

УДК 630. 228.7:582.475.4(571.51)

Grafts of Woody Plants and the Problem of Incompatibility Between Scion and Rootstock (a review)

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Received 4.03.2011, received in revised form 11.03.2011, accepted 18.03.2011

Grafting can occur naturally between branches or more often roots of the same species, or artificially via asexual propagation where the tissues of two plants are encouraged to fuse with one another. Artificial grafting is commonly used for propagation to improve qualities of trees grown commercially via selecting for its roots (called the rootstock) and for stem, leaves, flowers or fruits (called the scion). It is often used to reduce the time to flowering and shorten the breeding program, improve quality and yield of fruits and seeds, improve hardiness in response to environmental conditions and pathogens resistance, and change cultivars. Incompatibility between rootstock and scion has been more often observed for inter-specific than intraspecific grafts, and might result in a dieback of a graft. The objective of this paper was to review the recent literature related to graft applications and incompatibility between scion and rootstock. Anatomical studies of incompatible grafts demonstrated a poor vascular connection, vascular discontinuity and phloem degeneration at the union area, which might be detected as early as few weeks after a graft establishment. These vascular fusion problems can disturb water, nutrient and assimilate flows in the plant and might result in a further breakdown of a union area. Incompatibility might be also a result of insufficient plasmodesmatal coupling at an early stage of development within one of the graft partners. Differences in abundance of phenol compounds and starch below and above the graft union, as well as peroxidase amount at the union might serve as biochemical markers of the rootstock/scion incompatibility. Genetically and biochemically similar scions and rootstocks could improve graft compatibility.

Keywords: *scion, rootstock, graft, compatibility.*

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Introduction

Grafts are often used in agriculture to select for and maintain desirable traits. Vegetative propagation such as grafting is preferable to sexual propagating to ensure reliability and maintaining desirable quality of yield given that the sexual propagation may genetically transfer undesirable traits. Grafting can also be a desirable method to propagate plants which are hard to root such as Siberian pine (e.g., Severova, 1958; 1968; Kolegova, 1977). However, a problem of incompatibility between grafted parts may occur and result in a further dieback of a plant. Thus, it is of importance to know mechanisms of incompatibility between parts of the graft to mitigate the potential problem even before planting the grafts or reduce the size of the effect. Also, recent literature has lots of information about transfer of desirable and undesirable traits. Summarizing of this information might be useful for forest services. Thus, the objective of this paper was to review the recent literature related to graft applications and incompatibility between scion and rootstock.

Types of grafts

Grafting occurs naturally that might involve branches or more often roots of the same species (inosculation) (e.g., Janick, 2009), or artificially via asexual propagation where the tissues of two plants are encouraged to fuse with one another. Artificial grafting is often used for propagation to improve qualities of trees via selecting for its roots (called the rootstock) and for other characteristics such as stem, leaves, flowers or fruits (called the scion).

Natural root grafting happens when roots of plants make physical contact with each other, while branch or trunk grafting may occur when crossed branches become in a close contact in a dense stand in which bark might become injured by fusion due to their friction under the air movements (e.g.,

winds) (e.g., Pravdin, Nekrasov, 1953). Although natural grafting is common between tree of the same species it has been also observed for trees of different species but the same genus. Natural grafting is common for holly, lime, oak, beech, Scots pine and Jack pine (e.g., Pravdin, Nekrasov, 1953; Janick, 2009). Natural grafting might affect ecosystems negatively by possible transmission of tree pathogens (Epstein, 1978) or positively through sharing water and nutrients via root grafts (e.g., Bormann, 1966), by providing support for a weaker tree, and an adaptation to promote fire or wind resistance (e.g., Loehle, Jones, 1990). A study demonstrated that root grafts can be less impacted by hurricane damage compared to non-grafted trees (Basnet et al., 1993). Another study demonstrated that grafted shaded trees had significantly higher root nonstructural carbohydrate concentrations than non-grafted shaded trees, indicating that root grafts partially offset the effects of shading (Fraser et al., 2006). A recent study demonstrated that after thinning, a growth increment was much less for trees, which had root grafts with removed trees, and it was linked to the support of roots and stems by live residual trees (Tarroux et al., 2010). Keeley (1988) hypothesized that root grafts would be of selective advantage to dominants regardless of the status of the tree to which it is grafted. For example, grafts would be of selective value in waterlogged soils because they would enhance anchorage effect by dispersing the tree's compressive force over a greater surface area.

