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ARTICLE in JOURNAL OF EXPERIMENTAL BOTANY • AUGUST 2013
Impact Factor: 5.53 · DOI: 10.1093/jxb/ert245 · Source: PubMed

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Gated communities: apoplastic and symplastic signals converge at plasmodesmata to control cell fates

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Received 7 June 2013; Revised 7 June 2013; Accepted 2 July 2013

Abstract
Due to their rigid cell walls, plant cells can only communicate with each other either by symplastic transport of diverse non-cell autonomous signalling molecules via plasmodesmata (PDs) or by endo- and exocytosis of signalling molecules via the extracellular apoplastic space. PDs are plasma membrane-lined channels spanning the cell wall between neighbouring cells, allowing the exchange of molecules by symplastic movement through them. This review focuses on developmental decisions that are coordinated by short- and long-distance communication of cells via PDs. We propose a model combining both apoplastic and symplastic signalling events via secreted ligands and their PD-localized receptor kinases which gate the symplastic transport of information molecules through PDs. Cell communities can thus coordinate cell-fate decisions non-cell autonomously by connecting or disconnecting symplastic subdomains. Here we concentrate on the establishment of such subdomains in the plant’s primary meristems that serve to maintain long-lasting stem cell populations in the shoot and root apical meristems, and discuss how apoplastic signalling via transport of information molecules through PDs is integrated with symplastic feedback signalling events.

Key words: Apoplast, peptide ligands, plasmodesmata, receptors, signalling, symplast.

Introduction
Plant cells, in contrast to animal cells, possess a rigid cell wall and remain fixed at a given position after cell division. Therefore they are highly dependent on positional cues to determine their identity. Laser ablation experiments in shoot and root meristems have elegantly proved the dependency of plant cells on positional cues and that cell identities are reversible (van den Berg et al., 1995, 1997; Reinhardt et al., 2003). Therefore, intercellular signalling processes are needed to exchange information between cells and are achieved either by apoplastic signalling events which involve ligands and plasma membrane-localized receptors or by symplastic information molecules moving through PDs.

PDs form narrow channels that interconnect plant cells with each other in order to allow intercellular movement of nutrients, but also signalling molecules in different symplastic subdomains (Epel, 1994; Rinne and van der Schoot, 1998). Primary PDs are already formed during cell divisions in the newly forming cell plate, whereas secondary PDs are formed in already established cell walls in localized breaks. Both classes of PDs are plasma membrane-lined channels through the cell walls of neighbouring cells building a central symplastically connected channel between two adjacent cells. They contain a membranous tube, the desmotubule, connected to the endoplasmic reticulum of both cells (Fig. 1). Both primary and secondary PDs can form higher-order structures by branching and generally allow for transport of transcription factors, metabolites, and even small RNAs needed for the necessary communication for developmental decisions, plant defence upon virus infection, and assimilate transport.

Mobile signals can theoretically pass through PDs in four different ways: (i) by travelling through the cytoplasmic sleeve; (ii) by entering the lumen of the endoplasmic reticulum-derived desmotubule; (iii) by lateral diffusion in the plasma membrane that lines the PD; or (iv) within the membrane of the desmotubule (Wu and Gallagher, 2012) (Fig. 1).

Although PDs form pores between cells across the rigid physical barrier of the cell wall, their potential for letting molecules of different sizes pass is dynamic and dependent on the production and/or degradation of callose (β-1,3-glucan) in the neck region of PDs. PD pores have a so-called size exclusion limit, allowing passage only of those molecules whose size falls below that limit (Crawford and Zambrisky, 2000). The activity of β-1,3-glucan synthases and glucanases regulates callose deposition and degradation and thereby affects the symplastic connectivity between plant cells. Furthermore, redox-potential and callose-binding proteins have been proposed to play a role in the PD callose modulation (Benitez-Alfonso et al., 2009; Simpson et al., 2009). However, it is still largely unknown which mechanisms and players serve to regulate traffic at PDs and select specific molecules for passage, while others are excluded from access to adjacent cells.
Regulation of meristematic fate decisions by symplastic movement of transcription factors and RNA through PDs

Plant transcription factors (TFs) have been reported to move between cells through PDs, and one of the first described cases is the TF KNOTTED1 (KN1). KN1 RNA is synthesized in the L2 layer of the shoot apical meristem (SAM) in maize, but the KN1 protein can be found also in the epidermal L1 layer (for SAM layer organization, see Fig. 2). It was shown that KN1 can interact with PDs to increase their size exclusion limit and mediate its own cell-to-cell transport. Furthermore, it was shown that KN1 can also transport its own sense RNA from cell to cell (Lucas et al., 1995). This report suggested for the first time that plant development and cell fate specification exploit intracellular communication by protein and RNA movement through PDs.

Another example of a mobile TF is the homeodomain TF SHORTROOT. It is expressed in the stele cells of the root and migrates to the immediately adjacent cell layer (the endodermis, the cortex/endodermis initial, or the quiescent centre). Here, it controls endodermis and stem cell maintenance together with the TF SCARECROW (Helariutta et al., 2000; Nakajima et al., 2001). The symplastic movement of the TF SHORTROOT from the stele to the endodermis and of microRNA165 in the opposite direction is PD dependent and can be regulated by CALLOSE SYNTHASE3, a bona fide callose synthase which belongs to a small gene family that can affect the size exclusion limit of PDs and therefore molecular trafficking between cells when misexpressed (Vatén et al., 2011).

