

Thematic Articles

# Cytoskeletal Regulation of Plant Growth

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The cytoskeleton, an intracellular network of fibrous structural proteins and other associated structural and motor proteins, is intimately involved in numerous aspects of plant growth. For example, mitosis, cytokinesis, cytoplasmic streaming, and directional expansion of plant cells, including tip growth of pollen tubes and the morphogenesis of branched leaf trichomes, are all cytoskeleton-based processes. Some recurring and interrelated themes that pertain to these phenomena are cell polarity, polar intracellular movement of organelles, molecules and cytoplasm, and intercellular movement of molecules and other signals to achieve communication and coordination within a tissue.

Actin is one of the major cytoskeletal proteins in plants, and a variety of associated proteins modulate its polymerization into microfilaments and thus its activity. Bryan Gibbon examines how two proteins that bind to free actin monomers, profilin and actin-depolymerizing factor (ADF), interact with actin in vitro and in vivo, and presents a model of how these molecules might be functioning to achieve the actin dynamics that regulate tip growth in pollen tubes and root hair cells. The other major player in the plant cytoskeleton is tubulin, which assembles with its associated proteins to form microtubules. Marjatta Raudaskoski and others present an overall summary of activities in the pollen tube that involve

cytoskeletal elements, including actin-based tip growth as well as microtubule-dependent processes such as division of the generative cell and migration of sperm cells toward the tube tip. For comparison, the single-celled, branched trichomes of *Arabidopsis* leaves are structurally more complex and do not display tip growth; as demonstrated in Dan Szymanski's contribution, their initiation and normal outgrowth likewise have specific requirements regarding the organization of microtubules and actin microfilaments, respectively.

Two of the papers included in this issue address different aspects of how partitioning of the cytoplasm is achieved at cytokinesis. Liu and Lee summarize current biochemical information about a superfamily of microtubule-based motor proteins, the kinesin-related proteins, and their location relative to microtubules during cytokinesis. One intriguing and complicating factor about these motors is that different members of the superfamily have different directions of motion relative to the polarity of the microtubules with which they interact. The authors present a model of how kinesin-related proteins with different directions of force generation could be employed to coordinate the forces required to establish the cytokinetic machinery (the phragmoplast) and then direct its activity to result in formation of the new cell wall dividing the parent cell. Brown and Lemmon's paper contrasts division of cytoplasm during vegetative growth with division during reproductive growth, during which there can be syntactia that eventually need to partition numerous nuclei. Noting the differences in cytoskeletal arrays

prior to cytokinesis, in the cellular landmarks the cell or syncytia has for reference, and in the precision of control of wall placement in the two systems, they hypothesize how the two methods for division might be related.

A third group of papers deals with the cytoskeleton and interactions between groups of cells. Overall and colleagues consider three models for how the cytoskeleton is co-aligned between neighboring cells to achieve coordinated division and organ expansion, with successive models increasingly invoking the participation of intercellular channels, the plasmodesmata. Baluska and others report on a region of the root tip that they call the transition zone, in which cells have a specific cytoskeletal arrangement that allows them to respond to cues for growth polarity and to coordinate growth processes.

By no means does this collection of papers represent the entire picture of how the cytoskeleton is involved in regulation of plant growth. However, what I hope it is able to do is to provide a glimpse of the range of activities that the cytoskeleton influ-



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ences in plants. In particular, its ability to select or impart cellular polarity provides a framework upon which other regulatory elements can operate to modulate growth.