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The Plant Cytoskeleton and Crosslinking Factors

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Abstract

Cytoskeleton exists in all eukaryotes and is involved in many significant cytobiological processes, especially the movements and developmental changes of plant cells. The cytoskeleton consists of microtubule (MT), microfilament (MF), and intermediate filament (IF). MT and MF are vital components of plant cytoskeleton. Crosslinking factor acts as a bridge between MF and MT. They play an important role in cellular life process and have always been a hot topic and key point in plant cytobiology, and the IF is a difficult point in this field. In this paper, the latest research on the cytoskeleton of plants is introduced, which focuses on the structure and dynamics of MT, MF, and IF, and summarizes the crosslinking factors between MT and MF. Also, the paper prospects the future research direction of plant cytoskeleton and the possible research hotspot, which provides a certain reference for people to continue to explore the function of plant cytoskeleton in the future.

Keywords

Plant Cytoskeleton, Crosslinking Factor

1. Introduction

The cytoskeleton is a three-dimensional reticular structure intertwined with protein fibers, almost distributed in the inner space of the whole cell, and connected with the cytoplasmic membrane, nuclear membrane, and organelle. The cytoskeleton is an intrinsic supporting structure for cell survival and composed of MT, MF and IF. The cytoskeleton is a crucial filament network that maintains cell morphology, internal arrangement and normal physiological function [1].

The dynamic changes of plant cytoskeleton are the basis of cell functions, such

as migration, adhesion, dissemination, and proliferation. In addition, cytoskeleton can assist in the transfer or movement of proteins, vesicles and organelles in the cell [2] and assist plants to respond to gravity changes. The cytoskeletal tissues and dynamics enhance plant tolerance to stress by regulating intracellular activities.

The cytoskeletal research has been one of the hot topics in the cell biology. This paper expounds the important role of the cytoskeleton in plant cells from four aspects: the tissues and dynamics of MT, MF, IF and crosslinking factors in plant cells.

2. Tissues and Dynamics of MT in Plant Cells

MT is the main component of the cytoskeleton, which is a hollow tubular structure. Each tubulin consists of two globulin subunits to form a heterodimer. The structural diagram of microtubules is shown in **Figure 1**. γ-Tubulin is another kind of tubulin which exists in centrosome and participates in the formation of MT. MT has three forms of existence: monomers, doublets and triplets [3]. Single tube is easy to depolymerize and unstable microtubules under the action of low temperature, Ca^{2+} and colchicine. The double and triple tubes are stable to low temperature, Ca^{2+} and colchicine. MT is present in almost all eukaryotic cells and can form basic structures, such as spindle, centriole, cilia, flagella and neural tube with other proteins [4]. MT has a key role in cell cycle, cell division, cell morphology maintenance, information transmission, intracellular material transport and signal transduction, etc. [5]. The dynamic characteristics of the MT include polymerization, depolymerization, severing, bundling, nucleation, etc.

2.1. MT-Associated Protein (MAP)

MAP is either a direct or indirect binding MT protein, which is co-located with MT *in vivo* and affects the function through the regulation of MT dynamics and tissues. The type of MAP includes tubulin, MAP65, TAN1, Katanin, Kinesin and so on [6]. Although they have different functions, they interact and work with MT to regulate a series of cellular activities.

MT plus end tracking proteins (TIPs) regulate the MT stability, vesicle transport, etc. The classic TIPs in plants include EB1 (the end-binding protein 1), SPR1 (SPIRAL1), CLASP (CLIP-associated protein), AUG8 (AUGMIN Subunit 8) and so on. SPR1 and EB1 surround in the cell intimal system in a similar way [7]. The plant-specific MAP (AUG8) regulates the transformation of the hypocotyls and the periplasmic MT arrays in the root [8]. CLASP and sorting nexin1 (SNX1) combine to regulate the transport of PIN2 protein to the cell membrane by MT [9]. Proteins that bind to the ends of stable MT are called MT capping protein (MCP) [10]. The calmodulin-regulated spectrin-associated protein (CAMSAP) family is one of MCPs, including CAMSAP1, CAMSAP2 and CAMSAP3. CAMSAP3 is combined with the negative end of non-centrosomal MT that mediates the anchoring of MT on adhesive junctions (AJ) [11]. Inhibition of CAMSAP3 expression results in smaller spindle bodies in mitotic cells