The given examples all describe PD-dependent movement of TFs and RNA over a short distance to locally affect developmental decisions. However, there is also long-range movement of TFs, a prominent example being FLOWERING LOCUS T (FT). FT is produced in the phloem companion cells of leaves and cotyledons (Kotake et al., 2003) and moves to the SAM where it promotes the transition to flowering by interaction with the FLOWERING LOCUS D protein to ultimately promote the expression of LEAFY (Corbesier et al., 2007; Jaeger and Wigge, 2007; Mathieu et al., 2007). Transport of FT requires the activity of FT INTERACTING PROTEIN1.
maintains the surrounding stem cells (Doerner, 1998; Sarkar et al., 2007). WUSCHEL RELATED HOMEOBOX5 (WOX5), which is expressed in the quiescent centre cells, expresses the WUS homologue WOX5 in the root meristem, the four cells of the quiescent centre maintain the adjacent single layer of dedi-

cted stem cells giving rise to all the different cell layers of the root. The fate of stem cell maintenance in the root meristem. Although the architecture of the root stem cell niche is clearly distinct from the SAM, they share similar regulatory modules for their maintenance. In the root meristem, the four cells of the quiescent centre maintain the adjacent single layer of dedicated stem cells giving rise to all the different cell layers of the root. The quiescent centre cells express the WUS homologue WUSCHEL RELATED HOMEOBOX5 (WOX5), which maintains the surrounding stem cells (Doerner, 1998; Sarkar et al., 2007). The fate of columella stem cells (CSCs), which form cell layers immediately distal to the quiescent centre, are regulated by a feedback mechanism, similar to the CLV pathway operating in the SAM. Here, the CLV3 homologue CLE40 (CLAVATA3/EMBRYO SURROUNDING REGION40) acts as a signal from differentiated descendants, the columella cells (CCs), to restrict WOX5 expression in the quiescent centre (Stahl et al., 2009) (Fig. 3). The CLE40 signal is perceived by the receptor kinases ARABIDOPSIS CRINKLY4 (ACR4) and CLAVATA1 (CLV1), a key receptor kinase in SAM maintenance, and acts to restrict CSC fate in the Arabidopsis root meristem. Both CLV1 and ACR4 overlap in their expression domains in the distal root meristem where they localize to the plasma membrane and PDs. Here, ACR4 preferentially accumulates (Stahl et al., 2013). ACR4 and CLV1 interact directly and can assemble into complexes that differ in their composition and their subcellular localization. Importantly, PD-localized complexes appear to comprise more ACR4 molecules than those at the plasma membrane (Stahl et al., 2013).

We now introduce a new conceptual model that indicates how these receptors integrate apoplastic signalling of the secreted peptide CLE40 with symplastic signalling through PDs. We propose that a yet-unknown mobile stemness factor (e.g. a transcription factor or another mobile information molecule) can move from the quiescent centre cells through PDs to the next cell layers. This movement could be controlled by the PD-localized receptor kinase complexes consisting of ACR4 and CLV1. At the cell wall shared between the quiescent centre and CSCs, only few or no CLE40 peptide is available from the apoplastic space to bind to and activate the receptor complexes; therefore, the stemness factor remains unphosphorylated and can move further to the CSCs to maintain their stem cell character. CLE40 concentration in the apoplast is higher between CSC and CCs, and the ACR4/CLV1 complexes are activated by the CLE40 ligand. Thus, the stemness factor will be phosphorylated when it diffuses towards the PDs either by direct interaction with the receptor kinase domains or by other downstream signalling components, restricting its further movement towards the CCs. Lacking a sufficient amount of stemness factor, these cells will now differentiate (Fig. 4). Noteworthy, a somewhat similar mechanism that allows controlling movement of information molecules via selective phosphorylation has been described for viral infections. Here, phosphorylation of movement protein inhibits its mobility and therefore viral spread after infection (Waigmann et al., 2000).

Fig. 3. Distal stem cell regulation in the root meristem. Red shading indicates expression of CLE40 (in differentiated columnella cells); blue shading indicates expression of WOX5 (in the quiescent centre). The red blocked line indicates negative regulation by CLE40 on WOX5 expression.

Coordination of developmental decisions at plasmodesmata
established, leading to a symplastic subdomain that regulates root meristem maintenance. Many components are shared or closely related in stem cell maintenance in the root and the shoot (e.g. CLE peptides and the receptor kinase CLV1). Therefore, it is likely that a similar mechanism for apo- and symplastic integration in meristem regulation also exists in the shoot.

**Conclusions**

Developmental decisions in plants are made as a result of intensive communication between cells. Plants have two major pathways to achieve this: either apoplastic and/or symplastic signalling. PDs play a major role in allowing and regulating transport of information molecules that serve to establish functional cell communities with different developmental fates. In this review, we have proposed a novel conceptual model integrating both ways of communication, by focusing on the example of distal root stem cell maintenance. Here, PD-localized receptor kinases could serve to bridge the gap between apoplastic signalling molecules and mobile information molecules, thereby establishing the necessary symplastic subdomains. In contrast to the classical peptide-triggered signalling pathway controlling transcription of target genes, we propose here that stem cell signalling in the root depends on the differential mobility of stemness factors. Future research on PD-localized receptor kinases and the identification of mobile targets will allow the addition of more detail to this only just emerging picture.

**References**


