**Spatiotemporal integration of signaling networks regulating pollen tube growth**

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At any given moment, the readout of cell function or behavior is a composite of events occurring at different scales. Cells utilize signal transduction cascades to relay information across different scales. Many cellular behaviors, such as pollen tube growth, are orchestrated by multiple signals interacting in a broader signaling network. Order is achieved by integration of these signaling networks with metabolic pathways, morphological and structural rearrangements, and gene expression profiles. Our recent work on *Nicotiana tabacum* pollen tube growth has identified an important role for cell hydrodynamics and volume sensing as a central mechanism that regulates several key signaling cascades, and has the potential to integrate and synchronize the function of the broader signaling network (**Figure 1**).

Water is not simply a passive solvent, but drives pollen tube growth via hydrostatic pressure and cell volume regulation. Volume and osmotic changes affect the mechanical/chemical status of the plasma membrane, cellular ionic strength and/or concentrations of specific ions, macromolecular crowding and proximity of protein binding partners. Osmotic potential in pollen tubes is asymmetrical and higher in the actively growing apical region. The cells are far from equilibrium and fluctuations in metabolism and growth lead to continual fluctuations in cell osmotic potential and stimulate water to flow into or out of the cell. Compensatory reactions to stabilize and regulate cell osmotic potential then become activated (regulatory volume decrease/increase), leading to activation of multiple signaling pathways including ion flux and phospholipid signaling, and triggering increases in exocytosis or endocytosis. Thus, water flux and osmotic balance can act as a traveling wave, activating the population of coupled oscillators at different osmotic potentials as shown in **Figure 1**. When cycles of hydrodynamic flow and regulatory networks are coupled in phase then growth becomes oscillatory. These results can facilitate reaching new insights for plant cell growth.

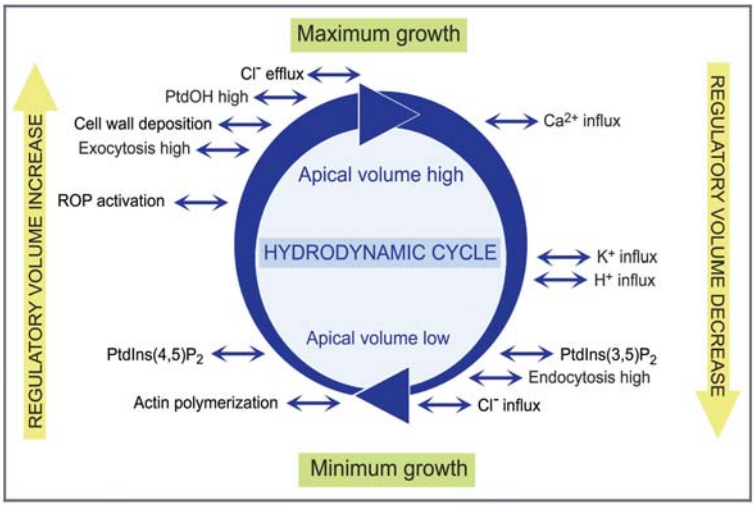


**Figure 1.** Pollen tube growth is driven by asymmetrical hydrostatic pressure. Fluctuations in osmotic potential affect all aspects of cell function: cell ionic strength, macromolecular crowding, cell volume, cell mechanics, and electrophysiology. Regulation of cell volume is linked through feedback loops to signaling cascades as shown in the illustration.