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Symplastic communication in organ formation and tissue patterning

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Communication between cells is a crucial step to coordinate organ formation and tissue patterning. In plants, the intercellular transport of metabolites and signalling molecules occur symplastically through membranous structures (named plasmodesmata) that traverse the cell wall to connect the cytoplasm and endoplasmic reticulum of neighbouring cells. This review aims to highlight the importance of symplastic communication in plant development. We revisit current literature reporting the effects of changing plasmodesmata in cell morphogenesis, organ initiation and meristem maintenance and comment on recent work involving the identification of novel plasmodesmata regulators and of mobile developmental proteins and RNA molecules. New opportunities for unravelling the dynamic regulation and function of plasmodesmata are also discussed.

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Introduction

At the end of the XIX century, plants were thought to be a mere aggregation of isolated cells; however, Eduard Tangl completely shifted the paradigm when he observed cytoplasmic intercellular connections in cotyledons of the tree *Strychnos nux-vomica* [1]. His discovery demonstrated that, despite the cell wall, plant cells communicate to each other and form higher order structures that characterize organisms. Some years later, in 1901, Strasburger named these connections plasmodesmata (PD), etymologically fluid bonds [1,2].

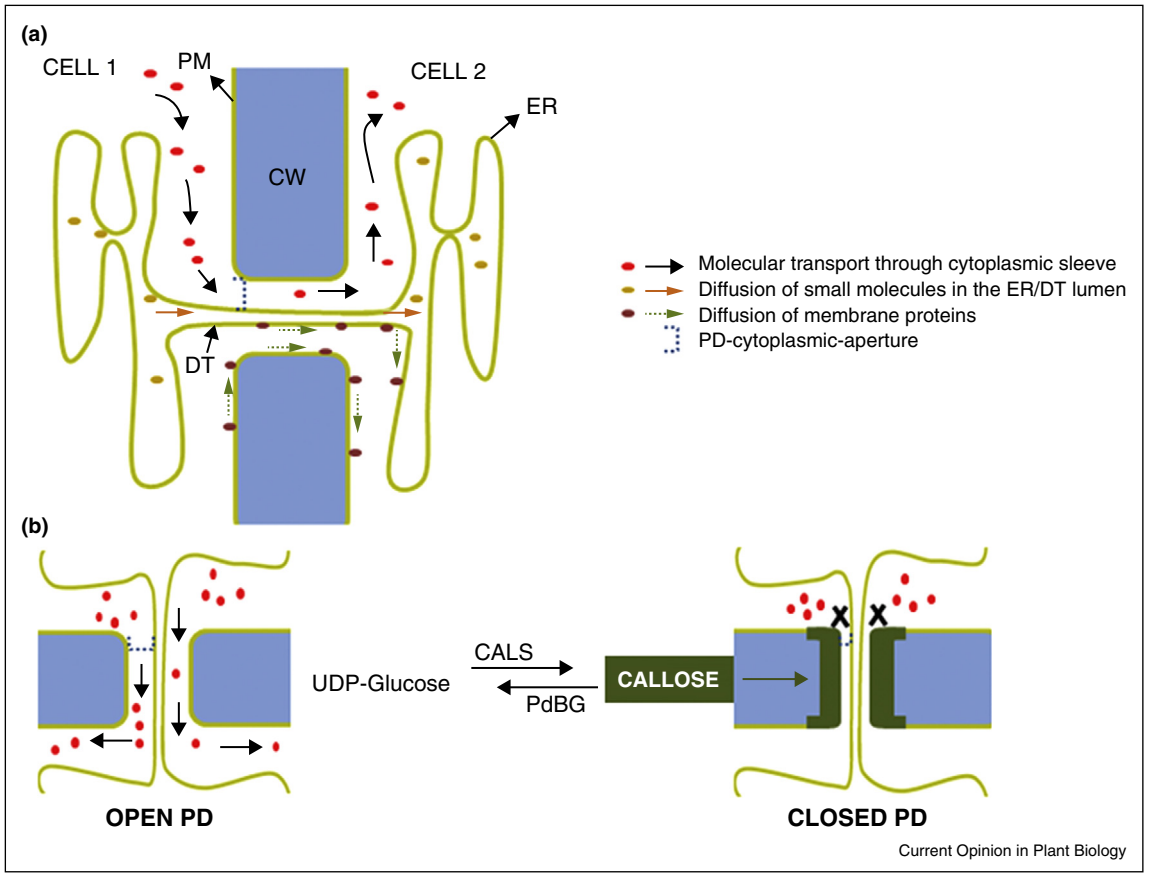
In simple terms, PD are channels made of plasma membrane (PM) that provide cytoplasmic and membranous continuity between neighbouring cells forming the symplasm (Figure 1a). Microscopically these channels appear as concentric cylinders, due to the presence of the desmotubule (DT), a structure derived from endoplasmic reticulum (ER) that becomes trapped in the middle of the channel during cytokinesis [3••,4]. Symplastic molecular transport mainly occurs through the cytoplasmic sleeve: the space left between the PM and the DT. Alternative methods for transport can be proposed including diffusion in the ER/DT lumen and lateral segregation of proteins in the PM and ER membrane but their contribution to symplastic intercellular communication is not well defined [5–7] (Figure 1a).