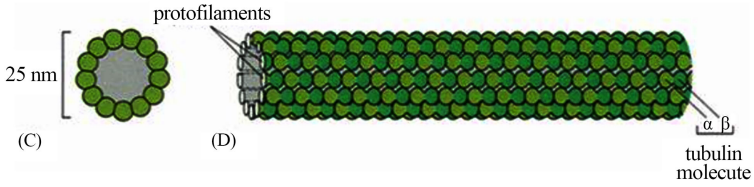

Figure 1. The structural diagram of microtubules.

and breaks MT in interphase cells [12]. CAMSAP2 and CAMSAP3 in interphase cells are involved in the regulation of MT system [13]. CAMSAP2 maintains the stabilization of the negative end of the non-centrosome MT [14]. AtMAP18 regulates the arrangement of periplasmic MT in cells and the polar growth of cells by inhibiting the MT polymerization [15]. MAP25 and MAP18 have some homology and inhibit the polymerization of MT [16].

2.2. MT Takes Part in the Plant Cell Growth

MT of plant has different MT arrays at different cellular stages. The MT in the rapid growth cells was arranged horizontally, and in the slow-growing cells was oblique or random, while in the cells was vertical when they stopped growing. Many factors affect the arrangement of periplasmic MT in hypocotyl cells. For example, when the dark hypocotyls are exposed to light, the MT in the cells changes from transversely to longitudinally [17]. When treated with MT depolymerization agents (such as oryzalin, propyzamide) or MT stabilizer (such as taxol), the anisotropic cells will lose their polarity. Therefore MT is momentous in cell polarity growth.

2.3. MT Is Involved in the Signal Transduction of Plant Hormone

Plant hormones and MT participate in the plant growth, development and stress response together. Auxin affects the plant growth under shading condition by regulating the distribution of periplasmic MT [18] [19] [20] [21]. Auxin reaction factor 8 (ARF8) and MT are involved in regulating the elongation of hypocotyls and stamens in *Arabidopsis thaliana*, but there is no direct evidence [22]. MT and gibberellin (GA) take part in regulating the growth of plant hypocotyl and the development of floral organs [23]. MT destability protein 40 (MDP40) is the key factor of Brassinosteroid (BR) to regulate periplasmic MT array and the elongation of hypocotyl cells [24]. MT and abscisic acid (ABA) regulate the stomatal opening and closing [25]. Ethylene is involved in the regulation of MT during the development of epidermal hair [26] [27].

2.4. MT Is Related in the Vesicle Transport

MT can transport intracellular vesicles and macromolecules and through other factors to transport substances, such as the Kinesin, CLASP and so on. At-KINESIN4 transports intracellular substances along MT and regulates microfibril deposition and cell polarity growth in the cell wall [28]. CLASP regulates the vesicle recovery process of PIN2 protein (auxin transport vector) by binding to SNX1 in

plant cells [9].

2.5. MT Participates in the Process of Plant Mitosis

In the prophase and prometaphase of mitosis, the spindle is composed of MT that assembled between two separated centroids and mediated the arrangement and separation of chromosomes to the equatorial plates of cells. The motility of the chromosomes in mitosis is connected by MT at the two poles and is gradually arranged on the equatorial plate of the spindle. The functional entity that mediates the connection between the motility point and the MT is the KMN complex. When the KMN complex is phosphorylated by AuroraB, its MT-binding capacity is weakened, thus releasing the relationship between the motility point and the MT [29]. When all the chromosomes are successfully arranged on the equatorial plate, the spindle test points are inactivated, the cells enter the mitosis anaphase and the sister chromatids are separated [30].