Grafts can be classified as homografts if the scion and rootstock are of the same species or heterografts if they are of different species. Several studies demonstrated that functioning and growth of homografts is often more successful compared to heterografts because of higher similarities in genetic structure between the graft components (Kovalishin, 1966; Yakovleva, 1967, 1974, 1975). Although heterografts more often experience incompatibility because of the differences in

anatomy, morphology and physiology between the graft components, they could be more beneficial than homografts. Heterografts of *Pinus sibirica* Du Tour demonstrated a higher growth compared to homografts (Matveeva and Kichkildeev, 2006). Grafting of flood-sensitive *Annona* species onto *A. glabra* rootstock improved flood tolerance of the species (Nuñez-Elisea et al., 1999). Grafting Fraser fir onto Turkish fir demonstrated reduced losses by phytophthora root rot in the southern Appalachian Mountains of North Carolina (Hibbert-Frey et al., 2006). Fig grafts showed an improved growth response to nematodes, which varied depending upon a rootstock (Hosomi et al., 2002).

Grafts applications

Grafts are often used in agriculture to reduce the time to flowering and shorten the breeding program, improve quality and yield of seeds and fruits, improve hardiness in response to environmental conditions and pathogens resistance and change cultivars (Severova, 1958; Kovalishin, 1968; Browning, Watkins, 1991; Titov, 1993; 1995; Lahav et al., 1995; Hosomi et al., 2002; Sanou et al., 2004; Giorgi et al., 2005; Hibbert-Frey et al., 2006; Ahmed et al., 2006; Mitani et al., 2008; Cantin et al., 2010; Gandev, 2009; Franzon et al., 2010; Bellefontaine et al., 2010; Pio et al., 2010; Souza et al., 2010; Tandonnet et al., 2010). For example, for Siberian pine it could take two-three years after grafting to develop reproductive organs strobills, and about 30-40 years for a sexually-propagated plant. Correspondingly, it could take 20 years for grafts and 170-240 years for sexually-propagated Siberian pines to reach the maximum seed production of (Severova, 1958; Beh et al., 2009). Also, Siberian pine/Scots pine heterografts had a higher growth and height compared to Siberian pine homografts (Matveeva, Kichkildeev, 2006). Another study by Browning and Watkins (1991)

tested several new quince hybrid rootstocks for pears and demonstrated that they all differed in their influence on fruit production and quality. A study of citrus hybrid seedlings grafted into shiikuwasha (*Citrus depressa* Hayata) demonstrated that about one third of the plants flowered two and a half years after grafting, while usually it takes almost 20 years from crossing to cultivar release to the industry (Mitani et al., 2008).

Several studies also demonstrated effect of rootstock on branching (e.g., Jayawickrama et al., 1991; Hirst, Ferree, 1995), crown, size and chemical content of leaves (Jayawickrama et al., 1991), fruit size and weight, rind thickness, juice content, brix, total acids and brix: acid ratio (Giorgi et al., 2005; Ahmed 2006; Georgiou, 2009), and flavonoid content (Gil-Izquierdo et al., 2004). Grafting is often used to induce dwarfing to apple trees or other orchards because it increases productivity by providing more fruits per unit of land and higher quality of fruits (e.g., Sitarek, 2006; Prassinis et al., 2009). One of the explanations is that when inducing dwarfing in grafts it results in shift in resource allocation towards reproductive organs compared to shoot growth (Webster, 1995).

Rootstock effects on plants have not always been positive. For example, Cardinal et al. (2007) demonstrated that yield of *Hevea brasiliensis* varied from 41% to 86% depending upon genetic background of a rootstock. Another study demonstrated that selection of a rootstock or scion might suppress yield and growth of apple trees (Univer et al., 2006). A recent study suggested that scion might also affect root vigour of a rootstock which was not related to carbon supply from the shoot (Tandonnet et al., 2010).

