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Special Issue Editorial

Plasmodesmata

Plant cells are interconnected by plasmodesmata (PD), membrane-lined channels in cell walls that allow cytosolic molecules to flow from one cell to the next. PD are essential for multicellular plant life: all land plants make PD, virtually every cell (with special exceptions) is connected to its neighbors through PD, and no mutant lacking PD has ever been isolated. PD transport molecules range from small metabolites and phytohormones to biological macromolecules, such as small RNAs, proteins, and viruses. Indeed, at the recent 11th International Plasmodesmata Meeting (PD2024) hosted by the Donald Danforth Center for Plant Sciences, leaders in the field pointed out that, from the perspective of PD biologists, the question is not, 'which molecules move through PD?', but instead, 'which molecules are prevented from moving through PD?'

PD2024 brought together a diverse group of biologists who either focus specifically on PD biology or whose research led them to consider the various roles of PD transport in plant physiology, development, and stress responses. Major open questions that emerged at PD2024 included the following. (i) What is the molecular composition of PD? (ii) What molecules are moving through PD, and what mechanisms selectively restrict this movement? (iii) How does PD transport contribute to dynamic stress responses?

In this special issue of the *Journal of Experimental Botany*, we collected a series of reviews that share the field's current understanding of these questions and highlight exciting future research directions.

Knock, knock: who's there? The molecular composition of plasmodesmata

Unlike subcellular compartments with clearly defined boundaries, such as mitochondria or plastids, PD are structurally continuous with their surroundings. In land plants, PD are composed of four basic structures: (i) an inner membrane (the 'desmotubule') continuous with the endoplasmic reticulum; (ii) an outer membrane continuous with the plasma membrane; (iii) a 'cytosolic sleeve' between these membranes that is continuous with the cytoplasm; and (iv) a modified cell wall beyond the outer membrane. The molecular composition of these structures, and their resulting impacts on intercellular trafficking, were a major focus of discussion at PD2024.

In their Darwin Review, Schreier *et al.* (2026) set the stage by considering the mechanisms of PD biogenesis in C_4 plants with Kranz anatomies. In these plants, numerous, specialized PD form post-mitotically at the interface between bundle sheath and mesophyll cells to facilitate rapid exchange of photosynthetic intermediates, concentrating carbon to minimize waste caused by photorespiration. Schreier *et al.* expand to consider PD from a genetic perspective, reviewing the genes that participate in PD formation and PD function, whether directly (e.g., genes that encode proteins enriched at PD) or indirectly (e.g., genes that control chloroplast physiology, which, in turn, impact PD biogenesis).

The cell wall surrounding PD is often enriched with callose (β-1,3-glucans). PD callose levels are dynamic through localized callose synthesis and degradation, however, which are thought to modulate the size and shape of PD to regulate intercellular transport. Simonaviciene *et al.* (2026) review our understanding of callose biology at PD, but they also turn our attention to the many other cell wall components that also impact PD biomechanics and could regulate PD trafficking, including pectins, hemicelluloses, and cellulose.

PD membranes are highly specialized structures enriched for specific lipids and proteins, as addressed in particular by Liu *et al.* (2026), Alazem *et al.* (2026), Turley and Faulkner (2026), Li and Aung (2026), and Barr and Tilsner (2026). Ironically, the best-characterized PD proteins are not encoded by plant genomes, as Alazem *et al.* (2026) emphasize, but are instead viral movement proteins. With rare, highly specialized exceptions, all plant viruses encode movement proteins that modulate PD transport to facilitate the spread of viral infections. Alazem *et al.* argue that understanding how viral movement proteins become enriched at PD, move through PD, and modify (or 'hijack') PD continues to be a powerful approach to elucidate the regulation of PD formation and function.

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Li and Aung (2026) shift the focus to endogenous plant proteins associated with PD membranes. Past efforts started to define the 'PD proteome' through sophisticated cellular fractionation methods or affinity purification using known PD constituents as bait; Li and Aung review how recent advances in proximity labeling, especially the powerful TurboID biotin ligase proximity-labeling tool, are being leveraged to expand our knowledge of the PD proteome.

With the discovery of proteins that are strongly enriched at PD, many groups have sought to define localization signals that selectively target proteins to PD, analogous to the well-defined signals that direct proteins to plastids, mitochondria, the endoplasmic reticulum, and so on. Against the expectation that we could define PD localization signals, however, each family of PD proteins investigated thus far apparently localizes to PD through distinct mechanisms. Building on these discoveries, Barr and Tilsner (2026) make a compelling case that PD biologists should move away from the hypothesis that the PD proteome is established by a PD localization signal(s); instead, they argue that some proteins are enriched at PD through retention signals. For example, proteins that are post-translationally modified with glycosylphosphatidylinositol (GPI) anchors are often enriched at PD because they preferentially associate with sphingolipids that are also enriched at PD, possibly due to biomechanical constraints introduced by the shape and curvature of the PD outer membrane. This reconceptualization, away from PD localization signals and toward motifs that encourage PD retention, will be important to consider when analyzing the diversity of proteins identified in PD proteomes.