3. Tissues and Dynamics of MF in Plant Cells

MF (also known as actin fibers) is cylindrical, with a diameter of 5 - 8 nm, consisting mainly of actin and actin-binding protein (ABP), and widely distributed in various tissues and cells, such as myocyte and non-muscle cell. The MF is arranged in parallel or evacuated to a network in the cells. Actin is a globular protein consisting of 375 - 377 amino acid residues with a molecular weight of 42 kD and is the raw material of the MF. There are two main forms of globular actin (G-actin) and fibrous actin (F-actin) in cells. MF has polarity, divided into positive and negative poles. A G-actin is combined with an ATP to become ATP-Actin. The affinity of ATP-Actin to positive end was high and ATP was hydrolyzed to ADP after binding to MF. The assembly speed of MF was influenced by actin monomer concentration, ion concentration, cytochalasin and ABPs. There is a wide variety of ABPs, more than 100 of which are involved in initial MF nucleation, end-capping, cutting and bunching [31]. MF refers to many life activities, such as maintaining cell morphology, material transport, apical growth, signal transduction and so on.

3.1. MF-Binding Protein

According to the regulation of the dynamic assembly function of MF, ABP can be divided into the following categories: MF nucleation promoters, actinrelated protein 2/3 complex (Arp2/3 complex), formin, villin, fimbrin, profilin, capping protein (CP), MF cleavage protein, etc. Arp2/3 complex is essential in the process of negative capping of MF. Formin is responsible for producing parallel MF bundles and regulating the arrangement of MF. Profilin binds with G-actin to maintain the stability of actin monosomic library in the cytoplasm and works by directly binding to actin, and has polyproline PLP binding sites. Villin has more regulatory activities than other proteins and has the activity of nucleation, capping, cleavage and binding of MF. Fimbrin has the functions of binding and

bunching of MT. CP can bind to the positive end of the MF to maintain the stability of F-actin, thus prevent the addition and loss of actin monomer at the end. The MF cleavage protein has an actin-dependent factor (ADF) and the function of the ADF includes shearing, polymerization, depolymerization and nucleation. In addition, many ABPs have been found, which connect MF and MT. Some ABPs are also key components of the signal transduction pathway.

3.2. MF Is Vital in Maintaining the Normal Morphology and Cell Movement

Treatment of *Arabidopsis* seedlings with MF-specific drug latrunculin resulted in fewer cells, shorter plants, villous twist leaves, roots, cotyls and pollen tube lengths smaller than those of normal ones [32]. MF is closely related to some intracellular movements, such as cytoplasmic circulation, endocytosis, exocytosis, etc. [33] [34]. There are many MFs passing through the vacuole at each stage of cell cycle and a large number of MFs are distributed around the chromosomes in the metaphase and anaphase of the spindle pole and the mitosis anaphase of the root tip cells of wheat. In UV-B irradiated cells, the dynamic assembly of F-actin is involved in the occurrence of abnormal mitosis [35]. In *tobacco* cells transformed with GFP mTalin fusion protein, it was observed that chromosomal movement and cell plate formation at anaphase of mitosis were dependent on MF [36].

3.3. MF Is Related to Plant Response to Gravity Variation

In the central columnar cells of Arp2/3 MF-associated protein complex (*dis*1-1, *dis*2-1) mutant, the lack of "cage-escape" and synergistic movement of amyloplasts is due to the restriction and separation of the amyloid by abnormal coarse MF bundles. The pretreatment of MF depolymerization agent (Latrunculin B) broke the "cage" effect of amyloid movement in mutants. In *dis*1-1 mutants, the intracellular translocation of PIN family proteins (PIN2, PIN3, PIN7) of several auxin transport vectors is abnormal, which affects the asymmetrical distribution of auxin in the cells above and below the root, resulting in a delay in the ground-bending growth of the root.

3.4. MF Is Involved in Plant Signal Transduction

A similar structure of the continuous body of the extracellular matrix-plasma membrane-cytoskeleton in the plant was found. Guard cells of plant are stimulated and the MF acts as a signal regulator to control the opening and closing of guard cells through aggregation or depolymerization. The stomatal closure rate of *ArpC*4 and *ArpC*5 mutants became slower and the accumulation rate of reactive oxygen (ROS) was later than that of wild type. So the dynamic regulation of MF might affect the production of ROS [37]. The MF attends the stomatal movement by regulating the distribution of NADPH oxidase in different parts of the guard cytoplasmic membrane and controlling the site of ROS production on the cell wall, thus regulating the relaxation of the cell wall.