Scion-rootstock interaction

Grafts represent two different genetic identities functioning as two systems in one

organism influencing each other. Understanding about mechanisms of the rootstock-scion interaction is yet limited. Several studies demonstrated mechanisms of scion-rootstock interaction on grafts, which were used to induce dwarfing. One of the hypotheses is that the growth regulator, auxin, which is transported at different rates between grafts on different rootstocks, affects cytokinin production in roots and causes differences in shoot growth (Lockhard, Schneider 1981; Webster 1998). Another hypothesis assumes that phenols accumulating at the graft union reduce tissue viability and the rate of auxin breakdown (Lockard, Schneider 1981, Treutter, Feucht 1991, Errea et al., 1994). Finally, the rootstock-induced dwarfing is caused by reduced soluble transport across the graft union (Atkinson et al., 2003, Basile et al., 2003). In addition, Prassinis and coauthors (2009) showed that rootstock-induced dwarfing might be caused by differential cessation of terminal meristem growth and is triggered by rootstock-specific gene regulation.

Most of studies demonstrated that there is no horizontal gene transfer between the graft components, scion and rootstock. However, a recent study of grafted tobacco plants demonstrated exchange of genetic information via either large DNA pieces or entire plastid genomes (Stegemann, Bock, 2009). In this study, the analysis of the graft sites revealed the frequent occurrence of cells harboring both antibiotic resistances and both fluorescent reporters. Although this research showed the exchange of genetic material between grafted components, the gene transfer was only restricted to the contact zone between the grafted components, which indicated that the changes could become heritable only via lateral shoot formation from the graft site. Previously, there was a study that described hereditary changes in grafted pepper, and suggested that these changes might be induced by a mechanism similar to that

of transformation in higher organisms (Ohta, Van Chuong, 1975). Yet, there are unresolved issues of whether gene transfer depends on the cell contacts between scion and rootstock. Although micromolecules can go through plasmodesmata, it is unknown if plastids or macromolecules of DNA can go through the plasmodesmata considering that their anatomical structure can change due to specific proteins.

Incompatibility between scion and rootstock

Incompatibility between rootstock and scion has been more often observed for inter-specific than intra-specific grafts, which might further result in a dieback of a graft. Anatomical studies of incompatible grafts demonstrated a poor vascular connection, vascular discontinuity and phloem degeneration at the union area, which might be detected as early as few weeks after a graft establishment (Pina, Errea, 2005; Pina et al., 2009). This results in a disturbance of water and nutrients transfer by xylem in one direction and photoassimilates by phloem in another direction. Plasmodesmata are important communication pathways in plants (e.g. Pina et al., 2009). These are channels in the plant cell wall allowing passage of macromolecules and solutes between the neighboring cells. A recent study demonstrated that insufficient plasmodesmatal coupling at an early stage of development within one of the graft partners might result in graft incompatibility (Pina et al., 2009).

At the graft connection area a callus forms as a reaction to wounding. Another study of apricot grafted onto a plum rootstock demonstrated that only some callus differentiation into cambium and vascular tissues occurred; while a large portion of the callus never differentiated (Pina, Errea, 2005). This interrupts the vascular connections because of the lack of differentiation that brings discontinuities in the cambium and

the formation of a band of parenchymatous cells. In a study of pear grafts typical symptoms of graft incompatibility such as bark discontinuity, cambial dysfunction and accumulation of starch in the scion were observed. Little cell necrosis was observed at the interface of incompatible grafts at the 5-month stage of graft development (Ermel et al., 1999). In spite of a lack of scion/stock vascular connections, some plants demonstrated that they could flower and produce seeds, i.e., there were nonvascular functional connections between the two plants, probably of parenchyma cells (Flaishman et al., 2008). Abundance of periderm rings was also a symptom of incompatibility according to a study by Ermel et al. (1999), which were more abandoned in incompatible grafts. In some cases, signs of incompatibility have been revealed a few years after grafting and were explained by differences in radial growth between scion and stock that breaks tissue connectivity at the graft union (Savva et al., 2004).