Dams and locks at the canals: which molecules can, or cannot, move through PD?

In principle, any cytosolic molecule has the potential to move through PD, but many molecules do not. For example, in most cell walls, PD are so narrow that they can only accommodate proteins up to ~80 kDa (and often considerably less than 80 kDa). In their review, Vasina *et al.* (2026) broaden our perspective beyond size constraints by providing a wide-ranging review on the physics of transport through PD, emphasizing the diversity of PD structures and the limitations imposed on molecular movement through these structures. Other features of molecules, such as their charge, can be just as important as their size. Vasina *et al.* also highlight that our understanding of PD transport relies heavily on various imperfect methods that could introduce confounding artifacts. Future research in the PD field should carefully consider these important perspectives.

Pioneering investigations of PD biology concentrated on physiological roles of PD in the movement of metabolites, especially sugar movement from photosynthetic sources to actively growing and/or non-photosynthetic carbon sinks. In the 1990s, the discovery that PD can transport endogenous proteins, such as the meristem-patterning transcription factor Knotted1, brought PD biology to the attention of plant developmental biologists. Subsequent investigations have emphasized that diverse patterning signals move through PD, including proteins, small RNAs, and crucial phytohormones. Linh and Ueda (2026) review our understanding of how PD transport impacts the localized movement, accumulation, and dispersal of auxins, with special emphasis on how auxin transport through PD affects leaf venation patterns.

Early studies of gene silencing in plants revealed that RNAi signals can spread from their origin to new parts of the plant. Voinnet (2026) offers a comprehensive historical review of the key discoveries about the intercellular movement of RNAi signals, emphasizing various open question in the field about how small RNAs move through PD, and why some small RNAs are more mobile than others. Elvira-Gonzalez *et al.* (2026) extend this discussion by focusing on the generation and movement of RNAi signals during viral infections.

Ejike *et al.* (2026) briefly turn our attention away from PD to review a distinct model of protein and RNA transport: the nuclear membrane. Diverse proteins and RNAs move across the nuclear membrane through nuclear pores, with smaller molecules free to pass through the pores in either direction, and larger molecules directed through the pores by a complex system of chaperones. Ejike *et al.* pay special attention to the role of phase separation and how this impacts transport through nuclear pores. Although there are key differences between nuclear pores and PD—among others, whereas the nuclear pore facilitates transport across a membrane, molecules move through PD without ever crossing a membrane barrier—Ejike *et al.* make the important point that analogous mechanisms involving phase separation might contribute to the regulated movement of proteins and RNAs through PD.

Spreading the word, but quarantining the infected: PD during infection

Successful pathogens use PD to their advantage: PD are the conduits of viral spread [as discussed in detail by Alazem *et al.* (2026)], and diverse microbial pathogens hijack PD to enhance their virulence and weaken plant defenses. When plants recognize an infection, PD transport is dynamically reoriented to prevent pathogen spread and to send out alerts that prime defenses in uninfected cells. These mobile defense signals include RNAi signals, as discussed in the reviews by Elvira-Gonzaelez *et al.* (2026) and Voinnet (2026), and as directly investigated in the report by Weiss *et al.* (2026), who show that inoculating plants with sequence-specific dsRNA can effectively defend plants against infection by tomato brown rugose fruit virus, an emerging and severe viral disease that primarily affects tomato agriculture. Liu *et al.* (2026) consider the roles of PD in the synthesis and movement of lipid-derived signals in defense, key metabolites that, among other roles, drive the durable 'systemic acquired resistance' response. Turley and Faulkner (2026) review our growing understanding of the important roles of a family of heavy metal-associated (HMA) domain proteins that are enriched at PD. HMA domain proteins appear to play

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regulatory roles during infection, and they are also targeted by pathogen effectors to promote virulence. Despite several groups discovering that HMA domain proteins play roles at PD, the underlying mechanisms remain unresolved and will be a major focus in the coming years.

Conclusions and prospects

More than a century after the discovery of PD, we are still only beginning to appreciate the complexity of molecular transport through PD and the regulatory mechanisms that drive and restrain intercellular trafficking. Contemporary, groundbreaking technical advances in several fields—especially genetic engineering, plant transformation, multiomics, molecular biology, microscopy, and electron tomography—will enable major advances in PD biology in the coming years. As Schreier *et al.* (2026) argue convincingly, PD biology is so deeply intertwined with plant development and physiology that new discoveries about PD can be widely impactful, informing strategies to engineer the crops that will be needed for a sustainable agricultural future.

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