Plasmodesmata Conductivity Regulation

Subjects: Plant Sciences

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Plant cells form a multicellular symplast via cytoplasmic bridges called plasmodesmata (Pd) and the endoplasmic reticulum (ER) that crosses almost all plant tissues. The Pd proteome is mainly represented by secreted Pd-associated proteins (PdAPs), the repertoire of which quickly adapts to environmental conditions and responds to biotic and abiotic stresses. Although the important role of Pd in stress-induced reactions is universally recognized, the mechanisms of Pd control are still not fully understood. The negative role of callose in Pd permeability has been convincingly confirmed experimentally, yet the roles of cytoskeletal elements and many PdAPs remain unclear. Here, we discuss the contribution of each protein component to Pd control. Based on known data, we offer mechanistic models of mature leaf Pd regulation in response to stressful effects.

Keywords: plasmodesmata (Pd) ; Pd-associated proteins ; desmotubule ; callose

1. Introduction

Due to their immobile lifestyle, plants are exposed to many abiotic and biotic stress factors. A coordinated and generalized plant response to adverse environmental factors is accompanied by activation of both apoplastic and symplastic transport of macromolecules. An understanding of the mechanisms of anti-stress reactions in plants has been facilitated by data obtained in recent years, indicating the role of intracellular traffic of secreted proteins with the participation of the endoplasmic reticulum (ER) and Golgi apparatus (GA) and the formation of an idea of alternative protein secretion pathways bypassing the GA.

2. Plasmodesmata Conductivity Regulation: A Mechanistic Model

The increasing number of studies indicating a link between abiotic and biotic stress responses and secretion pathways offers research avenues towards understanding mechanisms involving the participation of plasmodesmata (Pd) in the plant stress tolerance**.** With Pd, there is a direct connection between the symplast and the phloem that serves as a long-distance conductor in the vasculature, thus promoting rapid movement of materials between tissues both over short distances and over long distances throughout the plant. Pd provide a controlled symplastic exchange of both low molecular weight compounds and larger molecules, such as signaling molecules, transcription factors, non-cell-autonomous plant proteins, small regulatory RNAs and messenger RNAs, between plant cells, allowing general reactions in their growth processes and in response to stressful environmental factors. Through Pd and phloem, photosynthesis products from the mesophyll of source leaves are exported to sink leaves and the plant growth point. Sucrose, as a primary carbohydrate transported long distances in many plant species, is loaded into the phloem and unloaded into distal sink tissues. The productivity of agricultural plants largely depends on the efficiency of sucrose and other carbohydrates export from the mesophyll to the phloem through Pd, and further to the ripening fruits and grains.

The important role of Pd in stress response is universally recognized. At the same time, the mechanisms for regulating Pd functions and permeability after stress impacts are still not fully understood. If the negative role of callose in the control of intercellular molecular flow via Pd is convincingly confirmed experimentally, the role of cytoskeletal elements and protein components, called Pd-associated proteins (PdAPs), is mostly unclear. The analysis of the Pd proteome revealed that most PdAPs are secreted proteins that might be involved in controlling Pd permeability under abiotic and biotic stress. It is still unclear which genes and protein factors encoded by stress-induced genes are activated in source leaf cells to provide a fast and generalized stress response, leading to an increase in Pd conductivity and the outflow of photoassimilates to sink leaves. We assumed that the search for these genes should be carried out among genes with different levels of mRNA accumulation in leaves and roots as well as after stress challenge. The analysis of the PdAPs allows evaluating the role of secreted proteins in the functioning of Pd. The proteomic study of a Pd-enriched *Arabidopsis* cell wall fraction showed that most PdAPs are secreted proteins. The Pd structure, including its extracellular and endocellular parts,

involves both cytoplasmic non-secreted proteins and secreted proteins control, such as in the case of callose metabolism. It was previously believed that the list of cytoplasmic PdAPs located directly in the intracellular cytoplasmic sleeve was limited by actin and myosin.

The reactions of mature leaves Pd to stress are controversial due to the nature of the stressful agents, and, most importantly, to the different time points after stress impact. It is generally accepted that stress responses include Pd closure as a result of reversible callose deposition.

If we proceed from the Pd structure along channels in the cell wall that contain the dumbbell-shaped ER DT inside them and ducts, or Pd sleeves, surrounding DT, then there are several ways to block the movement of molecules through these structures (Figure 1).

