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Plasmodesmata and hormones: pathways for plant development

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> "…[The] plant has means to control the symplastic continuity of its parts and to regulate the degree of isolation of its constituent cells. This form of regulation is a counterpart to that which results from the release and action of hormones. One is led to speculate whether hormones themselves might act in part by opening or closing symplastic pathways."
>
> (Carr, 1976, p. 287)

Plant development depends on local positional cues and on mobile non-cell-autonomous signals that can act at short or long distances. Plant hormones are growth factors that mediate local cell events as well as coordinate long-distance processes that affect the entire plant. While it is clear that hormones often act beyond the confines of single cells the mechanisms by which this is accomplished are longstanding questions, as exemplified by the quote above (Carr, 1976). The cytoplasmic connections between cells formed by plasmodesmata (PD) essentially render groups of cells as symplasts whose boundaries depend on the permeability of PD at any given cell interface. Symplastic fields change with developmental progression, and links to hormone action can be easily identified (Burch-Smith et al., 2011), although data examining causation is not readily available in the literature. Thus, how hormones influence PD remains poorly understood but there has recently been increasing attention to the role of PD in mediating hormonal flux and signaling (Figure 1).

Plasmodesmata directly connect neighboring cells allowing the intercellular trafficking of small molecules like metabolites and hormones as well as macromolecules like small RNAs and protein transcription factors that act as signaling molecules during development and defense, making PD crucial for communication between plant cells. Plasmodesmata are structurally complex and diverse, and transmission electron microscopy reveals that they are usually 30–50 nm in diameter and can consist of a single opening or multiple openings connected to each other via a central cavity (Burch-Smith et al., 2011). The desmotubule at the center of the PD consists of compressed endoplasmic reticulum (ER) and thus allows ER continuity between cells. The major conduit for cell-to-cell trafficking is likely the cytoplasmic sleeve, the fluid-filled space between the desmotubule and the delimiting plasma membranes of the connected cells. Plasmodesmata trafficking is often regulated by the controlled accumulation of callose, a β−1,3-glucan, in the cell wall surrounding a plasmodesma (Figure 1). Callose deposition reduces intercellular trafficking, while the converse occurs when callose is removed. A hallmark of plant development is the restriction of PD-mediated intercellular flux into groups of cells undergoing a specific developmental program distinct from their neighbors', a state termed symplastic isolation. Symplastic isolation is often marked by callose accumulation at PD of cells at the boundary of this group of cells, but it can also involve structural modification of PD. The importance of PD regulation in development is exemplified by studies of callose deposition during lateral root formation, where induction of callose deposition restricted the cell-to-cell trafficking of the SHORT-ROOT transcription factor and microRNA165 and disrupted protoxylem formation in developing roots (Vaten et al., 2011). While the callose-mediated isolation can be reversed after the developmental transition, structural modifications to PD are usually permanent (Burch-Smith et al., 2011). Although symplastic isolation has been assumed to be important for controlling hormonal and signaling fluxes, experimental evidence for this remains sparse. Further, it remains unclear how much influence PD and intercellular flux have on establishing hormonal gradients during development.

Perhaps the best-known plant hormone is auxin. Its primary effects are promoting cell division and expansion, and auxin signaling has been intensely investigated and described. The local flux of auxin depends on membrane-localized transporters, the AUX1/LAX transporters for influx, the general plasma-membrane-localized ABCB

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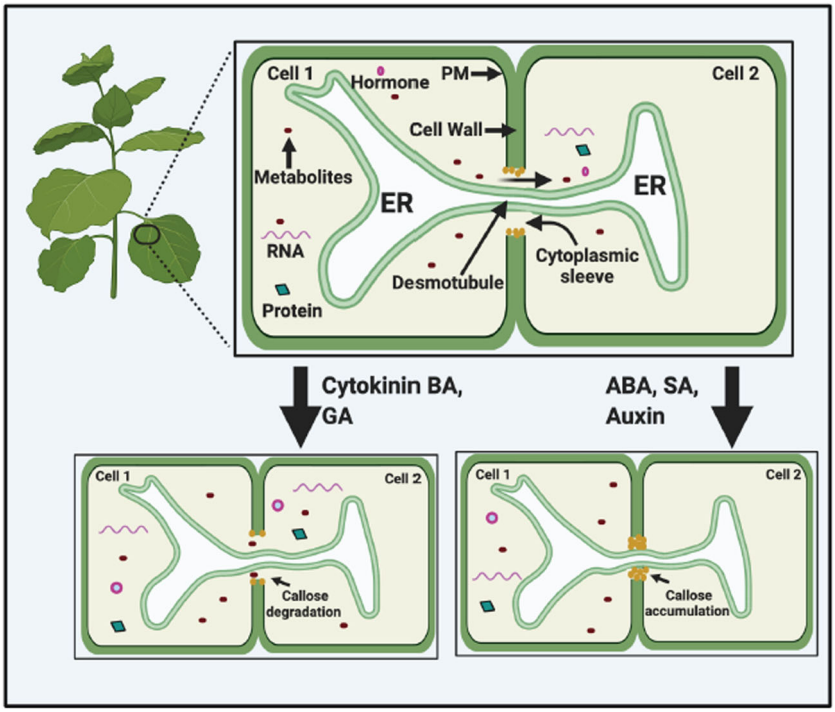

