



Bridging plant cells: ultrastructure, regulation, and role of plasmodesmata in assimilate partitioning

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Received: 09 February 2023 / Accepted: 28 June 2023 / Published: 30 September 2023

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Plasmodesmata are microscopic channels that connect adjacent plant cells, enabling direct symplastic transport of molecules, including photoassimilates. They play a crucial role in intercellular communication and the regulation of assimilate translocation from source to sink tissues. The structure, frequency, and permeability of plasmodesmata influence the efficiency of sucrose and other carbohydrate movement, impacting plant growth and yield. This review explores the ultrastructure of plasmodesmata, the molecular mechanisms governing their regulation, and their role in assimilate partitioning under normal and stress conditions. Emphasis is placed on recent advances in imaging techniques, molecular gating, and the integration of plasmodesmal function with phloem loading and unloading strategies. Understanding these pathways offers insights for improving crop productivity through targeted manipulation of assimilate transport mechanisms.

Keywords: *Plasmodesmata, symplastic transport, phloem loading, source–sink relationship*

Introduction

Cells, as we know, are the basic structural and functional units of all living organisms. These cells are comprised of various membrane-bound organelles [some cells have a secondary cell wall in addition to the primary cell wall]. In plants, the cell walls are bound or glued together with a substance called pectin, a structural polysaccharide [unlike animals]. The middle lamella, located between the cell walls of the adjacent cells, is rich in pectin. There are cell-to-cell interactions for the transport of components between cells. These cell interactions and transportations occur with the help of Plasmodesmata [singular-plasmodesma]. Plasmodesmata, also known as protoplasmic bridges, are narrow, membranous, co-axial tubules that facilitate molecular exchange between cells, both micro and macro molecules. It directly links the cytoplasm of the neighboring cells, sharing the cytoplasmic contents. This continuous environment formed by the plasmodesmata is called the symplast, opposite to which is the apoplast. The apoplast is an intercellular space filled with gas and water present in the plasma membrane. The plasmodesmata are found only in plants and algae. In algae, they are found in members of the family Charophyceae, Charales, Coleochaetales and Phaeophyceae as well as all embryophytes. The animals lack these structures. They consist of gap junctions which replace the plasmodesmata in plants. Gap junctions are aggregates of intercellular channels that permit direct cell–cell transfer of ions and small molecules.

Plasmodesmata structure

A typical plant cell may have around 1,000 and 100,000 plasmodesmata connecting it with adjacent cells, equating to between 1 and 10 per μm^2 (Alfonso et al., 2006). The diameter of the microscopic channel plasmodesmata is approximately said to be 40 nm. The composition of the plasmodesmata comprises three layers, namely, plasma membrane, desmotubules, and cytoplasmic sleeve. The plasma membrane portion of the plasmodesma is a continuous

extension of the cell membrane or plasmalemma and has a similar phospholipid bilayer structure (Pankratenko et al., 2020). The cytoplasmic sleeve is a fluid-filled space enclosed by the plasmalemma and is a continuous extension of the cytosol. Trafficking of molecules and ions through plasmodesmata occurs through this space. Smaller molecules (e.g., sugars and amino acids) and ions can easily pass through plasmodesmata by diffusion without the need for additional chemical energy. Larger molecules, including proteins (for example, green fluorescent protein) and RNA, can also pass through the cytoplasmic sleeve diffusively (You & Jaffrey, 2015). The majority of the plasmodesmata consist of a desmotubule, a central, narrow, cylindrical duct that connects the endoplasmic reticulum of two adjacent cells. The ER within the plasmodesma (the desmotubule, or appressed ER) is continuous with the cortical ER, but appressed tightly, leaving no luminal space (Quader & Zachariadis, 2006). The construction of the desmotubule consists of proteins embedded in the endoplasmic reticulum. The major proteins present are actin and myosin, which control the opening and closing of the desmotubule by evolving a contractile force. Some, but not all, transport of the plasmodesmata occurs through the desmotubule (Radford & White, 2011).

Plasmodesmata types

Table 1. Plasmodesmata are of two types based on their origin

Primary Plasmodesmata	Secondary Plasmodesmata
During multicellularity, after nuclear division, a septum is formed between the two daughter cells in the later stage of cytokinesis, in which the endoplasmic reticulum gets trapped and associates or creates a link between the two adjacent cells. This is how plasmodesmata are said to have evolved, and the plasmodesmata formed during cell division are called primary plasmodesmata. Eg: <i>Chara zeylanica</i> produces both primary and secondary plasmodesmata.	Unlike primary plasmodesmata, secondary plasmodesmata are not formed during cell division; they are inserted into the existing cell walls between non-dividing cells. Eg: <i>Chara corallina</i> produces only secondary plasmodesmata.

