Review Article

A comprehensive review on cytoskeletal organization and its interaction with polysaccharides and enzymes during primary cell wall development

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ABSTRACT

A well-coordinated process is required to construct a complicated structure like the cell wall, which consists of several elements that must be joined appropriately from various sources inside the cell. In order to successfully moderate dynamic responses to developmental and environmental signals, further complexity is necessary. The plasma membrane is continually and actively transporting sugars, enzymes, and other cell wall elements throughout diffused development. Actin filaments and microtubules make up the cytoskeletal pathways used to transport cell wall elements in vesicles during cell division. In addition to these elements, other proteins, vesicles and lipids are transported from and to the cell plate while cytokinesis occurs. Adding additional cell wall material or building a new cell wall requires a rearrangement of the cytoskeleton, which we examine in this review first. We next look at the commonalities between these two processes. Our next topic is the transport of cell wall-building polysaccharides and enzymes via motor proteins and other interactions with the cytoskeleton. Final thoughts on cytokinesis-generated cell walls include a look at some of their unique properties.

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Keywords: Cell cortex; cytoskeleton; phragmoplast; microtubule nucleators; cellulose biosynthesis; kinesins; callose

1. INTRODUCTION

In 1665, when Robert Hooke used a microscope to investigate oak cork (*Quercus suber*) under a light microscope, he accidentally started the study of cell wall function and structure. Because of its resemblance to a monk's room (cell), he came up with the name "cell" to represent the tiniest living biological structure. Hooke was able to see the cell wall for the first time since the cellular contents had been cleared. Cell wall research has since profited from structural component analysis of the isolated cell wall [1]. Our knowledge of how the cytoskeleton and transport of cell wall components are intertwined has recently improved thanks to recent advances in cell biology, especially live-cell imaging (LCI). Cell expansion and division are two of the most important factors in generating plant biomass. Cellulose is the most prevalent biopolymer on the earth because it is a key element of main cell walls. Additionally, cell wall synthesis and alteration are as important to plants as global biomass. Cell wall production and modification take up around 10% of certain plant genomes, and hundreds to thousands of additional genes are involved in controlling the vesicle and cytoskeleton transportation [2].

During cytokinesis, the cell wall is built from scratch, whereas during diffuse growth, new cell wall material is incorporated into the existing cell wall. In both circumstances, motor proteins transport vesicles carrying cell wall components to the cytoskeleton. Vesicles normally emerge in the Golgi and are transported via the cytoskeleton, often passing through the trans Golgi network (TGN), on their way from and to the cell plate and the plasma membrane. For this reason, having microtubules and microfilaments that are appropriately structured is essential for the placement and assembly of cell wall substituents. For example, the quick and precise addition of cellulose during diffuse development is dependent on well-organized microtubules owing to direct connections between enzymes, microtubule linking proteins and microtubules that create cell wall polymers called cellulose synthases.

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During cell division, the phragmoplast, a conserved land-plant-specific structure, initiates the formation of the de novo cell wall [3]. Phragmoplasts are primarily responsible for generating new cell walls after the cytokinesis process separates the DNA [4]. Prior to the conclusion of cytokinesis, a preliminary version of the new cell wall is produced, known as the cell plate. As the cell plate grows in size, vesicle transport and fusion and changes in cell wall structure occur simultaneously [1,2,5]. Actin filaments in the phragmoplast create an antiparallel array of microtubules facing the center of the cell [6]. In the phragmoplast, spindle microtubules are used to build microtubules, which are then used to expand the phragmoplast through microtubule-dependent microtubule nucleation [7]. After then, when the cell plate grows, the microtubules are disassembled [6,8]. The cell plate fusion site or division site is a specified area where the phragmoplast connects to the cortex of the cell [3,9]. Because of this, the next section focuses on proteins and microfilaments that influence cytoskeletal dynamics and structure.

