification of grafted plants

Several biotic and abiotic factors involved in the re-establishment of plants are reported in the literature, though botanical characteristics are scientific debatable regarding "what" can be considered graft compatible or not graft compatible. Notably, no precise definition of "graft compatible" exists, and published research generally refers to this as the establishment of a successful graft, involving prolonged survival and proper functioning of the composite plant (late compatibility) (Goldschmidt, 2014). Among the possible botanical characteristics involved, taxonomic affinity is presumed to be a prerequisite for graft compatibility.

The taxonomic proximity of scion and rootstock species is essential to the success of re-establishment of both graft partners, though current understanding of incompatibility in woody plants remains insufficient. A homograft occurs when intraspecific grafts are used, with scion and rootstock belonging to the same botanical species, the members of which are presumably always compatible. The more general approach of heterografting occurs when grafts are interspecific, with scion and rootstock belonging to different species of the same genus. In addition, interfamilial grafts are rarely compatible, thereby typically graft incompatible.

The importance of taxonomic identification is particularly evident when analyzing studies of species belonging to the family Annonaceae. Some plants in Annonaceae are erroneously recognized as "graft incompatible" when certain species are used as rootstocks. For instance, this occurred for Brazilian producers and rural technicians who erroneously concluded that the native plant popularly known as *biribá* [*Annona mucosa* (Bail.) H. Rainer] is incompatible with atemoya when used as a plant rootstock. However, a number of botanical species exist with the popular name "biribá" that are perfectly serviceable as rootstocks plants. Notably, "biribá" is commonly used in different regions of Brazil to refer to soursop (*Annona muricata*), *araticum-do-brejo* (*Annona glabra*), wild-soursop (*Annona montana*), and wild-sweetsop (*Annona reticulata*), which are reportedly graft incompatible as rootstock with atemoya scions (George and Nissen, 1987; Sanewski, 1991).

The importance of correct identification of plants involved in the grafting process can also be verified in *Prunus*. For example, Reig et al. (2018) studied the (in)compatibility reactions between apricot (*Prunus armeniaca* L.) cultivars and 21 different *Prunus* rootstocks before releasing these rootstocks on the market. Reig et al. (2018) affirmed that apricot exhibited perfect unions (the line of the union between bark and wood is hardly visible) with plum rootstocks (*P. insititia*); however, several discontinuities in the bark, with breakage of the tree at the graft union in the nursery or orchard being observed in some plum rootstocks including "Miral 3278 AD" (*P. cerasifera* × *P. amygdalus*), "Ademir", and "Myrobalan 713 AD" (both *P. cerasifera*). Curiously, the plant species popularly known as 'plum' invoked both success and 'failure' as a rootstock. As a result, correct taxonomic identification is necessary to avoid mistakes and provide both nurseries and fruit growers with valuable information regarding the risks of weak unions.

This situation is increasingly aggravated by the number of exsiccates of studied species deposited in herbariums being low, making it difficult to identify the correct taxa of a species. Thus, the characteristics of certain species that are graft incompatible are generalized among all botanical species that present the same popular nomenclature, resulting in misunderstandings when obtaining scion and rootstock seedlings.

3. Grafting technique and professional skills

Grafting plants has been an important tool for improving olericulture and fruticulture, and will likely maintain this position as an important agronomic and agricultural production technique over the long term. The necessity for nursery growers to select rootstock species with ample advantages, along with the ability to reproduce it on a large scale, makes grafting an attractive strategy for increasing yields and growing fruits or vegetables in environments where it was not previously possible.

Furthermore, the professional skills required for the grafting technique are fundamental to obtaining a good bud "take" and determining whether certain scion–rootstock combinations are truly incompatible, that is, whether failure was triggered by anatomical mechanisms or simply by inexpert grafting practice. Nursery growers responsible for the production of commercial rootstocks and scions generally use a slight physical pressure, using either a clip or wrapping tape around a graft tissue joint to promote successful formation.

In addition, nursery growers must graft rootstock and scion stems of a similar size, which allows for the proper alignment of tissue known as the vascular cambium. These tissues are popularly known as "plant stem cells", and give rise to the phloem and xylem during secondary plant growth, when the roots and stems thicken (Melnyk and

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