Both primary and secondary plasmodesmata (Table 1) are the initial structures that are simple but can form complex structures by forming branches and/or fusion of existing plasmodesmata or the fusion of established and newly formed plasmodesmata (Burch-Smith et al., 2011).

Functions of plasmodesmata

The cell walls of plasmodesmata are very turgid and compact. The cytoplasmic bridge of plasmodesmata mediates direct transport of components between cells. Although cell walls are permeable to small soluble proteins and other solutes, plasmodesmata enable direct, regulated, symplastic transport of substances between cells. It helps in the communication between two adjacent cells (cellular communication). The cytoplasmic sleeve of the plasmodesmata allows the direct flow of small molecules like sugar, amino acids, or ions by diffusion without the requirement of any chemical energy. Plasmodesmata contain both passive and active pores. Through the passive pores of plasmodesmata in plant cells, it transmits water and nutrients. Actin structures found in plasmodesmata help to move transcription factors such as short interfering RNA, messenger RNA, viroid, and plant viruses (Heinlein, 2014). Some mechanisms of plasmodesmata remain unknown. But some larger molecules can cause the plasmodesmata channels to open wider. The desmotubule helps in the transfer of lipids. Between the outside of the desmotubule and the inner face of the cylindrical plasma membrane is an annulus of cytosol, which often appears to be constricted at each end of the plasmodesmata. These constrictions may regulate the flux of molecules through the annulus that joins the two cytosols. It forms a living continuum between the adjacent cells, the symplast, and facilitates the symplastic transport. When a cell is infected by some pathogen, it manufactures proteins in order to fight them and the transport of these proteins through the plasmodesmata can alert the adjacent cells of the presence of the pathogens so that they can take some precautionary measures to rid away the infectious pathogens. The disadvantage is that in the case of presence of toxic materials, their transport is also facilitated by the plasmodesmata which is the solid reason for the spread and cause of many plant diseases.

Plasmodesmata in assimilate translocation

What is assimilate translocation

The products of photosynthesis (mainly the sugar sucrose) are a major component of the substance found in the phloem, called assimilate. Ions, amino acids, certain hormones, and other molecules are also found in assimilation. The movement of assimilation is called translocation, or assimilate transport.

Transport mechanism

Plasmodesmata have been shown to transport proteins (including transcription factors), short interfering RNA, messenger RNA, viroid, and viral genomes from cell to cell. One example of a viral movement protein (MP) is the tobacco mosaic virus MP-30. MP-30 is thought to bind to the virus's genome and shuttle it from infected cells to uninfected cells through plasmodesmata (Kleinow, 2016). Flowering Locus T protein moves from leaves to the shoot apical meristem through plasmodesmata to initiate flowering (Wu et al., 2022). Plasmodesmata are also used by cells in phloem, and symplastic transport is used to regulate the sieve-tube cells by the companion cells. The size of molecules that can pass through plasmodesmata is determined by the size exclusion limit. This limit is highly variable and is subject to active modification. For example, MP-30 is able to increase the size exclusion limit from 700 Daltons to 9400 Daltons, thereby aiding its movement through a plant. Also, increasing calcium concentrations in the cytoplasm, either by injection or by cold-induction, has been shown to constrict the opening of surrounding plasmodesmata and limit transport. Several models for possible active transport through plasmodesmata exist. It has been suggested that such transport is mediated by interactions with proteins localized on the desmotubule, and/or by chaperones partially unfolding proteins, allowing them to fit through the narrow passage. A similar mechanism may be involved in transporting viral nucleic acids through the plasmodesmata.

The phloem is a vascular tissue with living or conducting cells for food transport, unlike xylem, which has only dead cells, such as tracheids and vessels, for the transport of water. Stacks of cylindrical cells in the phloem called sieve-tube elements form column-like structures. The cells are separated from each other by sieve plates. The sieve plates, which look like those of a Swiss cheese, have holes in them for the passage of food. Sieve-tube elements have reduced cytoplasmic contents and rely on special parenchyma cells called companion cells, which assist with metabolic activities and provide energy. In addition to sieve-tube elements and companion cells, the phloem contains other parenchyma cells and may contain sclerenchyma fibers. In leaves, the phloem is found in vascular bundles (leaf veins), which are surrounded by a bundle sheath. Phloem loading: It is the process of transfer of entry or filling or loading of photosynthetic products from mesophyll cells to the sieve tube of phloem for further transport.