2. REGULATORY FACTORS RESPONSIBLE FOR MICROFILAMENT AND MICROTUBULAR BIOSYNTHESIS DURING DIFFUSE GROWTH

Actin filaments and microtubules are a pair in microfilaments, cargo, including cell wall components, are transported by motor proteins along the tracks. When the cell wall is changed, enlarged, or created, the factors that influence microfilament and microtubule placement have a significant but sometimes indirect function. The concept that cell shape controls orientation of microtubule is supported by the observation of cortical microtubules that are aligned with the long axis of rectangular or elliptical microchambers [10]. In protoplasts, which are unicellular with enzymatically destroyed cell walls, the arrangement of microtubules was recently scientifically examined. Microtubules align along the long axis when protoplasts are restricted in rectangular wells, which suggests that the default orientation of microtubules is longitudinal [11]. Planta, on the other hand, often has microtubules that run perpendicular to the cell's long axis [12]. In order to transform the orientation of microtubules from longitudinal to transverse in silico, a faint directional signal is all that is required [13]. One of the directional signals is mechanical stress, which has been postulated. Cellulose microfibril orientation is guided by microtubules in response to mechanical stress, according to the most basic paradigm [14]. A cell growth path is perpendicular to the expected maximum tensile stress direction, whereas microtubules align parallel to this [12,15]. Microtubules develop circumferential in hypocotyls, cotyledons, and meristems when the stress pattern is altered by laser ablation of adjacent cells [16]. Spherical protoplasts were contained in rectangular reservoirs in solutions of varying osmolarity to further investigate the mechanism of microtubule orientation. Osmolarity decrease causes stress, which overrides geometrical signals that would otherwise direct tubular orientation along the projected path of maximum tension after two hours [7,17]. Unlike animal cells, plant cells are unlikely to experience comparable osmotic shifts, and it is not yet clear how the change in osmotic potential affects tensile stress. Even if microtubules are able to directly react to changes in tensile stress, numerous additional proteins are very certainly necessary. To find out whether regulators, the microtubules itself, or other components are involved in the detection of maximum tension, further study is required.

Formins have also had their roles clarified through a number of useful ways that target groupings of formins. In moss, RNAi suppressed all of the class 1 formins without affecting tip development, but plants sizes were shorter and had fewer cells, indicating delayed cytokinesis. Multinucleate or stubs cells were not found [18]. Understanding how formins contribute to cytokinesis and mitosis was made possible with the use of the small chemical formin inhibitor SMIFH2 [4-7,19]. Formins may occasionally be found in the phragmoplast midline or phragmoplast, despite their generally obscure involvement in cytokinesis. This treatment also lowers duration of EB1 comet and changes turnover of fusion proteins such as KNOLLE and DYNAMIN RELATED PROTEIN 1A (DRP1A) [20]. No one knows for sure yet whether SMIFH2-induced cytokinesis deficits are primarily due to formin disruption. Formin mutations may be combined to offer clear evidence concerning their involvement in cell proliferation and cytokinesis.

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3. REGULATORY FACTORS RESPONSIBLE FOR MICROFILAMENT AND MICROTUBULAR ORGANIZATION AT THE CELLULAR CORTEX DURING TELOPHASE

Cell cortex microtubules and actin filaments accumulate during telophase, but before the phragmoplast touches the cell cortex (Figure 1) [21]. When microtubules emerge, they originate from either the nuclear envelope or the cortex-localized gamma tubulin or gamma tubulin ring complex [13,22]. A recent study has shown that the cell cortex may be organized by interactions with proteins that localize to the division site before the phragmoplast reaches the cortex, but it's not yet clear what these proteins do at this stage.