In a study of peach/plum grafts it has been demonstrated that free amino acids per tree decreased in rootstock of incompatible grafts while they became stabilized in compatible grafts between 79-89 days after grafting (Moreno et al., 1994). Another study of peach/plum grafts by Moing and Gaudillere (1992) demonstrated that sorbitol was lower in roots of incompatible grafts compared to compatible ones, and that sugars and starch accumulated in scions of the incompatible grafts following 78 days after grafting, but carbon partitioning was only slightly affected by graft incompatibility. They also showed that nitrogen assimilation ceased 78 days after grafting in incompatible grafts, which was not the case in compatible grafts. This suggested an inhibited transport of solubles from roots to scion in rootstocks and from photosynthetic apparatus to rootstock. A study of pear/quince grafts demonstrated that 63kDa protein might

be responsible for incompatibility because it was observed in compatible grafts, faintly observed in intermediate compatible grafts and was not detected in incompatible grafts (Gulen et al., 2005). Absence of peroxidase A in pear/quince grafts has been also related to graft incompatibility (Hosseini et al., 2008).

Graft incompatibility can be often determined at an early stage of graft development. For example, in a study of apricot grafts accumulation of phenol compounds could serve as an indicator of incompatibility as early as the first week after grafting (Errea et al., 2001). Another study also indicated that accumulation of phenol deposits at the place of graft union might inhibit graft compatibility (Mng'omba et al., 2008). Another study also demonstrated that differences in phenol accumulation below and above the graft union might serve as an indicator of compatibility (Usenik et al., 2006). Additionally, a study of *Prunus persicu/Prunus* spp. grafts indicated that significant increase in peroxidase activity might be observed in incompatible unions (Zarrouk, 2010).

Conclusion

Our literature review demonstrated that there are varieties of grafts which might inherent desirable or undesirable properties from their graft components. Incompatibility is a complex problem that might occur between graft plants and result in their further dieback. Here, we reviewed and discussed several mechanisms of graft incompatibility, and concluded that compatibility might be improved by selection of the types of rootstock and scion that might: (1) favor callus differentiation into cambium and vascular tissues; (2) be able to establish a close cell contact at the graft union to maintain water and nutrient balance between scion and rootstock; and (3) enable synchronicity in radial growth and cell differentiation between scion and rootstock. Graft

components with similar genetic backgrounds might be incompatible less often compared to inter-specific grafts. Biochemical markers such as abundance of phenol compounds and starch at the union, below and above the union and specific polypeptide, peroxidase activity might be helpful to diagnose incompatibility at an earlier stage of graft development.

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Acknowledgements

The authors would like to acknowledge the support provided to the 2010 winners of the Russian Federation government support to the leading scientific schools (grant №HIII-65610.2010.4). We are also grateful to the grant No. 53 of the Siberian Branch of the Russian Academy of Sciences for partial support.

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Прививки древесных растений и проблема несовместимости подвоя и привоя (обзор)

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Прививки древесных растений могут возникать естественным образом в результате срастания стволов или корней деревьев, находящихся в тесном контакте друг с другом, или искусственно, при пересадке части одного растения, называемого привоем, на другое – подвой. Прививание растений применяется для повышения продуктивности, улучшения качества плодов, ускорения наступления плодоношения, а также повышения резистентности к неблагоприятным факторам среды и патогенам. Из двух видов прививок – гомопластические (внутривидовые) и гетеропластические (межвидовые) – проблемы, связанные с анатомо-физиологической несовместимостью, чаще всего возникают у последних. Целью данной статьи является обзор современной литературы, связанной с применением прививания и проблемой несовместимости между компонентами прививки. На анатомическом уровне несовместимость представляет собой нарушение целостности васкулярных элементов, прерывающихся слоем некротических клеток в зоне контакта привоя и подвоя. В физиологическом отношении неполноценный межклеточный контакт создает барьер, препятствующий доступу воды и минеральных веществ в верхнюю часть растения – привой, и ассимилятов – в противоположном направлении. Несовместимость может быть также результатом нарушения формирования плазмодесм на ранней стадии развития прививки. Различие в концентрации фенольных соединений и крахмала, их избыток ниже и выше зоны срастания компонентов прививки, так же как и пероксидаз, может служить биохимическим маркером несовместимости между привоем и подвоем. Последствия несовместимости привоя и подвоя угнетают рост растения и являются причиной его гибели. Подбор генетически и биохимически сходных компонентов прививки может минимизировать проблему несовместимости.

Ключевые слова: привой, подвой, прививание, совместимость.