3.5. MF Participates in Plant Defense against Stress

The dynamic changes of MF partaked in the transport of papillomastoid formation related to cell wall formation and the expression of disease-related genes at the site of pathogen infection [38]. Compared with CK, LatB pretreatment is accelerated the formation of maize spot after infection with Rhizoctonia solani AG1-A and affected the development of infection structure. After treating with CytochalasinA, hypersensitive cell necrosis, H_2O_2 production and mastoid formation in cucumber leaves induced by powdery mildew were significantly inhibited, so indicating that MF depolymerization could promote the infection of powdery mildew in wheat. The MF assists soybean resistance to virus and the depolymerization of MF is beneficial to the development of soybean mosaic virus. ADF can be induced by abiotic factors such as drought, high temperature and low temperature [39].

4. Tissues and Dynamics of IF in Plant Cells

IF is another significant fibrous cytoskeleton protein, which is between MF and MT in diameter and encodes more than 70 genes. The IF forms a complex lattice structure within the cell to connect the nuclear membrane, the plasma membrane and another cytoskeleton [40]. According to structure and sequence homology, they can be divided into five categories: I-VI type. I and II type of IF including acidic and intermediate-basic keratin. III type of IF consists of vimentin, desmin, peripherin and glial filament acidic protein. The IV-type of IF includes a neurofilament protein subunit and an α-internexin. V-type of IF contains nuclear matrix proteins such as LaminA, C, B1/2 and other nuclear skeleton proteins. VI-type protein is located in the crystalline lens [41].

IF is concerned in many cellular physiological activities: including movement, deformation, anchoring and distribution of organelles and intracellular signal transduction, etc. [42]. The main component of IF in *Arabidopsis* cells is keratoid. Research shows that IFS limits the generation of traction and prevents the accumulation of traction in monolayer. IFS controls the structure and dynamics of myosin networks. IFS promotes actin-drive kinetics of AJs between adjacent leading cells have been found [43]. Actin-driven AJ and maintenance of cell-cell interactions require IFS.

Lamin is a type-V IF protein that can be classified into A and B types, which provides nuclear mechanical stability and shape. And Lamin establishes connection between the nuclear skeleton and cytoskeleton. In the mitosis of the lesion, the Lamin depolymerization depends on phosphorylation and is then dispersed in the cells [44]. In the anaphase/terminal transition, they begin to reassemble around the segregated chromosomes [45]. Lamin-B is an essential part of the mitotic spindle assembly. Lamin was initially considered to support the nuclear membrane and provide anchoring sites for chromosomes [46]. The Lamin is required in biological events at all stages of the cell cycle, including nuclear membrane assembly and rupture, DNA synthesis, transcription and apoptosis [46]

[47]. Lamin-B dominates the formation of mitotic spindle [48].

5. Crosslinking Factors

In cells, the coordination of MT and MF functions is essential for the cell to perform many physiological functions. Many proteins in cells are involved in the cross-linking of MT and MF. The main crosslinking factors in plant cells includes: *Arabidopsis thaliana* formin 14 (AFH14), *Arabidopsis thaliana* formin 16 (AtFH16), kinesin with calponin homology domain (KCH), MT-associated protein 18 (MAP18), MT-associated protein 190 (MAP190), MT-destabilizing protein 25 (MDP25), ROP-interactive CRIB motif containing protein (RIC), pollen-specific MT-associated protein (SB401), kinesin-like calmodulin-binding protein (KCBP) and so on.

5.1. AFH14

Formin is an important cytoskeleton regulatory factor and can regulate the dynamics of MT and MF arrays in *Arabidopsis* [49]. *AFH*14, which consists of 18 exons and 18 introns, is a typical II type formin with conserved sequences. Expressed in BY-2 cells was shown to decorate preprophase bands, spindles and phragmoplasts to induce coalignment of MT and MF. FH1FH2 is the main functional domain of AFH14, which binds to the purified MT and MF directly and induces the formation of MT or MF bundles. MF and MT are similar in length and uniform in the arrangement under overexpressed *AFH*14. In cells with decreased *AFH*14 expression, the connection between MT and MF was interfered, so affecting mitosis and cytokinesis. FH1FH2-RFP and GFP-MAP4 (MBD) labeled MT were colocated and the binding of FH1FH2-RFP to MT was dynamic *in vitro* [50].