Phloem loading

In plants, the movement of sugars from source tissues into the phloem sieve elements is known as sieve element loading. During this process, sugars accumulate in the sieve elements and companion cells at higher concentrations compared to mesophyll cells. Once loaded, these sugars are transported away from the source tissue in a process referred to as export. Sucrose can enter the phloem sieve element/companion cell complex through two main pathways: 1. Symplastic phloem loading – This can occur via passive or active mechanisms. 2. Apoplastic phloem loading – Here, membrane-bound transport proteins actively transport sugars through the cell wall space (apoplast) using energy. These pathways either rely on simple diffusion through the symplast or on active transport across the apoplast, with specialized transport proteins facilitating movement (Bhatla, 2018).

1. Passive Symplastic Loading

According to the pressure-flow hypothesis, passive loading occurs when the sucrose concentration in mesophyll cells is higher than that in the phloem sap. In many woody and some herbaceous species, mesophyll cytosol contains more sucrose than the phloem sap (Fu et al., 2011). These species tend to have fewer starch deposits in minor veins when supplied with external sucrose compared to active loaders and are rich in plasmodesmata (PD) between mesophyll and sieve elements (Schulz, 2015). A key question has been whether the pressure generated by passive loading is sufficient for long-distance transport in tall plants. Experimental models, including a synthetic tree-on-a-chip system, suggest that even small pressure differences can support sugar transport in trees (Comtet et al., 2017). Anatomical studies also show that sieve tube and plate structures in trees adjust resistance along the transport path, reducing the pressure required (Savage et al., 2017). Thus, tall trees can effectively rely on pressure-flow-driven symplastic transport.

2. Active Symplastic Loading

The polymer trap hypothesis explains active symplastic loading in species with specialized intermediary cells (Slewinski et al., 2013). Sucrose diffuses from mesophyll cells through PD into intermediary cells, where it is enzymatically converted into raffinose (594 Da) and stachyose (667 Da). The PD at the mesophyll–intermediary cell

interface is narrow enough to allow sucrose in but prevent larger raffinose family oligosaccharides (RFOs) from diffusing back (Sanyal et al., 2023). This trapping is energized by the enzymatic conversion via galactinol synthases (Salvi et al., 2021).

Phloem unloading

Phloem unloading is essentially the reverse of phloem loading — the movement of assimilates from the phloem into sink tissues such as roots, fruits, or storage organs. This process supports growth, storage, and metabolic activity in sink tissues and can occur either via the symplast or apoplast. When sugars reach the sink end, they are unloaded from sieve elements and transferred to surrounding cells.

The process involves three stages,

1. Sieve Element Unloading – Sugars leave sieve elements in the sink tissue.
2. Short-Distance Transport – Post-sieve element transfer moves sugars to specific sink cells.
3. Storage and Metabolism – Sugars are stored as starch or metabolized for energy.

The pressure-flow hypothesis remains the most widely accepted explanation for sap movement in the phloem, applying to both loading and unloading phases.

Conclusion

Plasmodesmata serve as vital conduits for symplastic communication and assimilate movement between plant cells, forming an integral component of the source–sink transport pathway. Their structural dynamics and selective permeability enable precise regulation of sucrose and other photoassimilates, ensuring efficient translocation in coordination with phloem loading and unloading processes. Environmental cues, developmental stages, and stress conditions can modulate plasmodesmal conductivity, thereby influencing assimilate partitioning and overall plant productivity. Advancements in molecular biology and imaging have deepened our understanding of plasmodesmal function, yet the complexity of their regulation warrants further exploration. Targeted manipulation of plasmodesmal properties offers promising avenues for enhancing crop yield and stress resilience by optimizing assimilate flow.

Acknowledgement

NIL.

Author contributions

Conceptualization – Ashok Subiramaniyan, Chandrasekaran Perumal, Ashokkumar Natarajan, Selvakumar Gurunathan. Writing (original draft) - Akshayaa Guhan, Sonali Vergin Philips, Roshini Kuppusamy. Writing (review & editing) - Ashok Subiramaniyan, Chandrasekaran Perumal, Ashokkumar Natarajan, Selvakumar Gurunathan.

Conflict of interest

The authors declare no conflict of interest.

Ethics approval

Not applicable.

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