CellPress

Review

# Receptor Complex Mediated Regulation of Symplastic Traffic

Yvonne Stahl[1,*] and Christine Faulkner[2,*]

**Plant receptor kinases (RKs) and receptor proteins (RPs) are involved in a plethora of cellular processes, including developmental decisions and immune responses. There is increasing evidence that plasmodesmata (PD)-localized RKs and RPs act as nexuses that perceive extracellular signals and convey them into intra- and intercellular responses by regulating the exchange of molecules through PD. How RK/RP complexes regulate the specific and nonspecific traffic of molecules through PD, and how these receptors are specifically targeted to PD, have been elusive but underpin comprehensive understanding of the function and regulation of the symplast. In this review we gather the current knowledge of RK/RP complex function at PD and how they might regulate intercellular traffic.**

## A Newly Emerging Role of Receptors at Plasmodesmata

Plasmodesmata (PD) are membrane lined pores that directly connect the cytoplasm of adjacent cells. Thus, PD generate a cytoplasmic continuum termed the symplast that connects cells within and between tissues and organs, throughout the whole plant. In the simplest context, the symplast allows the free diffusion of molecules that are small enough to pass through PD from cell to cell. In addition, PD allow the specific and active trafficking of larger proteins and RNAs between cells and thus create the possibility for many classes of molecules to have a direct route of passage to other tissues.

Mobile molecules can act as long- and short-range intercellular signals and define responses to both developmental and environmental stimuli. Accordingly, PD must be regulated to control molecular traffic between cells. Very little is understood about the mechanisms by which PD function in this capacity. For passive translocation of molecules via PD, regulation occurs with regard to the aperture of the pore, that is, whether the plasmodesma is open or restricted. For active translocation of larger molecules such as transcription factors (TFs) there is evidence that passage through the pore is dependent on chaperones that unfold and fold the protein [1]. There are also hypotheses that phosphorylation might either facilitate or prevent passage of some classes of molecules through PD [2]. Whether regulation is specific or nonspecific, PD respond to changes in the extracellular environment [3–5] and thus regulatory mechanisms might involve transmission of a signal across the plasmodesmal plasma membrane (PD PM), thereby converging apoplastic and symplastic signaling (Figure 1).

Receptor kinases (RKs) and receptor proteins (RPs) are anchored in the plasma membrane (PM) and display receptor domains on the extracellular face of the cell. RK receptor domains are directly linked to an intracellular kinase domain by a single pass transmembrane domain. RKs and RPs perceive extracellular signals via their apoplastic receptor domains and this triggers intracellular signaling, often via ligand-induced complex formation.

### Trends

There are increasing identifications of plasmodesmata-located receptor kinases and receptor complexes.

Receptor kinases CLV1 and ACR4 form a specific complex in the plasmodesmal plasma membrane.

The receptor kinase FLS2 and the receptor protein LYM2 modify plasmodesmal function in response to the pathogen-associated ligands flg22 and chitin, respectively.

Plasmodesmal membranes have many characteristics of membrane microdomains, that is, they are enriched in sphingolipids and sterols and contain proteins such as remorins and tetraspanins. Membrane microdomains are associated with receptor signaling in animal cells.

[1]Institute for Developmental Genetics, Heinrich-Heine-University, Universitätsstrasse 1, D-40225, Düsseldorf, Germany
[2]John Innes Centre, Norwich Research Park, Norwich NR4 7UH, UK

*Correspondence:
Yvonne.Stahl@hhu.de (Y. Stahl) and
Christine.Faulkner@jic.ac.uk
(C. Faulkner).