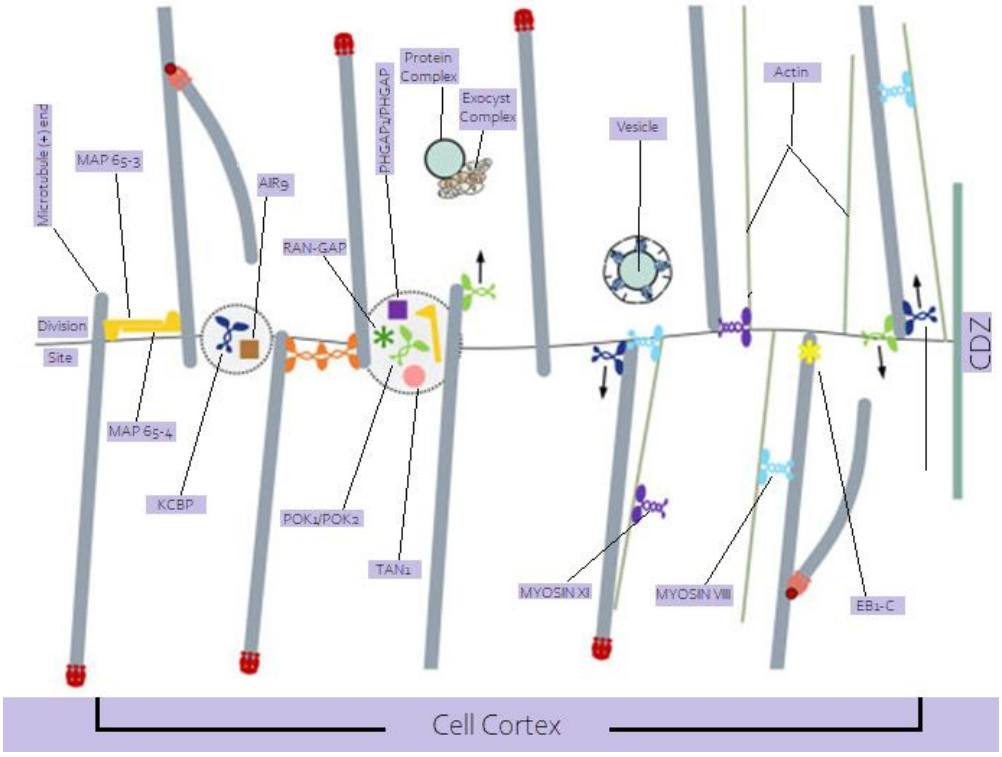

Fig. 1. The cell cortex underlying the plasma membrane before it comes into contact with the phragmoplast

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Through transitory microtubule plus-end stabilization, cortical telophase microtubules interact with TANGLED1 (TAN1) and other division site-localized proteins and this leads to the microtubules adopting a perpendicular orientation, which is analogous to the orientation of the phragmoplast itself [23]. Additionally, the in vitro involvement of TAN1 angle-independent crosslinking and bundling of microtubules is consistent with microtubule plus-end capture [18,24]. As the phragmoplast reaches the cell cortex, it incorporates microtubules from the cortical telophase. Parallel bundling of microtubules solely on a single part of the phragmoplast causes expansion of the phragmoplast to migrate toward the microtubules, which are subsequently incorporated into the phragmoplast via parallel bundling. There are yet no clues as to how additional microtubule-binding proteins that are present at the division site other than TAN1 engage with cortical telophase microtubules to fine tune the location of the phragmoplast to the division site.

4. LOCALIZATION OF THE REGULATORY PROTEINS PRIOR TO PHRAGMOPLAST-CORTEX INTERACTION

Pre-cytokinesis proteins, those that concentrate at or near the division site, play an important function in cytokinesis and phragmoplast placement. Microtubule-cross-linking protein TAN1, kinesin PHRAGMOPLAST ORIENTING (POK1) and POK2 as well as IQ67 Domain (IQD) proteins are among the many other proteins that have been identified as having a role in mitosis. In maize, the protein TAN1 is necessary for proper placement of the phragmoplast, and it also bundles microtubules in vitro [25]. The AUXIN INDUCED IN ROOT CULTURES9 (AIR9) mutant, by itself, does not exhibit a phenotype that differs from that of the wild type in Arabidopsis tan1 mutants [26]. Double tan1 air9 mutants, on the other hand, have abnormalities in the division plane and have short roots [27]. The tan1 air9 double mutant wild-type development is restored by mitotic expression of TAN1 [28]. After the phragmoplast touches the cortex, the AIR9 protein concentrates at the division site [29]. After metaphase, two PH-GAPs that engage with POK1 are found to assemble at the division site. These PH-GAPs are essential for situating the division plane in a redundant manner [30]. At last, a group of proteins known as "IQ67-DOMAIN" (IQD6, 7, and 8) interact with POK1 and have a role in establishing the division plane [31]. By examining where the proteins that constitute the division site are located in different mutants, we may learn more about how the division site is established and maintained until cytokinesis is complete.

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5. CYTOKINESIS AND PHRAGMOPLAST CORTEX INTERACTIONS

Associations between microtubules and phragmoplast and actin filaments that are positioned in the cortex direct the phragmoplast exactly to the spot where it will divide after it has reached the cortex. They are facilitated by proteins located at division site, such as MYOSIN VIII in moss (microtubule and microfilament binding protein) [32]. Final contact with the cell cortex is dependent on the contacts between F-actin, Myosin, and the cell cortex. If these relationships are disrupted in any way, the phragmoplast will not be able to reach the mother cell plasma membrane [27,33]. Final contact with the cell cortex is dependent on the contacts between F-actin, Myosin, and the cell cortex. If these relationships are disrupted in any way, the phragmoplast will not be able to reach the mother cell plasma membrane. The subsequent recruitment of the phragmoplast back to the division site suggests long distance interactions between the actindivision sites [34]. In order for cells to properly extend and undergo

cytokinesis, microtubule regulators including as nucleators, cross-linkers, end-binding proteins, and severing proteins are required [35].