First, is stimulating callose deposition around Pd. Second, by increasing the intracellular pressure, thereby compressing the ER DT and blocking the entrance to Pd. Third, the deposition of calreticulin and reticulons in the DT lumen leads to the expansion of the ER DT lumen. Fourth, narrowing the Pd sleeves, as probably occurs through the participation of the actin-formin complex, as well as the accumulation of remorin, PDLP1 and 5, GnTL, and ^{C1}RGP. Pd opening, as a process opposite to closing, can include (1) the removal of callose and (2) the displacement of negative regulators from the Pd structure. PME and NCAPP can also have an indirect positive effect on Pd dilation. Since most PdAPs are secreted proteins, modification of the intracellular protein trafficking pathways is also involved in Pd control.

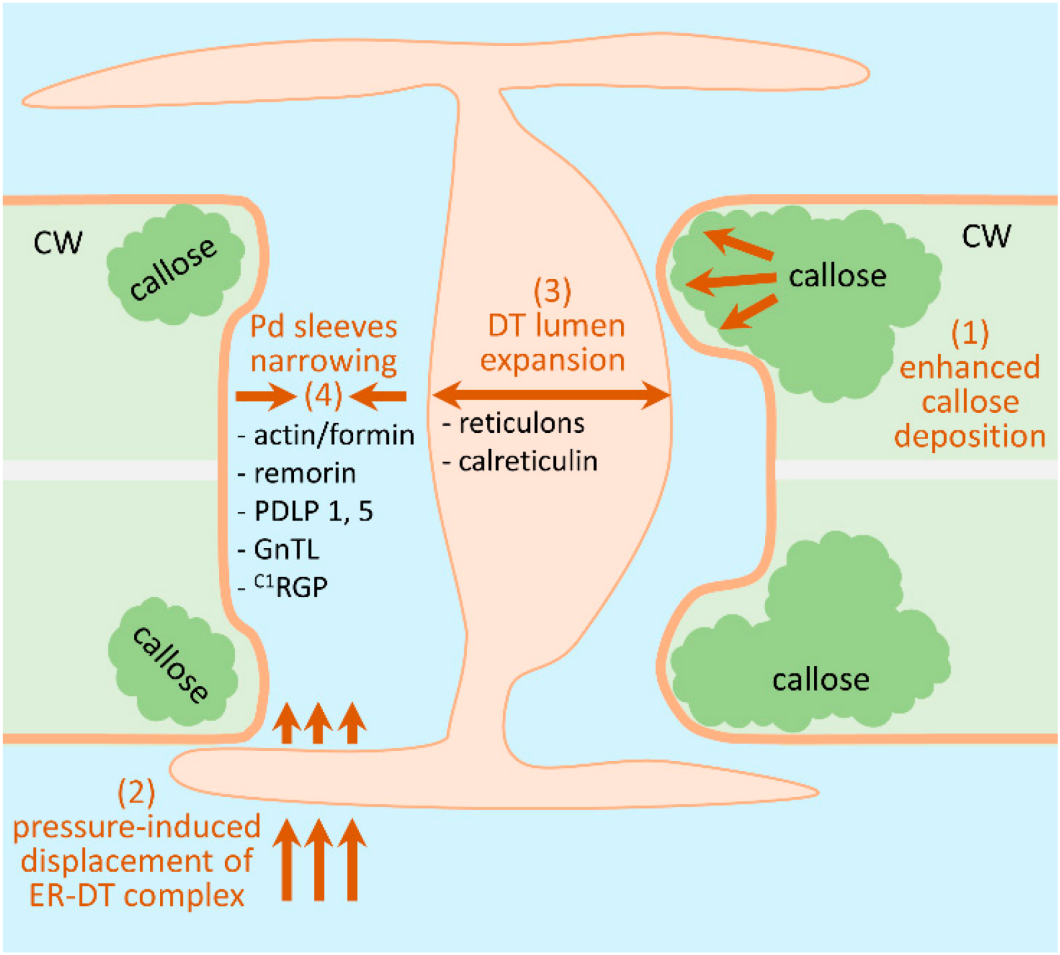

Figure 1. Schematic representation of plasmodesmata permeability negative regulation. (**1**) callose depositions around Pd neck; (**2**) stress-induced increasing of the intracellular pressure leading to the compression of the ER DT and blocking Pd entrance; (**3**) ER DT lumen expansion as a result of calreticulin and reticulons deposition; (**4**) narrowing of the cytoplasmic sleeves.

The putative mechanisms for the participation of PdAPs in the regulation of Pd presented in Figure 1 are diverse, but ultimately come down to the means of closing/opening the molecule passage through Pd sleeves surrounding the DT.

The publication can be found here: https://www.mdpi.com/2223-7747/8/12/595/htm