5.2. AtHF16

AtFH16 is also type II formin [51] and plays a key role in regulating the morphology and structure of MF and MT. When *AtFH*16 is knocked out, the MT cannot effectively nucleate into bundles and the MF cannot be recruited to the spindle to form cage structures. The transformation of spindles and membranes was inhibited, resulting in cell division stagnation. The high expression of *AtFH*16 in transgenic plant cells is accelerated the free assembly of MF and MT and the change of cytoskeleton dynamics, thus promoting the cell division. The binding affinity of FH1FH2 of AtFH16 to MT is higher than that of MF *in vivo*. FH1FH2-RFP and GFP-MAP4 of AtFH16 is co-located, indicating that AtFH16 and MT co-located [52]. Cells initiate cascade reactions at all levels, which transmit signals to AtFH16 or control the activity of AtFH16 to influence the polymerization of MT under enhanced UV-B radiation.

5.3. KCH

KCH subfamily is a kind of plant-specific protein [53]. The first KCH protein

identified was GhKCH1 at the cellular level. GhKCH1 can interact with the MF and connect between the MF and MT in the growing cotton fiber [54]. Overexpression of OsKCH1 in BY-2 cells delays nuclear localization and cell division [55]. KCH is also a connector between MF and MT during nuclear localization. Members of the KCH family can bind to actin *in vivo* and *vitro*. MF and MT are able to respond to abiotic stress and *AtKCH*3 was involved in the regulation of abiotic stress response by regulating the dynamic changes of MF and MT. KCH transports nucleation and MT-actin interactions in flowering plants [56]. The results of low-speed coprecipitation showed that CH domain of *AtKCH*3 and *AtKCH*4 could promote MF bunching *in vitro* [57].

5.4. MAP18

MAP18 is a MAP of DREPP family that stabilizes MT and regulates the anisotropic growth of *Arabidopsis* cells [15]. The cytoplasmic membrane Ca2 junction protein 2 (PCaP2) and MAP18 were the same protein. The PCaP2's function is diverse in cells and is involved in the morphogenesis of *Arabidopsis* cells by regulating the destability of MT and MF cleavage activity through calcium signaling pathway [58]. The MT destability activity of PCaP2 enhanced the cold tolerance ability of plants and stimulated the expression of cold genes in plants. MDP25, which was similar to MAP18, is combined with MT and MF. Also, MDP25 cuts MF under the action of Ca^{2+} and is joined in regulating the growth of pollen tube tip [59].

5.5. MAP190

MAP190 is a protein isolated from BY-2 cells that binds both MT and MF [60]. *In vitro*, MAP190 binds MT and MF into bundles, while in cells it can bind to spindles and membranes during cell division [61]. AtMAP190 and NtMAP190 have similar functions, which lead to the interaction between MF and MT. Using complementary lines expressing AtMAP190-EGFP, *AtMAP*190 is found to be located in the nucleus and not co-located with MF and MT.

5.6. MDP25

MDP25 is a cationic binding protein with 225 amino acid residues and molecular weight of 25 KD in *Arabidopsis*, which is encoded on chromosome 4. It can bind metal cations such as Ca^{2+}, Mg^{2+} and so on [62]. MDP25 regulates the growth of hypocotyl by destabilizing MT [16]. The binding of MDP25 to MF showed that the MDP25 per mole of MF also was increased with the increase of concentration. MDP25 affects the arrangement of MF in the pollen tube and regulates the dynamic changes of MF by influencing the cutting frequency of pollen tube subapical MF. When the Asn at position 5 of the N terminal of MDP25 mutated to Ala, the MF cutting activity of MDP25 was significantly reduced, so indicating that Asn made vital contributions to the MF cutting activity of MDP25 [63].