6. REGULATORY ROLE OF MICROTUBULE NUCLEATORS DURING DIFFUSE GROWTH AND CYTOKINESIS

Diffuse growth and cytokinesis need microtubule nucleators, such as gamma tubulin and the gamma-tubulin ring complex [36]. Microtubules, in contrast to animal cells, may nucleate either from the nucleus, the plasma membrane, or from microtubules that were already there [34-37]. Gamma tubulin ring complexes are recruited during nucleation from preexisting microtubules by the two MOZART1 homolog proteins and AUGMIN complex, GAMMA-TUBULIN COMPLEX3 INTERACTING PROTEIN1 (GIP1) and GIP2 [38].

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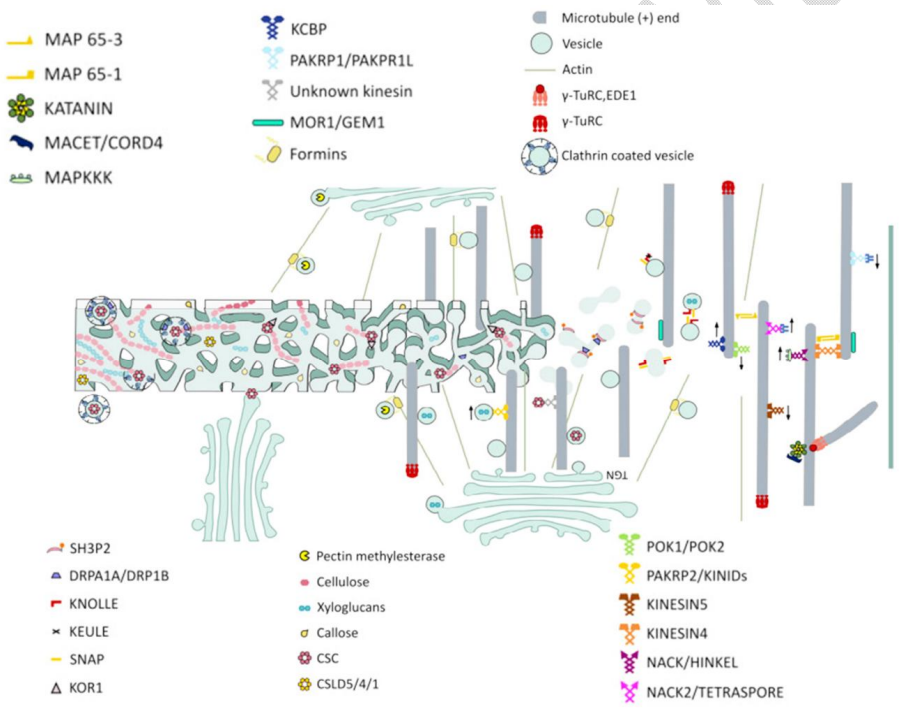

Fig. 2. Model of land-plant cytokinesis. Phragmoplast, membrane, and cell wall structures that form the cell plate from left to right: vesicle accumulation, vesicle fusion to form a tubulo-vesicular network, a tubular network, and fenestrated sheet.

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During the process of cytokinesis, the size of the phragmoplast increases as a result of the addition of additional microtubules that nucleate on the phragmoplast leading edge (Figure 2). Nucleation that

depends on microtubules, therefore, is essential for phragmoplast growth [39]. AUGMIN complexes are linked to microtubules during phragmoplast and spindle formation by ENDOSPERM DEFECTIVE1 (EDE1). Although the phragmoplasts of ede1 mutants are deformed, there is no evidence of cytokinetic abnormalities [40]. Surprisingly. phragmoplast assembly does not need the GAMMA-TUBULIN COMPLEX PROTEIN6 (GCP6).

7. REGULATORY ROLE OF VARIOUS SEVERING PROTEINS DURING MICROTUBULE ARRAY REORIENTATION

It is necessary for Arabidopsis to have both the catalytic p60 KTN subunit and the microtubule cross-over targeting p80 KTN subunit in order to perform appropriate microtubule severing [41]. Microtubule reorientation in response to mechanical stress requires KTN1, which suggests that severing helps microtubules realign [42]. Phragmoplast growth, location, and shape are all dependent on KTN1 [43]. Fragile fiber2 (fra2) mutants, also known as ktn1, exhibit decreased callose deposition and irregular cell plates [44]. At the distal phragmoplast, microtubules are severed by KTN1, which is hypothesized to be recruited by the microtubule-binding protein MACET4/CORD4 [22,35,45]. Though it has been shown that MACET4/CORD4 overexpression does not result in a rise in severing in tobacco (Nicotiana tabacum) cultivated cells, this has not been seen in tobacco (*Nicotiana tabacum*) cultured cells [46]. Rapid phragmoplast growth necessitates the presence of both KTN1and MACET4/CORD4 [19-22,47].

