Microtubule Regulation in Plant Cell Division

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Microtubules (MTs) are essential elements of the eukaryotic cytoskeleton and are critical for various cell functions. During cell division, plant MTs form highly ordered structures, and cortical MTs guide the cell wall cellulose patterns and thus control cell size and shape. Both are important for morphological development and for adjusting plant growth and plasticity under environmental challenges for stress adaptation. Various MT regulators control the dynamics and organization of MTs in diverse cellular processes and response to developmental and environmental cues.

microtubules microtubule-associated proteins development

1. Introduction

Microtubules (MTs) are highly conserved cytoskeletal structures in both plant and mammal cells [1][2]. Like mammal MTs, plant MTs consist of α- and β-tubulin subunits [3][4], and some tubulin isoforms are expressed in specialized cells or tissues during development [5][6][7][8]. The formation of α/β-tubulin heterodimers needs a large chaperone complex and guanosine 5′-triphosphate (GTP) [9][10]. Hence, recombinant tubulins cannot be efficiently produced in *Escherichia coli* because of the lack of a proper protein folding machinery in prokaryotes [11]. The longitudinal head-to-tail interactions between α/β-tubulin heterodimers via GTP hydrolysis to guanosine diphosphate build up the basic units of MTs, protofilaments [12][13]. The GTP cap at the plus end ensures MT growth, while the loss of the GTP cap results in MT shrinkage. The co-existence of growing and shrinking MTs driven by the restoration and hydrolysis of GTP was proposed as a “dynamic instability” model based on the observation of in vitro-reconstituted MTs [14]. The dynamic behaviour of MTs is thought to be an intrinsic property, as demonstrated by a MT polymerization experiment conducted from purified tubulin without external factors [15].

MT polymerization can occur spontaneously in vitro without any pre-formed templates when sufficiently high concentrations of purified tubulins are warmed up in the presence of GTP [16]. However, in cells, tubulin molecules tend to form a nucleation seed for efficiently initiating polymer growth and the construction of dynamic polar MTs under spatial and temporal control [17][18]. The evolutionarily conserved MT nucleating template is known as the γ-tubulin-containing ring complex (γ-TuRC) [19][20][21]. It initiates MT nucleation at a particular subcellular location, primarily regulated by Augmin [22][23][24]. Katanin internally breaks MTs dependent on adenosine 5′-triphosphate (ATP), particularly at MT crossover positions, where the detached daughter MTs can translocate via treadmilling to form new configurations of MT arrays [25][26][27][28][29]. Thus, both γ-TuRC and katanin are thought to be central components in synthesizing new treadmilling MTs at the plant cell cortex [25][30]. The dynamic nature enables MTs to alter their organization in response to internal and external signals for the needs of the cell, and it is regulated by various proteins [31][32].

Eukaryotes have conserved MT-associated proteins (MAPs) that bind along the MT lattice and have stabilizing or destabilizing effects on MT assembly [32][33][34]. However, plants possess a set of MAPs specific to plant morphology and physiology [35][36][37]. Conventional MAPs include motor proteins such as kinesins that utilize MTs as tracks to transport cargo and structural MAPs or severing proteins such as MAP65 and katanin (with the catalytic subunit p60 and a regulatory subunit p80) involved in MT organization via binding, bundling, or cleavage of MTs. MTs plus tip-associated proteins, such as cytoplasmic linker-associated proteins (CLASPs), regulate MT dynamics via their binding and interactions at the plus-end of growing MTs [13][36][38][39][40][41][42][43].

MTs arise from centrosomes in animal cells [44], but MTs in acentrosomal plant cells are thought to self-organize into structured arrays [45]. The plant-specific structures (i.e., cell wall and stomata) and the sessile nature of land plants lead to distinct MT regulation, affecting plant growth, development, and stress adaptation.

2. MTs in Plant Cell Division

Sessile plants cannot move as quickly as multicellular animals to escape environmental challenges. Thus, besides forming organs and various cell types for morphological development, cell division in plants is also important for adaptation to environmental conditions: adjusting growth under stress by enhancing, reducing, and redirecting cell growth [46]. In dividing plant cells, MTs form distinct structures, including the preprophase band (PPB), the acentrosomal mitotic spindle, and the phragmoplast [47][48][49] (**Figure 1**). The PPB, which is a plant-specific cortical MT ring, marks the orientation of the cell division plane and determines the spindle positioning in metaphase [50][51][52]. The PPB tunes the orientation of spindles in a mode similar to that of centrioles and astral MTs in animal cells, which implies the importance of spindle orientation [51][53].

