Research review

Plant grafting: how genetic exchange promotes vascular reconnection

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Summary

Grafting has been widely used to improve horticultural traits. It has also served increasingly as a tool to investigate the long-distance transport of molecules that is an essential part for key biological processes. Many studies have revealed the molecular mechanisms of graft-induced phenotypic variation in anatomy, morphology and production. Here, we review the phenomena and their underlying mechanisms by which macromolecules, including RNA, protein, and even DNA, are transported between scions and rootstocks via vascular tissues. We further propose a conceptual framework that characterizes and quantifies the driving mechanisms of scion–rootstock interactions toward vascular reconnection and regeneration.

Introduction

Plant grafting is a vegetative propagation technique that connects two severed plant segments together. The chimera, consisting of the scion and rootstock, survives as a new individual after wound healing. Natural grafting, which occurs when stems or roots of plants attach and fuse (Mudge *et al.*, 2009), has facilitated the invention of classic grafting techniques (Fig. 1). In recent years, micrografting protocols have been used increasingly as a tool to evaluate signaling and transport (Turnbull *et al.*, 2002; Turnbull, 2010).

The success of the graft depends on the compatibility between the rootstock and scion. Studies have indicated that grafts in different genera of the same family are rarely compatible, but grafts of different species within the same genus can survive by forming an effective graft union (Goldschmidt, 2014). The majority of homografts are compatible, with the exception of monocots. Since the wound required for grafting disrupts the plant vascular system (Asahina & Satoh, 2015), reconnection of the vasculature is necessary to maintain normal water and nutrient transportation. Most monocots do not have vascular cambia, which may be a reason why grafting fails (Sachs, 1981; Melnyk & Meyerowitz, 2015). This further suggests that vascular differentiation during wound healing is a prerequisite for successful grafting.

When the cambium of the scion joins fully with that of the rootstock, intact cells divide and proliferate into calli, which eventually differentiate into vasculature and plasmodesmata forms (Melnyk & Meyerowitz, 2015). Although the detailed molecular mechanisms underlying this process require further research, some studies have found that hormones, such as auxin, cytokinin and GA, play a pivotal role in regulating stock–scion interactions (Aloni *et al.*, 2010). Histological and microarray analyses of *Arabidopsis* micrografting identified auxin, ethylene and jasmonic acid as important molecules that participate in development of the graft union, and a model has been proposed to better interpret this phenomenon (Yin *et al.*, 2012; Fig. 2).

After cell walls fuse in the graft union, plasmodesmata stretch in small groups over the spaces of the inner cell wall, interconnecting the protoplasts of contiguous cells (Kollmann & Glockmann, 1985). Heterogeneous cells then interdigitate through the plasmodesmata (Melnyk & Meyerowitz, 2015). The plasmodesmata provide tunnels for small molecules and even selectively permit the movement of macromolecules, such as proteins and nucleic acids. Additionally, vascular reconstruction at the graft union enables macromolecules to be transported (Harada, 2010). In recent years, increasing effort has been made to determine how macromolecules are transferred between scions and rootstocks in grafting plants to reveal the mechanisms that control graft-induced changes in plant traits (Paultre *et al.*, 2016).

In this review, we first describe several different types of graft-induced phenotypic changes. We highlight existing evidence for the molecular and physiological mechanisms underlying grafting and then propose a framework to interpret how the transportation of genetic materials between the scion and rootstock is related to vascular reconnection and regeneration.