Microtubule orientation and reconfiguration in response to mechanical signals are all impaired in the ktn1 mutant cell [48]. Blue light-induced reorientation is impossible without KTN1 [26,49]. On the other hand, blue light-induced microtubule and mechanical force-dependent reorientation, are likely to have distinct processes.

8. SIGNIFICANCE OF MICROTUBULE BUNDLING PROTEINS DURING DIFFUSE GROWTH AND CYTOKINESIS

MOR1/GEM1 (Microtubule Organization1/Gemini1) is a critical component of microtubule assembly. Disruption of cytokinesis and diffuse growth occurs in *mor1* mutants [25,39,50]. The HEAT-repeat/TOG microtubule-binding domains of MOR1 are highly conserved [51]. Mitotic microtubule arrays, as well as cortical microtubules, include MOR1, which promotes the bundling of microtubules and their polymerization [52]. It has been shown that the temperature-sensitive mor1 mutants may be exploited to better understand how microtubule dynamics and abnormal cell plate formation are regulated [53]. The phragmoplasts of mor1/gem1 mutants occasionally split, resulting in many aberrant fresh cell walls and uneven membrane buildup in cell plates, in addition to generalized growth abnormalities [54]. It is interesting to note that despite the loss of parallel cortical microtubules and a reduction in the microtubule polymer mass in the mor1 mutant at restricted temperature, cell wall crystallinity remained high. This suggests that there is an inverse relationship between microtubule mass and cellulose crystallinity [44,55].

MAP65-1 and MAP65-2 have functions in cytokinesis that are somewhat redundant with those of MAP65-3. This was discovered by studying the interactions of mutants with map65-3. synthetic cytokinesis abnormalities are seen in the double mutants of map65-1 and map65-2 [56]. Although they generate fewer cells, map65-1 map65-2 double mutants do not show any evident cytokinesis deficiencies, indicating that they may still be active in cell division [49-51,57]. It is interesting to note that MAP65-1 may be seen at the very leading edge of the phragmoplast, where it crosslinks microtubules that run in the opposite direction [58]. Even though there is no abnormal phenotype in map65-4 mutants alone, when they are paired with map65-3 mutants, cytokinesis deficiencies induce gametophyte death [59]. The phragmoplast or phragmoplast midline is where MAP65-4 is found [32-35,60]. MAP65-4 is more dominant

in the phragmoplast midline in the map65-3 mutant to partly substitute the antiparallel bundling role of MAP65-3 [61]. In vitro, MAP65-4 stimulates the formation of antiparallel and parallel microtubules [62]. Even though it may be found in the division area, the function of MAP65-4 is not understood at this time [63]. This significant family of microtubule-bundling proteins will benefit from a more combinatorial mutant study, which will reveal distinct and complementary roles.

9. KINESINS MEDIATED MOVEMENT OF CELLULAR COMPONENTS

Kinesins are microtubule and actin filament or microtubule-binding motor proteins that transport vesicles and organelles as well as actin filaments or microtubules. Kinins may be used to replace the uncommon minus-end directed dyneins found in plants [64]. It is thought that Golgi vesicles are delivered to the cell plate by plus-end directed kinesins that are located on the surface of the phragmoplast. In point of fact, even synthetic vesicles are able to be carried effectively to the cell plate that is in the process of development [65]. Despite the fact that electron microscopy has shown phragmoplast microtubules with associated vesicles, specific kinesins have yet to be found [66]. Kinesins, on the other hand, serve a variety of functions in cytokinesis and phragmoplast placement, showing the difficulty of coordinating cell plate development [61,64,67].

