

*Tansley insight*

Systemic control of plant regeneration and wound repair

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Summary

Plants have a broad capacity to regenerate damaged organs. The study of wounding in multiple developmental systems has uncovered many of the molecular properties underlying plants' competence for regeneration at the local cellular level. However, in nature, wounding is rarely localized to one place, and plants need to coordinate regeneration responses at multiple tissues with environmental conditions and their physiological state. Here, we review the evidence for systemic signals that regulate regeneration on a plant-wide level. We focus on the role of auxin and sugars as short- and long-range signals in natural wounding contexts and discuss the varied origin of these signals in different regeneration scenarios. Together, this evidence calls for a broader, system-wide view of plant regeneration competence.

I. Introduction

Outside laboratory settings, plants rarely grow undisturbed, and physical damage is a ubiquitous part of their lives. Recovery from damage is a complex response involving wound closure, preparation of the defense systems for invasion, nutrients rerouting, and activation of tissue-specific repair mechanisms. In certain scenarios, wounding triggers restorative growth, a response ascribed to the 'regeneration competence' of the injured tissue. The competence to regenerate in plants is broad but limited by developmental stage and physiological conditions. Thus, dissection of the root meristem near its tip results in root meristem reformation, but the meristem fails to regenerate when a similar injury is inflicted at a more proximal position (Sena *et al.*, 2009; Durgaprasad *et al.*, 2019). Similarly, dissection of a young leaf tip triggers growth at its base to compensate for the missing leaf tissues, whereas older leaves lose the

competence to initiate such growth (Sena *et al.*, 2009; Kuchen *et al.*, 2012). Young shoots or leaves removed from their mother plant generate wound-induced shoot-borne (or 'adventitious') roots to replace the missing root system, but such capacity diminishes in older shoots or detached leaves (Steffens & Rasmussen, 2016; Li *et al.*, 2020). The molecular definition of 'regeneration competence' is still unclear, but it is usually ascribed to a certain autonomous cell state, either epigenetic (He *et al.*, 2012; Chen *et al.*, 2016; Hernández-Coronado *et al.*, 2022), transcriptional (Sena *et al.*, 2009; Durgaprasad *et al.*, 2019), or hormonal (Ikeuchi *et al.*, 2019).

Most experimental setups studying plant wound-response focus on a single wound, but wounding in nature is often a whole-plant affair and systemic signals may be involved in coordinating and prioritizing wound repair. Recent high-resolution studies of plant regeneration have begun to uncover the contribution of local vs

