$V(\text{Coma})/D(\text{Coma}) = 81 \pm 8$ km s^{-1} Mpc^{-1}. For a matter-dominated $\Omega = 1$ Einstein–de Sitter universe (Ω is the ratio of the actual density of the universe to the critical density), the corresponding age $t_o = (2/3)H_o^{-1} = (2/3) \times 9.78 \times [100/(81 \pm 8)] = 8.0 \pm 0.8$ billion years. Such a short age conflicts with the age of 15.8 ± 2.1 billion years that Bolte and Hogan (*8*) obtained from main sequence fitting of the metal-poor globular cluster M92 to the subdwarf main sequence derived from trigonometric parallaxes. If the oldest galactic globular clusters have ages of ~16 billion years, and if the time interval between the "Big Bang" and the formation of the first globular clusters was ~1 billion years, then the age of the universe is ~17 billion years. This value is twice as large as the value 8.0 ± 0.8 billion years previously found from H_o in an Einstein–de Sitter universe.

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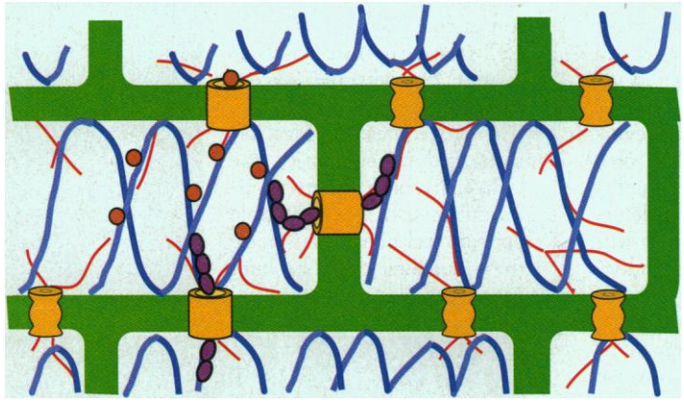
Plasmodesmata: Plant Channels for Molecules on the Move

Patricia Zambryski

Intercellular communication in plants occurs through cytoplasmic bridges called plasmodesmata (PD) (*1*). In contrast to their animal counterparts—gap junctions between closely appressed cells—PD are elongated structures that traverse the thick cell walls that surround plant cells. PD have an outer sheath that is contiguous with the plasma membrane, a central core of endoplasmic reticulum, and a collar or neck region. Historically, PD have been assigned a passive role: creating cytoplasmic continuity between plant cells to allow free transport of small metabolites and growth hormones less than 1 kilodalton (kD). When it was discovered that plant viruses pirate PD for movement of their genomes during infection, it was proposed that viruses altered the PD to allow transport of very large molecules. Now, several recent reports, one of which is in this issue of *Science*, provide compelling evidence that PD are inherently dynamic, rapidly altering their dimensions to increase their transport capabilities on contact with both viral (*2*, *3*) and endogenous plant proteins (*4*). Two other new studies, one in this issue (*5*), describe the cytoskeleton as a major tracking system to PD (*5*, *6*).

The movement protein (MP) of plant viruses has been extensively used to probe the function of PD (*7*). Recently, purified MPs have been microinjected into single plant cells to follow the movement of MP itself, complexes consisting of MP and single-strand nucleic acid, or co-injected fluorescent dextrans (*2*). These studies demonstrate that MPs increase the permeability of (that is, gates) PD within minutes of microinjection, implying that MPs operate an endogenous PD transport pathway.



Model for macromolecular transport between plant cells. Macromolecules track through the plant cytoplasm on microtubules, then interact with actin filaments to move to and through PD. Cell walls between individual plant cells, green; PD in either closed (constricted at either end) or open (smooth cylinder) configurations, yellow; microtubules, thick blue lines; actin filaments, red; elongated complexes between viral MP and single-strand nucleic acid, purple; and generic proteins capable of PD trafficking, orange.

Comparing MP-mediated transport in different plant cell types reveals that PDs are functionally diverse (*3*). In tobacco leaves, trichome hair cells have a greater basal size exclusion limit, 7 kD, than mesophyll cells (1 kD). Furthermore, although MP-induced gating in mesophyll cells permits movement of dextrans larger than 20 kD, MP does not gate trichome cells for these big dextrans. However, 30-kD MP itself moves in both cell types, and in trichome cells 30-kD MP mediates movement of a 68-kD reporter protein in cis but not in trans. Thus, an essential PD transport signal residing in MP dictates transportability in trichome cells, not size per se. Molecules to be transported are likely selected on the basis of at least four criteria: size, shape, signal (targeting) sequence, and gating function. From the perspective of PD, cell and tissue type, as well as developmental stage, regulate intercellular transport.

