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2 **Editorial on the Research Topic**

3 **Plasmodesmata: Recent Progress and New Insights**

5 Tessa Burch-Smith¹, Manfred Heinlein² and Jung-Youn Lee³

7 ¹Donald Danforth Plant Science Center, St. Louis, MO, United States

8 ² Institut de biologie moléculaire des plantes, CNRS, Université de Strasbourg, Strasbourg, France

9 ³Department of Plant and Soil Sciences, Delaware Biotechnology Institute, University of Delaware,
10 Newark, DE, United States

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13 In this Frontiers Research Topic, readers will find a collection of research articles, mini-reviews,
14 and opinion papers that focus on new findings and progress regarding plasmodesmata in the
15 context of plant development and plant-pathogen interactions. Specifically, several reports present
16 findings related to the targeted trafficking of endogenous and pathogen-derived proteins to or
17 through plasmodesmata, or the role and regulation of plasmodesmata in defining symplasmic
18 domains. The collection also includes articles that review progress with respect to cytoskeletal
19 connections to basic plasmodesmal function or to interspecific plasmodesmata formed between
20 hosts and their parasitic plants, or share perspectives on how plasmodesmal research may be
21 relevant to addressing critical issues in producing resilient crops in the face of imminent challenges
22 associated with climate change.

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24 In higher plants, virtually all sister cells are connected to each other via the primary plasmodesmata
25 formed at the division wall during cell division. However, as cells grow and differentiate, those
26 plasmodesmata can undergo temporary closing or various structural modifications such as those
27 that lead to the formation of secondary plasmodesmata or to disconnection by severing or complete
28 disintegration. These events sometimes lead to the symplasmic isolation of cells. Voitsekhovskaja
29 and co-authors (Voitsekhovskaja et al., 2021) investigate how secondary plasmodesmata may
30 differentially form depending on how they load sugar into the phloem, i.e., using an apoplastic or
31 symplastic path. This study reveals that secondary plasmodesmata formation is enhanced in

32 symplastic loaders, particularly at the cell walls joining epidermal cells and epidermal with
33 mesophyll cells. In addition, comparative analysis of carbohydrate composition suggests that
34 secondary plasmodesmata formed between the two cell layers are likely used to traffic
35 photosynthetic assimilates. Collectively, these findings raise the intriguing possibility that the
36 epidermis and mesophyll could together comprise a symplastic domain in symplastic loaders.
37 Godel-Jedrychowska and coauthors investigate how symplamic domains are formed in zygotic
38 and somatic embryos during their development (Godel-Jedrychowska et al., 2021). Their study
39 suggests that although the symplasmic domains form similarly in both types of embryos, there are
40 a few qualitative differences such as the timing of establishing domain boundaries and the size of
41 molecules that can move between cells. Krause group addresses the functional specialization of
42 secondary plasmodesmata (Fischer et al., 2021), examining what is known about interspecific
43 plasmodesmata formed between parasitic plants and their plant hosts and provides cogent
44 arguments for the value of parasitic plant-host systems in investigating various aspects of
45 plasmodesmal formation and structure, and the establishment of symplastic domains.

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47 Two reports describe findings about plasmodesmata in the context of plant development, one
48 related to the role of cytokinin in plasmodesmal function and the other to transcription factor
49 movement critical for xylem development. Various reports have shown that plant hormones, such
50 as auxin, abscisic acid, gibberellin, and salicylic acid, regulate plasmodesmal status, and/or vice
51 versa. Adding to the list of hormones linked to plasmodesmal function, Horner and Brunkard
52 show that direct application of a cytokinin, *trans*-Zeatin, or virus-induced gene silencing of the
53 components of the cytokinin signaling pathway both bring about changes in plasmodesmal
54 permeability (Horner and Brunkard, 2021). The transcription factor AT-HOOK MOTIF
55 NUCLEAR LOCALIZED PROTEIN(AHL)4 is a mobile member of a large protein family, which
56 is necessary for the proper xylem differentiation in *Arabidopsis*. Using domain swapping between
57 AHL4 and a non-mobile member, AHL1, followed by genetic analyses, Seo and Lee now show
58 that a specific C-terminal domain in AHL4 determines the mobility of the protein, and that AHL4
59 mobility from the stele to the endodermis and xylem precursor cells is vital for xylem development
60 (Seo and Lee, 2021).

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62 Chritiaan van der Schoot and his team examine the relationship between lipid bodies and
63 plasmodesmata in the shoot apical meristem in hybrid aspen and analyze the proteins associated
64 with lipid bodies in dormant buds (Veerabagu et al., 2021). Their findings indicate how lipid bodies
65 may function as a putative delivery system for plasmodesmal proteins along the actin cytoskeleton
66 to plasmodesmata. A minireview summarizes the association of actin with plasmodesmata (Diao
67 and Huang, 2021) focusing on class I formins, actin-binding proteins involved in actin
68 polymerization. Several class I formins localize to plasmodesmata including AtFH1 and AtFH2,
69 which are required to maintain plasmodesmal permeability.

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71 Reflecting recent interest in the role of plasmodesmata as the battleground against microbial
72 intruders, more proteins encoded by various microbial pathogens are identified to target
73 plasmodesmata. The team of Kyaw Aung presents evidence showing that bacterial effector
74 proteins can traffic between cells (Li et al., 2021), adding to the previous findings from fungal and
75 oomycete systems (Cheval and Faulkner, 2018; Iwanto et al., 2021a). They show that the effector
76 movement is restricted by accumulation of callose at plasmodesmata and that an effector targeted
77 to the plasma membrane is more efficiently able to move between cells than a mutant version that
78 does not associate with the plasma membrane. How plasma membrane association may facilitate
79 the protein's intercellular movement and how broadly this putative mechanism may apply are
80 interesting questions for future investigations. In addition, it would not be surprising if beneficial
81 bacteria also deploy effectors to bring about potential non-cell-autonomous effects.

82

83 Notably, three research groups review and discuss potential applications of plasmodesmal research
84 to improve crop health and yield. As the effects of global climate change become more pronounced
85 in the coming years, there is no doubt that a variety of biotechnological approaches will be needed
86 to enhance crop adaption. Along this line, Liu and coauthors succinctly summarize a large body
87 of research on the ways pathogens may manipulate plasmodesmata to facilitate infection and how
88 plants can deploy plasmodesmata-centered defenses to limit infection (Liu et al., 2021). Possible
89 strategies of engineering plasmodesmata to enhance defense responses, for example by targeting
90 callose metabolizing enzymes are also discussed. Iswanto and colleagues (Iswanto et al., 2021b)
91 discuss plasmodesmal proteins involved in abiotic stress and in host-pathogen interactions as
92 potential targets for gene editing using CRISPR/CAS9 technologies. The urgency to consider the

93 importance of plasmodesmata research for crop improvement is furthermore underscored in the
94 Perspective article from the Heinlein lab (Amari et al., 2021). It highlights the potential impact of
95 global warming on virus propagation in infected plants and agricultural productivity and collates
96 work spanning decades that clearly indicates the increased susceptibility of plants to viral cell-to-
97 cell movement at higher temperatures. Perhaps, the regulation of plasmodesmata may hold a
98 promise as a new target for crop engineering and the time may be ripe for that exploration.

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100 **Author Contributions**

101 All authors contributed to the conception and solicitation of this research topic. TB-S wrote the
102 first draft of the editorial, J-YL revised the draft and added additional sections, and MH edited. All
103 authors contributed to manuscript revision, read, and approved the submitted version.

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110 **Conflict of Interest**

111 The authors declare that there is no conflict of interest.

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116

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