10. PLUS-END-DIRECTED KINESINS

Depending on the plant species, kinesins of the KINESIN-4 family have varied functions in cell growth and cytokinesis [22,34,56,68]. For the first time, an inflorescence stem with low mechanical strength was shown to be lacking in FRA1 (FRAGILE FIBER1) [49,55,69]. The plus-end directed kinesin FRA1 is very processive [70]. However, further studies show that fra1-5 does not affect the organization, mobility, or concentration of CSCs at the plasma membrane and that the reduced mechanical strength in fra1 is not due to errors in cellulose microfibril patterning [71]. CMUs (cellulose synthase microtubule-uncoupling proteins) are proteins that bind microtubules and localize to the cell plate in order to prevent cells from twisting, and FRA1 does not directly alter cellulose production [72]. Microtubule lateral movement is controlled by modifying the FRA1-CMU association. The transport of polysaccharides to the apoplast may be affected by microtubule separation from the cortex, leading to fra1-cell wall abnormalities [73]. In point of fact, fra1-5 causes a reduction in the amount of fucose-alkyne-labeled pectin that is secreted [74]. In contrast, the cytokinesis of fra1-5 is unaffected [48,75]. During cytokinesis, mutants have a decreased number of cells but no visible structural problems in microtubules [15,65,76]. This protein family plays an important function in cytokinesis, however, in moss the Kin4-1a and Kin4-1c proteins are found in the phragmoplast midline, where they help to reduce microtubule overlapping areas [77]. Interesting, the phragmoplast of the kin4-1a and kin4-1c double mutant does not rotate, suggesting problems in the division plane [78].

Cytokinesis relies on a number of kinesin-7 plus-end directed kinesins. Tobacco possesses two kinesin-7s, NACK2 and NACK1, which have MSA (M-phase specific activator) sequences [79]. Mutations in the genes encoding tobacco HINKEL/NACK11 and Arabidopsis TETRASPORE / NACK2/STUD, as well as moss NACKa-c, were later shown to cause cytokinesis abnormalities [79,80]. Phragmoplast growth necessitates the microtubule-binding kinase-like protein RUNKEL, which is required for HINKEL recruitment to the phragmoplast [81]. Cell plate construction material may be transported by NACKs, since they are processive plus-end directed kinesins [81,82]. The C-terminal stalk domain of NACK1/HINKEL attracts MARKKK (mitogen-activated protein kinase kinase) proteins to the phragmoplast midline [83]. Proteases EB1, MAP65-1, and MAP65-3 are phosphorylated by the Mitogen-Activated Protein Kinase (MAPK) [84]. To ensure timely phragmoplast growth, Aurora Kinase activation of MAP65-1 lowers microtubule binding, which is important for appropriate microtubule disintegration at the

phragmoplast trailing edge [85]. Extra Spindle Poles1 is a caspase-like protein that stimulates microtubule polymerization with another set of kinesin-7s, which are not needed for cytokinesis [77,84,86].

11. MINUS END-DIRECTED KINESINS

In moss, Arabidopsis, and tobacco, members of the minus-end-directed Kinesin-5 family play an essential function in the process of cytokinesis; nevertheless, it is possible that they do not directly contribute to diffuse growth. Tobacco Kinesin-5, also known as Kinesin-Related Protein (NtKRP), is found in microtubules, where it is responsible for the translocation of opposite phragmoplast microtubules to reduce the amount of overlap between them [61,87]. Similar to Kinesin-5 AtKRP125c, rsw7 suffers spindle collapse, a faulty phragmoplast assembly and other problems in the cytokinesis process. It is possible that the apparent shape errors seen in cells are due to the mutant phenotypic changes that occur during mitosis and cytokinesis rather than flaws in swelling cells seen in RSW7 and AtKRP125c-deficient individuals [88]. Knocking down all Kinesin-5 (a–d) homolog RNAi has the same effect on the cell ability to divide into new cells. The minus-end-directed movement depletes Kinesin-5s from the phragmoplast midline, which is counterintuitive [89]. When Kinesin-5 is exempted from the deposition of antiparallel microtubules at the midline, it is not apparent how it connects or moves antiparallel microtubules.

During cytokinesis, a number of minus-end-directed kinesins from the Kinesin-14 family are involved. Spindle generation, chloroplast and nuclear mobility all rely on Kinesin-14s [57-60,90]. The vks1 mutant causes cytokinesis problems throughout endosperm cellularization, but not during vegetative phase, since it is essential for nuclear mobility, spindle formation, and phragmoplast organization [91]. Other similar proteins may be able to fill in during vegetative cell division, as this implies. For meiotic drive, a maize VKS1 paralog called KINDR moves neocentromeres toward the spindle poles; however, KINDR plays no function in vegetative cell division [91,92]. It is a calponin homology (KCH, KCH, calponin homology domains) kinesin, which attaches to both microtubules and actin and is found in mitotic microtubule frameworks [93].

