The cell wall is a real drag

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Martinière et al. (1), at long last, take a critical look at the general mobility of proteins in the plant plasma membrane. Hundreds of studies looking at the active or diffusion-limited transport of proteins in the animal cell plasma membrane paint a complex picture. There are mammalian proteins that wander the membrane aimlessly, proteins corralled into pens by the cytoskeleton, proteins that become stuck in a cholesterol-rich mud, and even proteins that anchor themselves to the ECM (2). From these broader findings, it appears clear that animal cells exploit the restriction of proteins to a 2D lipid plane for complex outcomes. At issue in plant cells is almost every property that has ever been ascribed to the transport of a plasma membrane protein in a cellular system. A systematic study of how different classes of membrane proteins move within the plant plasma membrane simply has not been done.

Life Behind the Walls

A defining property for plant cells is the semirigid cell wall. The chemical nature of this complex extracellular matrix and the mechanical properties it affords the cell could have broad implications for membrane protein mobility. Plant cells actively accumulate salts, and, therefore, generate substantial (negative) water potentials (3). The resulting attraction for water, balanced against the structural integrity of the cell wall, produces internal hydraulic pressures of 5 to 8 atm (4). How this internal pressure affects the properties of the plasma membrane itself and the movement of membrane proteins has been debated out of the literature for many years. The plasma membrane probably experiences a significant compressive force. Although the compression itself may have only small direct effects on the membrane, the larger action of this hydraulic pressure is to tightly appress the plasma membrane to the inner surface of the cell wall. The clear hypothesis here is that the movement of membrane proteins with exposed exoplasmic faces would be sterically hindered by the interactions with the cell wall.

Mechanics aside, plant cells devote extraordinary attention to constructing the cell wall at the plasma membrane (5). Cellulose, the main structural polymer in the cell wall, is chemically synthesized by enormous protein complexes

resident in the plasma membrane. These cellulose synthetases move as cellulose is created (6), potentially powered by the synthesis reaction and dehydration of the cellulose microfibril. The trajectory of the cellulose synthetases often follows the path of an underlying cortical microtubule, suggesting that the cytoskeleton inside the cell is patterning the cellulose deposition on the other side of the membrane via synthetase interactions (6). How the cortical microtubules are immobilized at the plasma membrane (7) to

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guide the synthetase complexes is a critical question. Lateral associations with the plasma membrane might be enough to hold the microtubules in place against the ravages of cytoplasmic streaming, but some connection to the cell wall could be a much sturdier arrangement for guiding large synthetase complexes. The answer, and unraveling many of the mysteries surrounding cell wall construction, depends heavily upon what we discover about the mobility of proteins in the plasma membrane.

Membrane Protein Mobility

Martinière et al. (1) express a series of modified proteins in plants to define how various forms of plasma membrane association affect protein movement. This includes proteins with lipid moieties, integral membrane proteins, and proteins with exposed regions on different faces of the membrane. By using several transgenic expression methods, their work demonstrates important general principles about membrane protein movement in flowering plants that can be compared with what we know about animal and fungal systems. First, eliminating the actin or the microtubule cytoskeleton did not alter membrane protein movement in any substantive way. Although this does not rule out such interactions for specific proteins, these data suggest that the plant cortical cytoskeleton is not playing a general role in collection or corraling mem-

brane proteins (8). In a second set of experiments, Martinière et al. (1) found little or no correlation between the mobility of a protein in the membrane and its tendency to accumulate in putative membrane "rafts." This work will not quell speculation that plant cells transiently create local regions of altered lipid content to trap specific proteins (9). However, the experiments do suggest that this is not a general mechanism for controlling membrane protein localization.

The most interesting finding from the work presented by Martinière et al. (1) is that the cell wall does indeed have a defining effect on the movement of proteins when they have exposed faces on the exoplasmic side of the membrane. These experiments clearly show that the cell wall interferes with the general mobility of membrane proteins, irrespective of any specific chemical interaction with cell wall components. The scope of this claim needs further investigation, but the implications are clear for a long list of cell biological phenomena. Correctly distributing proteins in the plasma membrane of the plant cell is going to be an extremely interesting process to understand at several levels.

Know Your Cellular Neighbors

There is much reason to understand how plasma membrane proteins are distributing themselves in plants. For the most part, flowering plants are built up in layers. The epidermal cells sit over the cortical cells, and the endodermal cells develop underneath the cortical cells, and so on. Key to this architectural plan, both during plant development and in mature tissues, is the proper interconnection of these walled cells. The interface between cells (i.e., the plasma membrane) at different positions needs to have the capacity to recognize who is who and act accordingly. For example, during root and shoot growth, the peripheral cells that constitute the epidermis and underlying cortex are highly polarized. Different membrane proteins, shown to be involved in vectoral auxin transport, localize distinctly to the apical, basal, and lateral faces of these box-shaped cells (10–12). How these proteins are accumulated and maintained in

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these different positions, as a general cell biological mechanism, remains a hugely interesting question (13–17) with implications for how cells in flowering plants can function together as tissues and organs.

That plant cells can partition various proteins into different regions of the plasma membrane is perhaps not too surprising. However, in light of the work from Martinière et al. (1), the generalizable mechanisms by which proteins get to these positions and stay in these positions

now becomes more intriguing. Consider that approximately 5% of the *Arabidopsis* genome encodes (putative) membrane-bound receptors with a spectacular array of activities (18, 19). It will be critical to discover how the cell wall influences the distribution of these integral membrane proteins so that they can find and transduce their cognate signaling molecules. If the cell wall serves as the great “hall monitor,” generally suppressing the urge of any membrane protein to wander about at more than a few microns per hour,

what part does lateral diffusion play in distributing membrane proteins, and on what time scale? Is it a good strategy or even plausible for receptors to cluster after agonist binding under these circumstances? What part does the cytoskeleton play in shaping membrane protein distribution beyond targeting of secretory vesicles? Finally, how has the general topology of plant plasma membrane proteins evolved to work with, or to work around, the dominant influence of the cell wall?

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