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# Integrating Hormone- and Micromolecule-Mediated Signaling with Plasmodesmal Communication

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## ABSTRACT

**Intercellular and supracellular communications through plasmodesmata are involved in vital processes for plant development and physiological responses. Micro- and macromolecules, including hormones, RNA, and proteins, serve as biological information vectors that traffic through the plasmodesmata between cells. Previous studies demonstrated that the plasmodesmata are elaborately regulated, whereby a long queue of multiple signaling molecules forms. However, the mechanism by which these signals are coupled or coordinated in terms of simultaneous transport in a single channel remains a puzzle. In the last few years, several phytohormones that could function as both non-cell-autonomous signals and plasmodesmal regulators have been disclosed. Plasmodesmal regulators such as auxin, salicylic acid, reactive oxygen species, gibberellic acids, chitin, and jasmonic acid could regulate intercellular trafficking by adjusting plasmodesmal permeability. Here, callose, along with β-glucan synthase and β-glucanase, plays a critical role in regulating plasmodesmal permeability. Interestingly, most of the previously identified regulators are capable of diffusing through the plasmodesmata. Given the small sizes of these molecules, the plasmodesmata are prominent intercellular channels that allow diffusion-based movement of those signaling molecules. Obviously, intercellular communication is under the control of a major mechanism, named a feedback loop, at the plasmodesmata, which mediates complicated biological behaviors. Prospective research on the mechanism of coupling micromolecules at the plasmodesmata for developmental signaling and nutrient provision will help us to understand how plants coordinate their development and photosynthetic assimilation, which is important for agriculture.**

**Keywords:** callose, cell-to-cell movement, hormone, intercellular signaling, plasmodesmata

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## INTRODUCTION

Intercellular communication through plasmodesmata involves vital processes for plant development and physiological responses (Lucas and Lee, 2004; Lucas et al., 2009; Xu and Jackson, 2010; Brunkard et al., 2013; Han et al., 2014b). For instance, recent studies have revealed that lateral root emergence in *Arabidopsis* requires the programmed regulation of symplasmic intercellular connectivity (Vaten et al., 2011; Benitez-Alfonso et al., 2013). The plasmodesmal switch also controls plant tropic responses in the hypocotyl (Han et al., 2014a). In addition, plasmodesmal closure is involved in the innate immune responses controlled by salicylic acid in *Arabidopsis* (Wang et al., 2013; Caillaud et al., 2014). Furthermore, plasmodesmal reopening is required to release bud dormancy in *Populus* by allowing signals to be exchanged (Rinne et al., 2011). In general, a broad range of biological processes are regulated by the plasmodesmata during plant growth. To coordinate these biological processes, micro- and macromolecules, such as ions, sugars, hormones, RNAs, and proteins, serve as biological signals and move through the plasmodesmata between the neighboring cells. It is believed that the plasmodesmata are elaborately regulated, whereby a long queue of multiple signaling molecules forms. However, the mechanism by which these signals are coupled or coordinated

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in terms of simultaneous transport in a single channel remains unclear. In the last few years, several plasmodesmal regulators that could also function as non-cell-autonomous signals have been disclosed (Benitez-Alfonso et al., 2009, 2013; Burch-Smith et al., 2011; Rim et al., 2011; Rinne et al., 2011; Vaten et al., 2011; Stonebloom et al., 2012; Faulkner et al., 2013; Wang et al., 2013; Caillaud et al., 2014; Duan et al., 2014; Han et al., 2014a; Kumar et al., 2015). In this review, we highlight recent advances in the regulation of plasmodesmata by non-cell-autonomous intracellular and intercellular signaling micromolecules, which is pivotal for plant development, physiology, and defense. We also provide insights into how callose dynamically regulates plasmodesmal symplasmic channels. Finally, we describe the fascinating discovery of the feedback regulation underlying the regulatory mechanism of plasmodesmal permeability.

## MICROMOLECULE DIFFUSE THROUGH THE PLASMODESMATA AS A SIGNALING VECTOR

Several micromolecules may function as signaling vectors or signals with directivity to carry bountiful programmed information to trigger diverse biological processes in plants by exchange among cells. The phytohormones, such as auxin, cytokinin (CK), gibberellic acid (GA), salicylic acid (SA), and abscisic acid (ABA), are prominent signaling micromolecules with different signal transduction pathways in the course of plant developmental and physiological processes. In addition, many metabolites are involved in the cellular signaling process. For example, sucrose has been fully accepted as a true signal in controlling many developmental processes (Tognetti et al., 2013; Ruan, 2014; Barbier et al., 2015). Different types of inorganic substances and ions are typical micromolecules that function as important cellular signals. $Ca^{2+}$ is widely recognized as a secondary signaling molecule in biology. Reactive oxygen species (ROS) also function as a stress signal to alter the profile of gene expression. In general, given the small sizes of these molecules, plasmodesmata are prominent intercellular channels that allow diffusion-based movement of those signaling molecules. Recent studies have provided evidence supporting this hypothesis by analyzing plant mutants with abnormal plasmodesmal permeability.