12. CELLULOSE BIOSYNTHESIS

A substantial structural component of the cell wall is made up of cellulose. Long beta-1,4-linked glucan chains make up the bulk of this substance. A huge complex called the CSC produces cellulose at the plasma membrane. Freeze fracture was used to create a hexameric rosette structure, which allowed researchers to see the CSC at the plasma membrane underneath microtubules [91,94]. CESA6 (CELLULOSE SYNTHASE 6), a CSC protein, was tracked in vivo using live imaging at the plasma membrane, where microtubules were shown to be a common route for its migration [78,95]. It is not known what the precise components of the CSC in primary cell walls are, however it is believed that they consist of a hexameric, equal-stoichiometric mixture of CESA1, CESA3, and either CESA6, CESA2, or CESA5 [84,96]. Cellular expansion and cytokinesis abnormalities may result from mutations in cellulose synthase subunits. Cytokinesis and cell elongation may be the sole roles for some of the cesA6 mutants because of their redundant roles with CESA2 and CSEA5 in the cell cycle [81,83,97].

Cell survival and movement may be improved by post-translational alterations such as phosphorylation [98]. Reduced mobility was seen in CESA5 and CESA3 and CESA3 by altering phosphorylation sites [99]. It is interesting that, phosphorylation of CESA by the protein kinase BRASSINOSTEROID INSENSITIVE2 is an intriguing example of the hormonal control of cellulose synthesis that occurs through phosphorylation of CESA [100].

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13. PROTEINS ASSOCIATED WITH CELLULOSE SYNTHASE

A nebulous linker protein was long thought to be the mechanism by which the CSC connects to microtubules in the plasma membrane [97,101]. CSI1 (Cellulose Synthase Interactive 1), the first linker protein discovered, creates a physical interaction between CSCs and cortical microtubules to start and sustain structured and fast cellulose production (Figure 3) [102]. Microtubule contact is confined to CSI1 N- and C-terminal areas, whereas the central domain of CESA interacts directly with CSI1 in several sites, including the N-, C-, and center regions of CSI1 [103]. A mutation in the csi1 gene causes CESA particles to lose their ability to follow microtubules, resulting in decreased velocities [104].

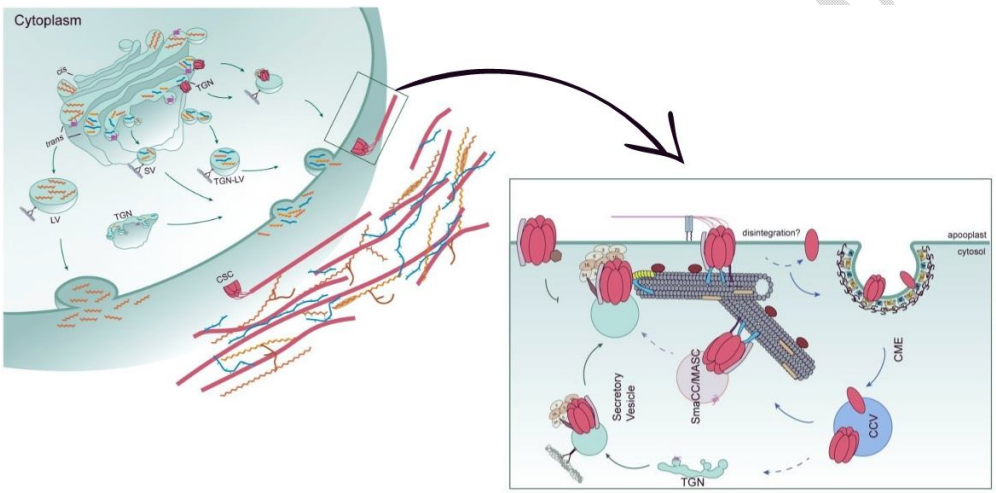

Fig. 3. Model of trafficking of non-cellulosic polysaccharides and cellulose in the primary cell wall.

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It has been shown that two homologs, CSI3 and the less well-known CSI2, have varied degrees of expression in various tissues. Mutant plants that lack the CSIA1 and the CSIA3 genes have no apparent abnormalities, while those that lack both genes exhibit slower particle movement, a smaller hypocotyl, and less cellulose content [104,105]. CSI1 and its homologs may or may not be required for cytokinesis, although this remains an open question. To find out whether they are necessary for cytokinesis, it would be necessary to create a triple mutant.

