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Review

Environmental and Endogenous Control of Cortical Microtubule Orientation

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Plant growth requires a tight coordination of cell shape and anisotropic expansion. Owing to their immobility, plant cells determine body architecture through the orientation of cell division and cell expansion. Microtubule cytoskeleton represents a versatile cellular structure essential for coordinating flexible cell morphogenesis. Previous studies have identified a large number of microtubule-associated regulators that control microtubule dynamics; however, the mechanisms by which microtubule reorientation responds to exogenous and environmental stimuli are largely unknown. In this review, we describe the molecular details of microtubule dynamics that are required for cortical microtubule array pattern formation, and recapitulate current knowledge on the mechanisms by which various environmental and endogenous stimuli control cortical microtubule reorientation.

Trends

Microtubule reorientation requires the activity of microtubule-associated proteins, including regulators of microtubule nucleation, severing, polymerization (and depolymerization), bundling, and interactions with cellulose microfilaments.

Predominant cortical microtubule orientations determine plant cell morphology and the direction of organ outgrowth.

In response to endogenous and environmental signals, cortical microtubules reorient and form various array patterns.

Microtubule Dynamics during Plant Life

Plant morphogenesis requires coordination of three processes at the cellular level: cell division, cell expansion, and cell differentiation. One of the most fundamental processes of plant cells is their reproduction through cell division [1]. To adapt to developmental and environmental changes, a plant cell rapidly modifies symmetric cell division by regulating the cytoskeleton apparatus. Microtubules (MTs) organize in diverse array patterns to regulate cell division, cell expansion, and cell differentiation [2]. Corresponding to those diverse roles, plant cells develop four types of MT arrays: cortical MTs (cMTs) are mainly responsible for cell expansion; the other three types of MT arrays including the preprophase band (PPB), mitotic spindle, and phragmoplast are essential for cell division and cell differentiation [2]. Among these MTs, cMTs are well characterized and they form highly ordered parallel patterns beneath the plasma membrane. They reorient in response to external stimulation, thereby tightly correlating their orientation with subsequent changes in the axis of cell expansion and plant organ formation [2]. In this review, we describe the molecular details of MT dynamics that are required for cMT array patterns, and summarize possible mechanisms involving environmental and endogenous control of cMT orientations.

Regulation of Microtubule Dynamics

Owing to the advancement of microscopy technologies, scientists have made great progress in understanding MT dynamics. More importantly, novel molecular components are being gradually identified, providing insights into MT dynamic behaviors, such as nucleation, growth and bundling, severing, and shrinkage as they relate to cMT reorientation (Figure 1).

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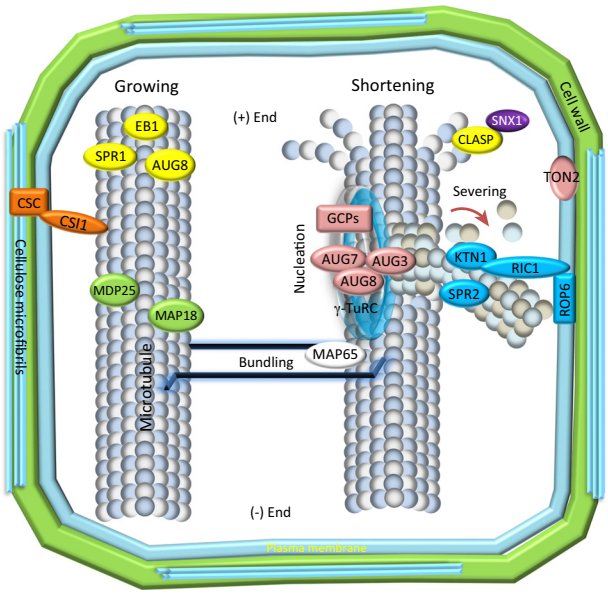

Figure 1. Microtubule (MT) Assembly Dynamics. Processes of MT (shown as two white cylinders) organization encompass MT nucleation, polymerization, depolymerization, severing, and bundling. AUGs and GCPs accumulate at nucleation sites to mediate MT initiation. TON2 localizes on the plasma membrane and also participates in MT nucleation (labeled as pink). Once new MTs generate from their mother MTs, KTN1, which forms a complex with RIC1 and ROP6, and SPR2 are recruited to crossover sites and catalyze a severing event (labeled as blue). In the process of MT growth and shrinkage, EB1, CLASP, and SPR1 accumulate at the plus (+) end to mediate MT polymerization (labeled as yellow); MDP25 and MAP18 are involved in depolymerization (labeled as green). MTs assemble into arrays of bundled filaments in a MAP65-dependent manner (labeled as white). In addition, MTs and cellulose microfibrils are connected by CSC–CSI complexes (labeled as orange). Abbreviations: AUG, Augmin; GCP, γ-tubulin complex protein; KTN, KATANIN; RIC1, ROP-interactive CRIB motif-containing protein 1; ROP6, Rho GTPase 6; SPR2, SPIRAL2; EB1, end-binding protein 1; CLASP, CLIP-associated protein; MDP25, MT-destabilizing protein 25; MAP, MT-associated protein; CSC, cellulose synthase complex; CSI1, cellulose synthase interactive 1.

Microtubule Nucleation, Polymerization, and Bundling

In animal and yeast cells, MTs are nucleated from centrosome-based MT-organizing centers (MTOCs), associated with γ-tubulin and γ-tubulin complex proteins (GCPs). These components establish the 'γ-tubulin ring complex' (γ-TuRC), which serves as a template for MT initiation [3]. By contrast, plant cells lack a true centrosome; therefore, how this organization is generated in the absence of a dedicated MTOC has remained unclear. It has been suggested that plant cells contain γ-TuRC-like structures and putative MTOCs help to form well-organized cMT arrays [4]. Indeed, enhanced MTOC activity favors the formation of longitudinal cMT arrays [5].

MT nucleation sites can form three different types of MT nucleation patterns: branching nucleation, parallel nucleation, and *de novo* nucleation, which are determined by the initial branching angle of existing MTs and regulated by several enzymes [6,7]. *Arabidopsis* TON2, a putative phosphatase 2A regulatory subunit, modulates the conformation change of γ-TuRC-like structures [8]. In *ton2* mutants, branching nucleation dramatically decreases and parallel and *de novo* nucleation increase compared with wild type (WT) [8,9]. Thus, TON2 may function as a specific regulator of nucleation geometry [9].

A new model of MT dynamics called hybrid treadmilling has been proposed for plant systems: MT plus ends show polymerization-biased dynamic instability, while minus ends exhibit slow and intermittent depolymerization [10]. The newly formed MTs grow along a new trajectory, implying that changes in the growth trajectory of growing MTs are important for controlling cMT orientation. Through a copurification assay, a number of MT-associated proteins (MAPs) were found to associate with tubulin [11]. MAP65 concentrates at the plus end of MTs and inhibits MT