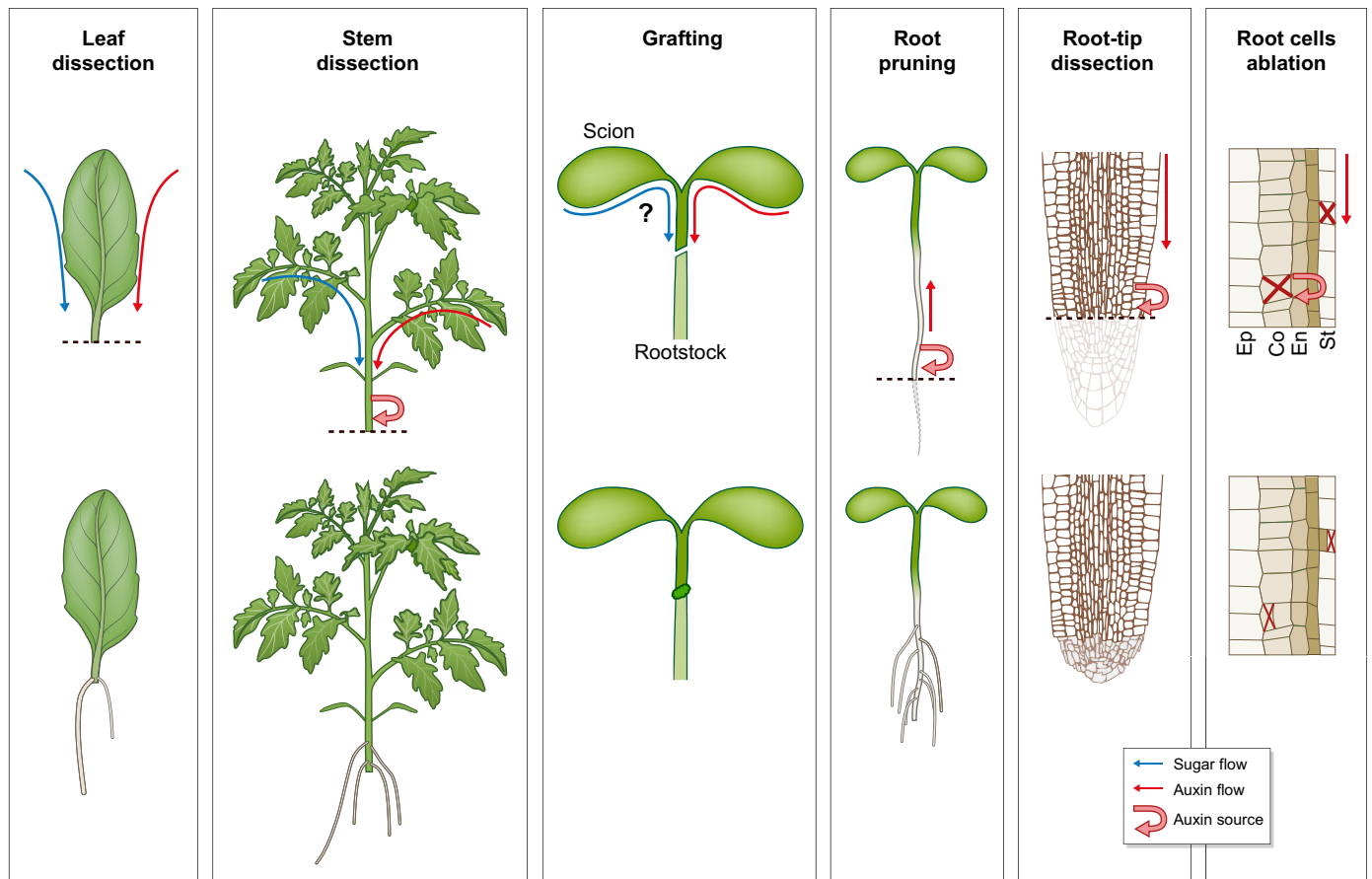


Fig. 1 The origin of local and systemic signals in different regeneration scenarios. Arrows mark the flow of the signal (red, auxin; blue, sugars). Curved arrow marks site of synthesis. Co, cortex; En, endodermis; Ep, epidermis; St, stele.

systemic signals to plant regeneration; key amongst these is the phytohormone auxin (Canher *et al.*, 2020; Hoermayer *et al.*, 2020; Matosevich *et al.*, 2020), and evidence from cuttings calls for a more holistic, whole-plant view, of plant regeneration that goes beyond local tissue competence (Druege *et al.*, 2019). Here, we discuss the systemic control of plant regenerative response. Many factors, including jasmonic acid and cytokinin, control tissue regeneration and can move systemically through the plant (Ikeuchi *et al.*, 2019; Zhang *et al.*, 2019). However, local vs systemic effects of many such factors are often difficult to untangle. In this piece, we focus on two signals, auxin and sugars, whose systemic effects on regeneration have been studied in most detail (summarized in Fig. 1). We limit ourselves to natural, or close-to-natural, wounding contexts. Though much has been learned about regeneration from tissue-culture experiments, the nature of these artificial systems often precludes distinction between systemic and local activity.