During maize development, RNA encoding the KNOTTED1 (KN1) homeodomain protein is found in all cell layers of the meristem except the outermost L1, whereas KN1 protein is found in both the inner and outer L1 layers. Likewise, in leaves of plants with the dominant *Kn1* mutation, RNA is located in the inner vascular cells, and protein is found in a broader domain including the L1. These findings (*8*) prompted speculation that KN1 protein might be transported through PD to the outer layer. Support for this idea comes from clonal analysis demonstrating that *Kn1* action in the inner layer nonautonomously influences adjacent cells (*9*). Now Lucas *et al.* have shown that, just as viral MPs gate and move, the KN1 protein itself both moves between mesophyll cells and facilitates the movement of dextrans and proteins larger than 20 kD (*4*). Furthermore, KN1 protein selectively transports *kn1* sense but not antisense RNA between cells. That an important regulator of plant development can move between cells has significant implications for how plants program differentiation. For example, the distribution, as well as the permeability, of PD between adjacent cells may regulate development by providing channels for exchange of regulatory signals. However, these intriguing studies provoke many questions. How common is macromolecular transport

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through PD during development? Does KN1 move selectively to the L1 layer, or does KN1 move everywhere? What is the benefit of KN1 transport? If *kn1* RNA is already actively expressed throughout the meristem, what does the plant gain by facilitating movement of *kn1* RNA? Why is microinjected KN1 not sequestered into mesophyll nuclei as in maize meristem cells?

Plasmodesmata have talents beyond the transport of endogenous plant transcription factors such as KN1. They are implicated in the movement of numerous proteins (up to 70 kD) from companion cells to the enucleate sieve elements of the phloem vascular system (*10*). The distribution of PD between cells of the fern gametophyte correlates directly with cell division patterns (*11*). In addition, as differentiation proceeds, epidermal cells of developing roots become progressively more isolated, that is, their PD are less prevalent or effective (*12*). Furthermore, during initiation of lateral roots, cells increase their intercellular communication through PD; after emergence of lateral roots, previously connected arrays of internal cells become sealed off (*13*).

How do molecules move within the cytoplasm to arrive at PD? Two recent reports use the viral MP system to demonstrate that MPs colocalize primarily with microtubules (*5*, *6*). To a lesser extent, MPs also colocalize with actin filaments, and in vitro experiments show that MP can bind to both actin and tubulin (*6*). In hindsight, these results are obvious because simple viscosity would hinder diffusion of an elongated viral genome coated with MP. That the MP proteins themselves track along the cytoskeleton suggests that the association of a viral nucleoprotein complex with the cytoskeleton is not passive, but may be determined by specific signal sequences. It will be interesting to determine whether endogenous plant proteins such as KN1 also track to PD by means of the cytoskeleton.

The cytoskeleton may also participate in the gating of PD. Actin filaments traverse PD channels (*14*), and actin may act as sphincter at the neck region of PD. Additional cellular factors could interact with actin to generate an open or closed PD conformation and so regulate transport.

The future looks bright for uncovering major fundamental principles for intra- and intercellular transport mechanisms in plant cells. Methods to purify PD are emerging (*15*) and will allow identification of the structural components and detailed architecture of PD. Viral MPs and endogenous plant proteins that traffic by means of PD will be useful to identify signal sequences for interaction with cytoskeletal components, targeting to PD, gating PD, and movement through PD. How are PD structure and function regulated during development in different cell types? Besides possible regulation of gating by cytoskeletal components or transportable proteins, how do general physiological signaling molecules such as calcium, guanosine triphosphate, and protein kinases affect PD transport? These questions and more, and their answers, mean there is a lot to do and look forward to.

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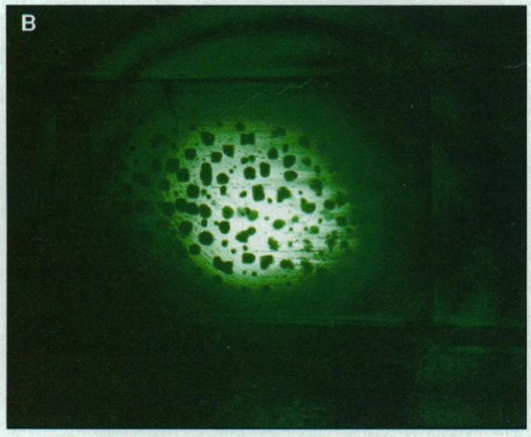
Eminent Domains

Ferroelectric crystals interact strongly with light and are used for optical memories, modulators, and switches. In such crystals, the unit cell has a front that differs from the back, and the lowest energy state is attained when all of the unit cells are aligned in the same direction, the *c* axis. In real materials, small groups of renegade cells cluster into domains where they align with each other but not with the rest of the crystal. If oriented 180° relative to the *c* axis, they cannot be detected except through elaborate or destructive procedures. S. MacCormack and J. Feinberg of the University of Southern California have devised a simple optical technique to image these domains. A probe laser beam sent through the crystal



shows a uniform image (**A**). If a second laser beam is simultaneously sent through the crystal, wherever the probe passes through an inverted domain, it loses energy to the second beam by the photorefractive effect (**B**). The researchers found that crystal samples believed to consist of only a single domain actually contained a large number of misoriented domains, a finding that may require the revision of existing values for the electrooptic coefficient of these materials. [Image courtesy of S. MacCormack and J. Feinberg, Department of Physics, University of Southern California, Los Angeles, CA 90089-0484, USA. E-mail: feinberg@physics1.usc.edu]