5.7. RIC

RIC is a downstream effector of Rho GTPases ROP and has a conserved CRIB domain [64]. *Arabidopsis thaliana* genome encodes 11 RICs, RIC1 is a member of the ROP-interactive CRIB motif-containing protein family. RIC1 interacts with MT or MF in different types of cells or organs. The absence or overexpression of RIC1 affects the dynamics of MF at the pollen tube tip. The plasma lemma oriented RIC1 releases the MF from the plasma membrane and regulates the formation of MF on the plasma membrane by interacting with formins [65]. RIC1 can interact directly with the P60 subunit KTN1 of Katanin in MT cutting proteins to promote the MT cleavage activity of KTN1 and lead to the detachment of branched MT, so to make the MT form a transversal ordered array. When RIC1 binds to MF *in vitro*, RIC1 makes the MF into bundles and caps the right end of MF without Ca^{2+}. In the presence of Ca^{2+}, RIC1 cuts the MF in a Ca^{2+} dependent manner and enhances the capping effect on the MF. RIC1 inhibits the process of polymerization of MT under salt stress by inhibiting the transition of MT from depolymerizing to polymerizing, which is an inhibitory factor of salt tolerance in *Arabidopsis*. RIC1 is also a MAP, which can enhance the cleavage activity of katanin to MT and promote the reassembly of intracellular MT [20]. RIC1 regulates the growth of different plant cells by regulating the dynamics of MF or MT in specific tissues.

5.8. SB401

SB401 is a kind of *potato* pollen tube specific protein, which encodes a lysine-rich pollen specific protein. SB401 protein binds MT *in vitro* and co-locates with MT *in vivo*, which can make MT bundle. Phosphorylated SB401 is mainly related to F-actin and dephosphorylated SB401 acts on MT [66]. SB401 can promote MT polymerization in low concentration and inhibit MT polymerization in high concentration. When SB401 is sufficient, MT and MF are connected together. When SB401 is insufficient, SB401 has higher affinity to MT and preferentially binds MT to form bundles of MT [67]. The results showed that SB401 was a new MT-binding protein that could bind both MT and MF.

5.9. KCBP

KCBP is about 140 kDa similar to kinin, found only in plants [54], moving along the MT in a negative direction [68]. PaKCBP is one of the proteins that affects the interaction between MT and MF. PaKCBP senses Ca^{2+} and affects the structure of MF and MT in pollen tubules. Then PaKCBP regulates the reposition of vacuoles and the rate of vesicle transport. Finally PaKCBP controls the growth of pollen tubes [69]. KCBP interacts with MT and MF to regulate the hairy branches and elongation of *Arabidopsis*. TCS1 and KCBP affect the stability of MT and control the number of branches by affecting the dynamics and stability of *Arabidopsis* MT [70]. The results revealed that KCBP, as a "bifunional protein" coordinates the spatiotemporal and temporal dynamics of MT and MF [71].

6. Outlook

In recent years, the cytoskeleton has great progress. As we know, it is a key bridge between microscopic protein molecule and macroscopic cellular structures. However, we still focus on how the cytoskeleton responds to the external signal to regulate the polarity localization and distribution of PIN protein, and how to participate in the vesicular transport of PIN protein and the fusion with target membrane.

MT is vital to the growth of plant cells, but whether there is MT involved in physiological activities of mature and senescent organs remains to be studied. The specific mechanism of MT-phytohormone interaction and MF in response to gravity of plants is not clear. Whether the MT participated in the upstream signal path is still unknown during the regulation of the MF dynamic change. How the MF and ROS take part in the regulation of stomatal movement is still indistinct. The mechanism of the MF to participate in the plant-sensing external stimulus and the disease defense through the regulation of various ABPs is the key direction of the future research. IF exists in most animal cells, but no IF gene has been found in the plant cell genome.

The mechanism of KCH to promote the formation of MT and MF is not clear. How *AtMAP*190 regulates MF and MT in the cytoplasm is unaccountable. Whether MDP25 preferentially introduces a certain cytoskeleton in plants remains to be further studied. SB401 is not clear whether the protein binds to MF *in vivo*. Other cross-linking factors such as EB1, CLASP, TANGLED, PLD delta in plants need further study. Above all, elucidating the mechanism of cross-linking factors in plant cytoskeleton in MT and MF is still an important research direction in the future.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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