FIGURE 1 The effect of hormones on plasmodesmata-mediated trafficking. Schematic of two plant cells connected to each other by PD and the movement of metabolites and signaling molecules between the two cells. The hormones ABA, SA, and auxin can restrict intercellular trafficking through the deposition of callose in the cell wall at the PD. ABA may also decrease pore size through an alternative mechanism. The hormones cytokinin and GA cause the removal of callose at PD and increase intercellular trafficking. Cytokinins can also increase the formation of secondary PD. Created with BioRender.com

efflux transporters, and the polar PIN-FORMED (PIN) efflux carriers that also mediate auxin recycling within cells and between compartments. These transporters are essential for setting up the auxin gradients through which auxin exerts its effects as well as regulate auxin homeostasis by subcellular auxin compartmentalization. One puzzle, however, was whether auxin, a small hydrophilic molecule, moved between cells via plasmodesmata to exert its effects. Indeed, although the genome of the moss *Physcomitrium* (*Physcomitrella*) *patens* encodes homologs of auxin transporters, auxin moves via PD during lateral branching in the moss gametophore (Coudert et al., 2015). Exciting recent studies in *Arabidopsis thaliana* confirmed that not only can auxin move via PD in other plants, but that this movement is necessary to complement transporter-mediated auxin flux (Mellor et al., 2020) and is also required to establish tissue-level auxin gradients in the shoot (Gao et al., 2020). Indeed, auxin effects on PD include establishing local gradients important for root stem-cell identity (Liu et al., 2017), lateral root initiation (Sager et al., 2020), and shoot tropic responses (Han et al., 2014). Further, auxin-mediated callose accumulation at PD is implicated in tropism and lateral root formation (Han et al., 2014; Sager et al., 2020). It will be interesting to see how auxin flux is balanced between the genetically encoded transporters and PD, and we anticipate that this will be a question of considerable research interest in the near future.

Studies investigating bud dormancy have been informative for understanding PD–hormone interplay. Bud dormancy and release from dormancy in hybrid aspen and other trees are marked by profound changes to PD and intercellular trafficking in the buds mediated by various hormones. In aspen, PD closure at the onset of dormancy is accomplished by callose accumulation mediated by abscisic acid (ABA), preventing entry of growth-promoting factors like the protein FLOWERING LOCUS T (FT) into the meristem (Tylewicz et al., 2018). Release from dormancy is accompanied by removal of callose mediated by gibberellic acid (GA)-inducible β−1,3-glucanases in poplar (Rinne et al., 2011) and hybrid aspen (Singh et al., 2019). The gaseous hormone ethylene was also found to mediate PD opening to release dormancy in *Narcissus tazetta* (Li et al., 2012). Gibberellic acid and ABA traffic via PD in *Chara vulgaris* and *P. patens*, respectively (Kwiatkowska, 1991; Kitagawa et al., 2019). In contrast, the defense hormone salicylic acid (SA) does not traffic via the symplast but instead moves in the apoplast (Lim et al., 2016). Despite this, SA is well known to regulate plasmodesmata through callose dynamics, acting through the callose synthase enzyme CalS1 (Dong et al., 2008), PLASMODESMTA LOCATED PROTEINs (PDLPs) (Lee et al., 2011; Lim et al., 2016) and modulating lipid organization through the lipid-raft like protein REMORIN to control callose accumulation at PD (Huang et al., 2019; Figure 1).

While callose deposition and removal seem to be the primary mechanism through which hormones act to control PD trafficking during development, there are instances where other changes to PD have been observed. Exogenous ABA modified PD pore size in *P. patens* as application of ABA reduced intercellular trafficking of a fluorescent probe, and although PD in ABA-treated samples were narrower than those in control plants, no increase in PD callose in response

to ABA could be detected (Kitagawa et al., 2019). Thus, hormones may alter PD ultrastructure other than through callose metabolism, for example, through the cytoskeleton, although this has not been experimentally verified.

There are two major classes of PD that form at different developmental times. The first class is primary PD that form during cytokinesis when strands of ER become trapped in the new cell wall being formed between daughter cells. The second class is the secondary PD which are added to existing cell walls by a mechanism that remains elusive but likely involves cell wall remodeling (Burch-Smith et al., 2011). Application of the cytokinin benzyladenine (BA) to the shoot apical meristems of *Sinapis alba* induced secondary PD formation, a phenomenon that had previously been observed to occur during the SAM floral transition (Ormenese et al., 2006). This observation along with mutants with increased secondary PD formation could yield new avenues for understanding the intriguing phenomenon of how cell walls are modified coincident with the insertion of plasma membrane and ER to form a new PD.

Given the importance of hormones and PD to plant development, it is surprising that so much remains unknown about how the two interact to coordinate the production of effective signaling gradients and to allow the non-cell-autonomous effects of hormones. We expect that in the future more comprehensive studies that examine the effects of single hormones and combinations of hormones at physiological concertation on PD will be undertaken. The use of mathematical models to help explain the effects of PD on hormone gradients and signaling will be a boon to this field, as it has been for studies on auxin (Gao et al., 2020; Mellor et al., 2020). Efforts to understand how hormones interact with PD could also provide interesting insights into the cell biology of PD, for example, secondary PD formation and how PD ultrastructure can be altered by factors other than callose. In the long term, understanding and being able to predict the outcome of hormone–PD interactions could provide new tools for approaches that engineer resource allocation for maximizing the proportions of crop photosynthetic output that is available for human consumption (e.g., rice C_4 project; Ermakova et al., 2020). Such processes depend on PD for nutrient distribution and manipulating PD may have consequences for hormone signaling and plant development.

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