 http://dx.doi.org/10.1016/j.tplants.2015.11.002

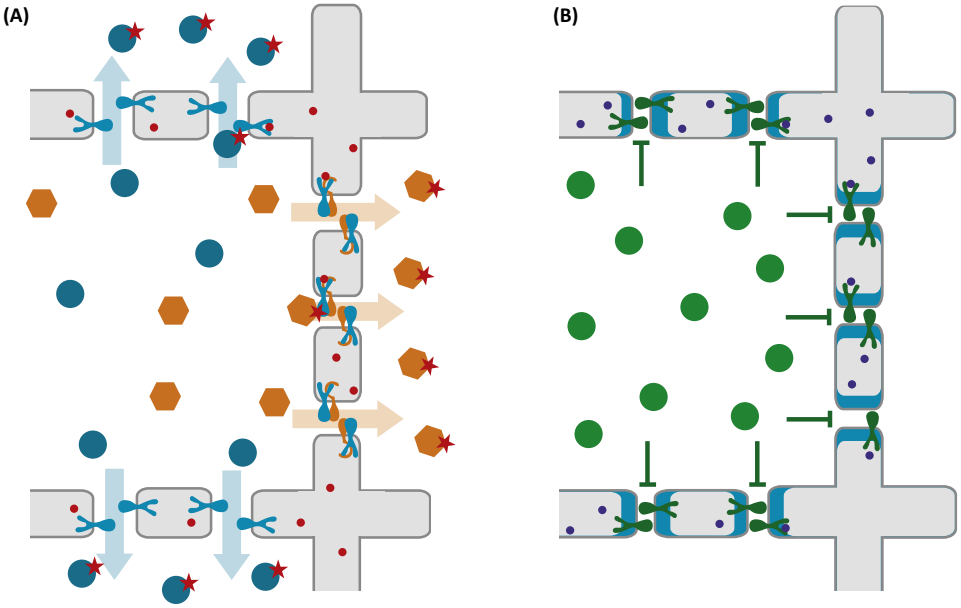


Figure 1. Models of Specific or Nonspecific Movement through Plasmodesmata (PD) Mediated by Receptor Kinases (RKs). Dark gray lines represent the plasma membrane (PM) and light gray boxes represent the cell wall. (A) PM-localized RKs (blue and orange) may facilitate cell-to-cell trafficking of macromolecules (circles and hexagons) by phosphorylation (red asterisks) of specific cargoes upon perception of an extracellular ligand (red dots). This may define cell fate as spatial information may be relayed into directional transport (indicated by arrows) of a morphogenic signal. RKs may alternatively regulate directional transport by polarized localization and/or receptor complex formation. (B) RKs (green) might modulate nonspecific flux of macromolecules (circles) between cells via triggering localized callose deposition (blue) following extracellular ligand (purple dots) perception. Callose deposition induces a reduction in plasmodesmal aperture and thus influences the size exclusion limit (SEL) for all classes of molecules.

RKs and RPs feature in multiple cellular processes, including developmental transitions [6] and immune responses [7]. In plant development, RKs and RPs can perceive small signaling peptides in order to maintain stem cell homeostasis in the shoot and the root apical meristems. In plant immunity, RKs and RPs act as pattern recognition receptors (PRRs) for many classes of pathogenic microbes, and upon binding of pathogen-derived molecules trigger intracellular signaling cascades that initiate defense responses.

The PM lines the PD pore and thus is continuous between cells. Purification and analysis of PD membranes has indicated that the PD PM contains many membrane-anchored and integral membrane proteins [8]. Approximately 30% of all type 1 membrane proteins (secreted proteins with a single transmembrane domain) in *Arabidopsis* are predicted to be RKs [9,10]. The *Arabidopsis* PD proteome contains a similar proportion of RKs in purified plasmodesmal extracts (approximately 29% [8]) indicating they are likely to be as significant to PD function as they are across the remainder of the plasma membrane. Indeed, a handful of PD located receptors have been identified (Table 1) and some of these have been shown to have PD-specific functions or to form PD-specific complexes [3,11–15].

PD-specific receptor complexes and receptor signaling is reminiscent of the specification of receptor signaling to different membrane domains in animal immunity. Some animal immune receptors are activated upon recruitment to **membrane microdomains** (see Glossary), correlating receptor complex formation and activity with the lipid environment [16]. Further, some animal receptors, such as the Toll-like receptors have subcellular and tissue specificity that

## Glossary

**ACR4:** ARABIDOPSIS CRINKLY4, the *Arabidopsis thaliana* homolog of CR4. Localizes to the PM and PD and was found to form homo- and heteromeric complexes with the leucine-rich repeat RK CLAVATA1.
**BAK1:** BRI-ASSOCIATED RECEPTOR KINASE1, leucine-rich repeat RK that acts as a coreceptor for multiple leucine-rich repeat RKs including FLS2.
**CERK1:** chitin elicitor receptor kinase1, lysin motif RK essential for chitin perception and multiple chitin-triggered immune responses.
**CLV1:** CLAVATA1, leucine-rich repeat RK that was found to regulate stem cell homeostasis in both shoot and root meristems of *Arabidopsis thaliana* by perception of small peptide ligands.
**CLE40:** CLAVATA3/EMBRYO SURROUNDING REGION40, small peptide shown to regulate distal stem cell fate together with the RKs ACR4 and CLV1 in the *Arabidopsis* root.
**Distal stem cells:** cells distal (towards the root tip) of the QC, similar to CSCs in the *Arabidopsis* root.
**FLS2:** FLAGELLIN SENSING2, leucine-rich repeat RK that binds flagellin, in complex with BAK1, and initiates immune responses.
**FRET/FLIM:** Förster resonance energy transfer/fluorescence lifetime imaging microscopy, method to measure protein–protein interaction *in vivo*.
**FTIP1:** FLOWERING LOCUS T (FT)-INTERACTING PROTEIN1, essential regulator that is required for FT movement in *Arabidopsis*.
**LYM2:** LYSIN MOTIF DOMAIN-CONTAINING GLYCOSYLPHOSPHATIDYLINOSITOL-ANCHORED PROTEIN, lysin motif RP that is enriched at PD and functions independently of CERK1 to trigger PD closure in response to chitin.
**MAMP:** microbe-associated molecular pattern, a molecule or molecule fragment that is common to a class of microbe and can be detected by receptors of another organism. These may be peptides such as flg22 (from flagellin) or oligosaccharides such as chitin.
**Membrane microdomain:** a subdomain of a phospholipid bilayer that is specified by its lipid (e.g., sterol- and sphingolipid-enriched) or protein composition (e.g., by the