II. Auxin as a systemic regeneration signal

The small molecule auxin is closely implicated in enabling regeneration, and it is used in controlling plant clonal propagation

and tissue culture growth (Ikeuchi *et al.*, 2019). It is produced in multiple places in the plant and is transported in a polar manner, mostly basipetally, to form short- and long-range gradients within the plant (Robert & Friml, 2009; Zhao, 2018). The relationship between auxin gradients and regeneration response is likely an ancient trait. When the thallus of liverworts is dissected, a new meristem is initiated from the cut site of only one of the cut halves (Larue & Narayanaswami, 1957; Nishihama *et al.*, 2015). This differential response is guided by depletion of the plant-wide auxin gradient formed by the meristem (Ishida *et al.*, 2022), and exogenous application of auxin inhibited the regeneration response (Larue & Narayanaswami, 1957).

The aerial parts of many plant species can form shoot-borne roots from stems or leaves when these parts are removed. Many signals control this process, but auxin remains a key factor (Bellini *et al.*, 2014). Auxin accumulation at the site of root initiation site was demonstrated for many species, and exogenous application of auxin, or auxin-like molecules, is often sufficient to promote root initiation (Steffens & Rasmussen, 2016).

Current evidence suggests that most of the auxin activating wound-induced root initiation is coming from remote tissues. When a rosette leaf of *Arabidopsis* was detached and placed on

hormone-free media, it initiates roots from its basal parts (Chen *et al.*, 2014; Bustillo-Avendaño *et al.*, 2018). This process required the activation of auxin biosynthesis in the distal part of the detached leaf, away from the cut site, and disruption of auxin transport by application of *N*-1-naphthylphthalamic acid (NPA) inhibited root formation (Liu *et al.*, 2014; Xu, 2018). Application of NPA also inhibited the formation of roots in stem cuttings of *Petunia hybrida* (Ahkami *et al.*, 2013) and cut tomato and *Arabidopsis* hypocotyls (Sukumar *et al.*, 2013; Alaguero-Cordovilla *et al.*, 2021), suggesting these restorative growth responses are also controlled by remote production of auxin.

Given that auxin can, and is often, synthesized near its site of action (Brumos *et al.*, 2018; Zhao, 2018; Matosevich *et al.*, 2020), it is not clear why auxin produced away from the site of injury should be required for wound repair. One possible hypothesis is that injury to part of the plant can prime the rest of it for regenerative growth. In this scenario, auxin can serve as a systemic signal that tunes the regenerative response to the environmental and physiological state of the plant (Mroue *et al.*, 2017).

The systemic levels of auxin are responsive to damage and environmental conditions. Physical damage and increased temperature lead to increased synthesis of auxin in the leaf, which then spreads systemically throughout the plant (Machado *et al.*, 2016; Serivichyaswat *et al.*, 2022). This response is not limited to leaves, as damage to the *Arabidopsis* hypocotyl also increased the expression of the auxin-responsive promoter *DR5* in all aerial parts of the plant (Huang *et al.*, 2020). This wound-induced systemic increase in auxin is sensitive to physiological factors such as plant age. The expression of microRNA156-targeted *SQUAMOSA* PROMOTER BINDING PROTEIN-LIKE (SPL) increases with plant age (Wu *et al.*, 2009). In cut leaves, these SPLs suppress the induction of auxin biosynthesis, leading to a reduced number of shoot-borne roots. Exogenous auxin application restored root initiation in leaves with high SPL levels (Ye *et al.*, 2020).

Consistent with systemic auxin acting as a priming or modulating agent during regeneration, different sources of auxin, either local or remote, are important in different scenarios of tissue regeneration. During shoot-borne root initiation, NPA treatment does not abolish root initiation, and at least some of the auxin accumulation can be ascribed to local biosynthesis near the cut site, independent of the shoot-derived auxin (Alaguero-Cordovilla *et al.*, 2021). In some cases, remote auxin is not required at all, such as during regeneration of the root meristem from dissection. Here, auxin signaling is induced in cells near the cut site that proliferate to replace the missing distal part of the meristem (Sena *et al.*, 2009; Efroni *et al.*, 2016). This accumulation results from the induction of auxin biosynthesis *YUCCA* genes at the cut root tip itself (Matosevich *et al.*, 2020).