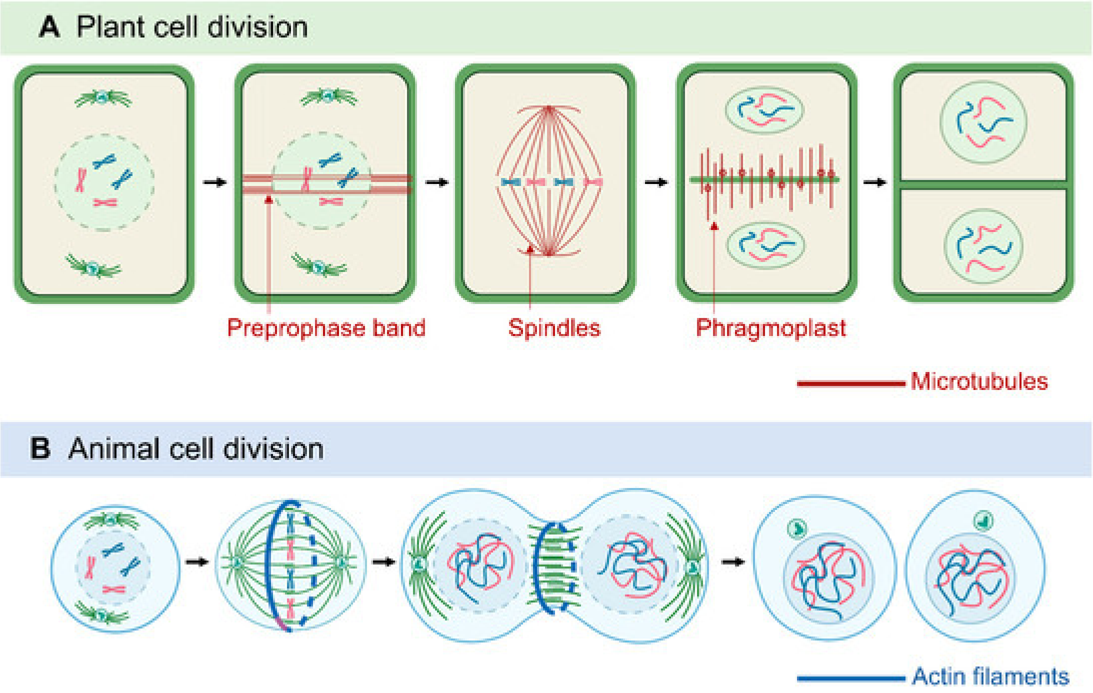

Figure 1. Comparison of plant and animal cell division. Plant cell division (**A**) is characterized by microtubule (MT)-based structures: the preprophase band, the acentrosomal mitotic spindle, and the phragmoplast. In animal cell cytokinesis (**B**), the contractile ring pinches the cell into two daughter cells, whereas plant phragmoplasts extend and guide vesicle fusion to generate the cell plate.

MT-based spindles separate chromosomes during mitosis [54]. Most animal spindle-assembly factors are well conserved in plants, but plants lack two major elements: centrosomal components and the cytoplasmic dynein complex [48]. Animal spindle MTs nucleate from centrosomes [55], whereas plant MTs appear to nucleate from the nuclear envelope surface [56]. In animals and fungi, cytoplasmic dynein is a processive minus-end-directed motor that pulls on astral MTs from the cell cortex for efficient and accurate spindle assembly and positioning [57]. In contrast, plants lack cytoplasmic dynein but contain many minus-end–directed kinesin-14 proteins, which were thought to be involved in the sliding of anti-parallel microtubules throughout mitosis [46][58][59][60]. Kinesins with a calponin homology domain (KCH) are a distinguished subclass of kinesin-14 found only in Plantae [61]. Rice OsKCH2 exhibits processive minus-end-directed motility on MTs to potentially compensate for the loss of dynein [62], whereas moss KCH drives MT-based nuclear transport reminiscent of animal dynein [63]. In animals, plus-end–directed kinesin-5 and kinesin-12 facilitate the spindle arrangement [64][65] and it seems to be conserved in plants, as shown by Arabidopsis KINESIN-12E controlling spindle MT organization and size during mitosis [66]. MTs are protein–protein interaction sites for the spindle assembly checkpoint (SAC) protein complex and signaling network. Plants have conserved the SAC network with some variations from animals and yeast [67]. The dissection of proteins associated with SAC led to the discovery of novel aspects of plant SAC regulation [68][69], which may be relevant for plant breeding studies because ploidy alternations likely rely on SAC properties.

Another plant-specific MT machinery, the phragmoplast, is formed between the reconstituting daughter nuclei at the end of telophase, as a hallmark of cytokinesis [70]. The phragmoplast expands and transports Golgi-derived vesicles containing building materials to facilitate the construction of the cell plate. The assembly, crosslinking, and turnover of phragmoplast MTs are regulated by various MAPs, kinesin motors, and regulatory enzymes [49][53][70][71][72]. Among them, plant-specific Cortical MT Disordering 4 tethers the conserved MT-severing protein katanin to facilitate phragmoplast expansion and accelerate cytokinesis [73]. Cytokinesis-specific MAP65-3 plays primary roles in phragmoplast integrity and efficient cell plate formation [74][75][76]. Phragmoplast dynamics during cytokinesis is closely related to the phosphorylation of MAP65-3, regulated by mitogen-activated protein kinase 4 and aurora kinase [77][78][79]. As a positive regulation mechanism, benzimidazole-3 proteins interact with MAP65-3 and promote MT bundling for phragmoplast expansion [80]. The MT motor protein KINESIN12 is critical for maintaining MT plus-ends in the phragmoplast midzone. Indeed, the Arabidopsis double-mutant pok1/pok2 (two kinesin-12 orthologs) revealed chaotic division sites and a slower phragmoplast expansion rate compared to the wild-type [81][82]. Overall, because they lack structurally defined centrosomes but have flexible and distributed PPB and phragmoplasts, plant cells can assemble bipolar spindles and determine the division plane with a great deal of plasticity, thereby compensating for the restraints in cell movement caused by the stiff plant cell wall [46][83].

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