### Phytohormones

Phytohormones are critical signaling molecules that control multiple pathways during plant biological processes. These pathways often involve a pivotal step that requires intercellular communication by one or more phytohormones. In particular, cell pattern formation is dependent on the trafficking of phytohormones among cells to transfer the diverse biological information (Sabatini et al., 1999; Leyser, 2005; Vanneste and Friml, 2009; Zhao et al., 2010; Band et al., 2012; Brunoud et al., 2012). There are two major pathways of phytohormone transmembrane transport: transporter-dependent transport and diffusion-based transmembrane movement. Using auxin as an example, studies have focused on the mechanism of polar auxin transport through auxin efflux and influx transporters (Bennett et al., 1996; Jurgens and Geldner, 2007; Christie et al., 2011; Adamowski and Friml, 2015). It is widely accepted that the asymmetric localization of the auxin efflux transporter in a plant cell contributes to the polarity of auxin transmembrane movement (Adamowski and Friml, 2015). PIN family genes, which encode a typical auxin efflux transporter in plants, are key factors regulating the polar auxin movement, because *pin* mutants display multiple phenotypes, including compromised auxin transport. In contrast, studies on the auxin maximum at the shoot apical meristem revealed that chemiosmosis-based auxin movement was able to dissipate the auxin maximum formed by the polar auxin movement (Jonsson et al., 2006; Smith et al., 2006; Bayer et al., 2009). According to the model of chemiosmosis-based auxin movement, the size of the auxin maximum can be disturbed by auxin diffusion factor. Compared with the chemiosmosis-based auxin movement, the auxin diffusion through plasmodesmata without any transmembrane movement could lead to more efficient dissipation of the accumulated auxin (Lucas and Lee, 2004). At present, one of the prominent questions regarding the auxin signaling pathway is whether auxin diffuses through the plasmodesmata. Indole-3-acetic acid (IAA), the most important auxin produced by plants, has a low molecular weight of 175 Da and is thus believed to diffuse through the plasmodesmata. This size is much smaller than that of proteins, such as transcription factors, which can successfully traffic through the plasmodesmata (Kim et al., 2005; Lucas et al., 2009; Xu and Jackson, 2010). The direct evidence supporting auxin movement through plasmodesmata was provided by recent studies on the *Arabidopsis* mutant *gsl8*, which has increased plasmodesmal permeability (Han et al., 2014a). An auxin-loading assay using isotope-labeled auxin and a DII-Venus auxin sensor measuring endogenous auxin levels revealed that auxin diffusion through the plasmodesmata could be enhanced by reducing the plasmodesmal callose. In this study, auxin movement was determined in etiolated seedlings with or without phototropic stimulation. Auxins were concentrated in the hook region of the hypocotyl of the *Arabidopsis* grown in dark conditions. Auxins had diffused extensively through plasmodesmata in the induced *dsgsl8* hypocotyls both in dark-grown seedlings and during the phototropic response, but not in the wild-type control. During the tropic response, polar auxin transport plays a major role in producing an auxin gradient, which may result from both the lateral auxin transport from the endodermis to the outer layer of cells and the basipetal auxin transport from the hook region of hypocotyls. However, this study did not determine whether the auxin gradient formation was blocked or whether its maintenance was disrupted in the *dsgsl8* line. More experiments are required to uncover the role of auxin diffusion through plasmodesmata.

The hormone movement through plasmodesmata was suggested to be essential for the coordinated gametophytic shoot branching of *Physcomitrella* (Coudert et al., 2015). Three known hormonal regulators, including auxin, CK, and strigolactone, of both sporophytic and gametophytic branching, interact to generate the branching pattern in plants. In this study, the transportation of three ancient hormones was suggested to be regulated by plasmodesmal connectivity. Interactions among these hormones are the major steps in determining the re-specification of epidermal cells into branch initial cells in the gametophytic shoots of *Physcomitrella*. It is well known that PIN-mediated basipetal auxin transport controls the lateral organ formation in flowering plants, but the normal branching pattern in the *Physcomitrella pin* mutant suggested that PIN-mediated