The systemic source of auxin required for regeneration may not even be the shoot. When the entire apical root meristem is removed ('root pruning'), lateral roots are induced above the injury site. This response is the result of induction of *YUCCA*-mediated auxin biosynthesis near the cut site, followed by acropetal (rather than shoot-derived basipetal) transport to the root initiation site (Xu *et al.*, 2017). Strikingly, the source of auxin during repair may differ even for adjacent tissues. Cell death in the root internal stele triggers

auxin accumulation in adjacent endodermis cells, leading to restorative cell division. No induction of auxin biosynthesis genes could be detected near the dying cells, and *in silico* simulations are consistent with auxin accumulation resulting from dying cells blocking the basipetal auxin flow, although its ultimate source is unclear (Canher *et al.*, 2020). By contrast, repair of ablated cells in external root tissues, which also results in increased auxin accumulation, occurred even when auxin biosynthesis and polar transport were chemically inhibited, suggesting auxin may be derived from internal stores (Hoermayer *et al.*, 2020).

Another example of systemic auxin acting as a modulator of tissue repair is during the reconnection of severed vasculature in graft formation. In this case, wound healing initiates with callus growth at the site of injury, followed by the formation of new vasculature strands connecting the scion and rootstock across the graft junction. The activation of the auxin response machinery is required for the process (Melnik *et al.*, 2015). As it was demonstrated that regeneration of damaged vasculature is promoted by auxin application, it was generally thought that graft formation is promoted by shoot-derived auxin (Wulf *et al.*, 2019). Recent evidence, however, paints a more complex picture. Removal of the cotyledons and treatment with NPA led to reduced proliferation at the graft junction, but vasculature still regenerated at normal rates (Melnik *et al.*, 2015; Serivichyaswat *et al.*, 2022). And while treatment with the auxin transport inhibitor 2,3,5-triiodobenzoic acid could inhibit cell proliferation at the graft junction (Matsuoka *et al.*, 2016), removal of both cotyledons could promote graft formation in *Arabidopsis* micrograft when low levels of sucrose were added, suggesting cotyledon-derived auxin does not play a major role in vasculature regeneration (Marsch-Martínez *et al.*, 2013). Indeed, vascular reconnection in heterografts did not correlate with auxin flow (Wulf *et al.*, 2019). However, a systemic increase in auxin level induced by elevated temperature had a promotive effect on proliferation at the graft site and connections were made faster (Serivichyaswat *et al.*, 2022). Taken together, this suggests that though wound healing at the graft site probably relies on local auxin supply, it can be enhanced by remote signals influenced by environmental conditions.

It should be noted that auxin is involved in a plethora of plant developmental processes, and its effect on regeneration cannot be considered specific (Vanneste & Friml, 2009). Further, other remote signals may act in parallel or together with auxin to control growth and regeneration. Thus, removal of the shoot of *Arabidopsis* resulted in severe inhibition of lateral root initiation and regeneration of cut root apical meristems. However, exogenous auxin had only a very mild effect on lateral root initiation in shootless plants and could not rescue root meristem regeneration at all, suggesting other long-range factors may be at play (Reed *et al.*, 1998; Matosevich *et al.*, 2020).

III. The role of sugars in regeneration

Apart from hormonal control, other systemic factors contribute to a coordinated wound response, an aspect that is mostly studied in the initiation of shoot-borne roots. Sugars, produced in the shoot via photosynthesis and transported systemically through the plant via

the phloem, were shown to affect regenerative responses. In hibiscus cuttings, leaf removal reduced the rooting capacity even when treated with auxin, but this could be rescued by sucrose supplementation to the cutting base (van Overbeek *et al.*, 1946). The sucrose effect depended on adequate ammonium levels; indeed, the wound-induced root primordium is also a sink for nitrogen-based compounds and microelements (Svenson & Davies, 1995; Zerche *et al.*, 2016).