The capacity of molecules to move through PD cytoplasmic sleeve depends on their size and shape and on the cell type and/or developmental stage where they appear. This is because PD number and size exclusion limit (SEL, the maximum molecular size allowed through any specific pore) are developmentally (and environmentally) regulated [8]. Symplastic molecular transport is extremely important in the phloem, where PD connect companion cells (CC), sieve elements (SE) and the surrounding tissues to regulate communication of metabolites and signals between distant organs [9]. It is also essential in the meristems where transcription factors (and other signalling molecules) move to determine cell fate and tissue development [10,11]. Here we summarize information from recent papers supporting the role of PD in organ formation, meristem development and tissue patterning. Three current topics will be discussed: the regulation of PD during organ development, the role of PD-located receptor proteins in this process and the identification of novel mobile developmental regulators (non-cell autonomous proteins and RNA molecules).

Plasmodesmata regulation during organ formation and vascular patterning

As a key factor in cell-to-cell communication, PD-cytoplasmic aperture is tightly regulated (Figure 1). This is, at least partly, achieved by modifications of the surrounding cell walls, which have different composition (and properties) in the microdomains that are in contact with PD, such as enrichment in certain pectic polysaccharides and callose [4]. Callose (a β-1,3-glucan polymer) is found delimiting PD sites and its accumulation greatly influences transport through the channel by imposing physical constrictions on PD-cytoplasmic aperture (Figure 1b).

Figure 1



Transport pathways and PD regulation by callose. **(a)** Intercellular transport occur through PD cytoplasmic sleeve (black arrows), by diffusion in the lumen of the endoplasmic reticulum (ER) and the desmotubule (DT) (orange arrows) and, potentially, by lateral segregation in the membranes (green discontinuous arrows). Plasma membrane (PM), cell wall (CW) and PD-cytoplasmic aperture (in discontinuous blue) are indicated. **(b)** PD transport is regulated by the deposition of callose in the surrounding cell wall. Callose is produced at PD sites from UDP-glucose by callose synthases (CALS) and degraded to glucose subunits by PD-located beta-1,3 glucanases (PdBG). Callose turnover depends on the activity of these enzymes. High levels of callose restricts PD-cytoplasmic aperture blocking molecular transport thus cell-to-cell symplastic connectivity.

Callose synthases (CALS) and β-1,3 glucanases (PdBG) that localize at PD sites were identified, providing the machinery for dynamic regulation of callose turnover *in situ*. Altering the expression of these enzymes affects PD transport capacity, thus cell-to-cell symplastic connectivity (Figure 1b). Indeed, gain-of-function mutations in *CALS3* trigger an excessive accumulation of callose at PD impairing root organ development by blocking the transport of transcription factors and miRNAs (such as SHORT-ROOT and microRNA165) that determine the correct formation of the vascular tissue [12]. Further studies using transgenic lines expressing a strongly activated version of CALS3 in specific tissue types and under inducible promoters reveal the importance of callose regulation in the formation of lateral roots and in the transport of hormones involved in vascular patterning and meristem maintenance [12–15]. Characterization of loss-of-function mutations and RNAi lines in CALS10 and CALS7 support the role of callose, and PD, in organ formation and patterning. Mutants in CALS10 (also known as Glucan-Synthase-Like 8 or GSL8) display stomata clustering, presumably due to the unrestricted mobility of the bHLH transcription factor SPEECH-LESS (SPCH) which controls asymmetric cell division in leaves to establish stomata cell fate [16,17]. Separate research, using an inducible RNAi line, identified the role of GSL8 in hypocotyl bending in response to phototropism, a phenotype associated with auxin gradient formation [18]. On the other hand, decreasing CALS7 expression affects the formation of sieve pores: a special type of enlarged PD found at the cell plate of adjacent SE, leading to defective phloem transport, reduced seedling height and aborted embryos among other defects [19,20]. Similarly, a CALS mutant in maize, named *tie-dyed2* (*tdy-2*), is affected in vascular development, specifically in the connections between CC and SE [21]. Correspondingly,