Sucrose application promoted shoot-borne roots in dark-treated *Arabidopsis* seedlings or leaf explants (Takahashi *et al.*, 2003; Chen *et al.*, 2014) and rescued the reduction in shoot-borne roots in shoot-less cucumber seedlings (Qi *et al.*, 2020). The sugars required for wound-induced shoot-borne root formation are unlikely to come from local stores, as dark pretreatment of cuttings, which drains internal carbohydrate stores, could even improve rooting when cuttings were returned to normal light regimes (Klopotek *et al.*, 2010).

Carbohydrates are transported from leaves via the phloem, but it is unclear how they are recruited to wound-induced root initiation sites. Some evidence, mainly from gene expression studies, suggests an active change in sugar transport may induce the formation of a new sink. In *Arabidopsis*, mechanical wounding upregulates the expression of the hexose transporter *SUGAR TRANSPORTER4* (*STP4*) and the sucrose transporter *SUCROSE PROTON SYMPORTER3* (*SUC3*) (Truernit *et al.*, 1996; Meyer *et al.*, 2004). Expression of sucrose exporters from the SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTERS (SWEET) family are induced during the formation of roots from detached leaves (Chen *et al.*, 2012; Liu *et al.*, 2022). In rice, herbivory feeding of leaves led to the upregulation of *OsSUC4* (Chang *et al.*, 2019). Fungi attack in *Arabidopsis* leaves increased *STP4* expression and the sucrose hydrolysis activity of the membrane-bound CELL-WALL INVERTASE (*CWINV*) (Fotopoulos *et al.*, 2003; Sauer, 2007). Transcriptome analysis of *P. hybrida* cuttings revealed a temporal upregulation of *CWINV* and *STP* near the site of injury, followed by an increase in hexose content, shortly before wound-induced root emergence (Ahkami *et al.*, 2009; Klopotek *et al.*, 2016).

What regulates the induction of these sugar transport and metabolism genes is unknown. However, recently, a group of DOF (DNA-binding with one finger) transcription factors was found to be induced by physical damage to the plant. Curiously, amongst the genes induced by these DOFs was a SWEET transporter (Zhang *et al.*, 2022), suggesting they could also play a role in regulating sugar transport. Indeed, a mutant in a rice orthologue of the same DOFs was defective in sugar uptake and had reduced expression of *SUC* and *SWEET* genes (Wu *et al.*, 2018). Though these correlative studies suggest a link between changes in carbohydrate metabolism, transport, and wound response, functional studies are required to determine their role in controlling tissue regeneration.

Sugar signaling may also play a role in controlling regenerative growth. The *Arabidopsis gin-2* mutant, defective in the sugar sensor *hexokinase1*, does not initiate wound-induced roots in response to glucose and auxin application (Moore *et al.*, 2003). The target of rapamycin (TOR) protein kinase, integrates environmental cues and cellular energy levels to developmental and metabolic responses

(Dobrenel *et al.*, 2016). Chemical inhibition (Deng *et al.*, 2017) or genetic perturbation (Stitz *et al.*, 2022) of TOR leads to a reduction in root initiation in potato wound-induced roots or *Arabidopsis* lateral roots, respectively.

Signals rarely act on their own, and sugars and auxin have a reciprocal effect on one another, with a large overlap between glucose- and auxin-responsive genes (Mishra *et al.*, 2021). Consistently, there is an additive effect for these factors during rooting (van Overbeek *et al.*, 1946; Calamar & De Klerk, 2002; Moore *et al.*, 2003; Corrêa *et al.*, 2005; Agulló-Antón *et al.*, 2011); at the moment, however, the nature of this interaction during regeneration is unclear.

IV. Conclusions

Studies of regeneration have mostly focused on uncovering the molecular mechanisms underlying tissue regeneration competence. By contrast, this review highlights the systemic and coordinated nature of the regeneration response. Though we have limited ourselves to just two mobile signals, many molecules and hormones are systemically transported in the plant and can potentially affect tissue repair. Although research of this topic is still at an early stage, future studies can provide a broader, plant-wide view of the regeneration process and the factors controlling the decision of whether or not to regenerate.

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