COBRA (COB), called for the mutant roots snake-like appearance, and KOBITO (KOB), which means "little" in Japanese, are two proteins that are less well known yet crucial for cell growth and cellulose production [106]. Stunted development, decreased cellulose deposition, and damaged cell walls are all characteristics of kobito mutants [79,92,107]. There is strong evidence that the plasma membrane protein encoded by KOBITO is localized to this membrane. As a glycosyl-phospholipid-anchored protein, COB is a member of the COB family. In both the Golgi and the cell wall, COB accumulates [108]. Disorganized cellulose microfibrils and a decreased cellulose content are seen in cob mutants [109]. Increased grain yields and root hair formation are the results of roothairless3, a monocot-specific COB homolog in maize [110]. Rice homologs of COB, such as BRITTLE CULM1 (BC1) and BC1-Like4 (BC1L4), similarly stimulate cell growth [109,111]. Through an N-terminal domain, BC1 binds cellulose in vitro and localizes

vesicles to the cell wall and to the plasma membrane [88,112]. By interacting directly with cellulose crystals, it is theorized that COB affects the synthesis of cellulose [103,113].

14. THE ASSEMBLY AND LOCALIZATION OF CSC

Electron microscopy revealed rosette CSCs in the Golgi, indicating that this is where they are assembled [114]. When cytokinesis occurred, immunogold labelling confirmed the Golgi deposition of CESA3 [115]. High molecular weight CSC complexes in stello1 stello2 mutants are decreased due of their involvement in the assembly of STELLO1 and STELLO1, two Golgi-localized proteins called after the Greek word stello meaning "to arrange in order."

It is hypothesized that endocytosis regulates the CSC, a large plasma membrane-localized complex [116]. When cells divide, clathrin-mediated endocytosis eliminates CESA particles from the plasma membrane and center of the cell plate, respectively [117]. Clapthin-mediated endocytosis and cytokinesis need DRP1A, a dynamin-like protein that binds to the light chain of clathrin [118]. Because of the deficiencies in rsw9/drp1a, cells are unable to extend and undergo cytokinesis properly, which leads to cellulose deficit [119]. OsDRP2B, a gene related to dynamin, was found to be mutated in rice at the brittle culm 3 mutant locus and is likely essential for clathrin-mediated endocytosis. OsCESA4 protein accumulation is reduced in rice culm 3 mutants, but OsDRP2B overexpression increases OsCESA4 protein accumulation in plasma membrane [120]. Proof for endocytosis emerged from in vitro and yeast-two hybrid experiments that showed that CESA interacts with the medium subunit of ADAPTER PROTEIN COMPLEX 2 (AP2M) in clathrin-mediated endocytosis. CESA concentration rises in ap2m deleted mutants because of a disruption in clathrin-mediated endocytosis [121]. A clathrin-mediated endocytosis adaptor known as TRANSDUCIN/WD40-2 (TWD40-2) is a part of the TPLATE complex, which dates back millions of years [122]. In addition to regulating development and cytokinesis, the TPLATE complex also controls CESA endocytosis, as shown by a rise in plasma membrane CESA particle density in the absence of TPLATE [123]. TPLATE and MUNISCIN-LIKE (TML)interact with CESA6 and facilitate its internalization from the plasma membrane via the TPLATE Complex [124]. The recent development of a temperature-sensitive tplate mutant is going to be a very useful tool for elucidating the function that it plays in both diffuse proliferation and cytokinesis.

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15. TRANSPORTATION AND BIOSYNTHESIS OF NON-CELLULOSIC POLYSACCHARIDE

Polysaccharides that are not cellulosic are mostly produced in the Golgi rather than at plasma membrane or late cell plate, as is the case with cellulose [125]. Xyloglucan and pectin are among the principal cell wall polysaccharides described here. Antibodies that have been well-studied and well-characterized may be a valuable tool in detecting certain carbohydrate characteristics [126]. Parallel to cellulose, xyloglucans have extra sugar alterations on the branching side chains of the glucans. According to the immunolocalization of terminal fucose antigens, modification of xyloglucans most likely takes place inside the trans cisternae of the Golgi and the TGN [127]. In agreement with this idea, oligosaccharide-mass characterization of Golgi-enriched subsets indicated fewer substituted xyloglucans in comparison to apoplastic cell wall segments [128]. Due to abnormally large secretory vesicles in phosphatidylinositol 4-kinase b1 and b2 (pi4kb1 and pi4kb2) mutants, xyloglucan trafficking from the trans Golgi to the TGN and to the cell surface is seen [129]. Golgi cis and medial cisternae are stained with immunogold, revealing the presence of xyloglucan-synthesizing enzymes such xylosyltransferases (XT1) and galactosyltransferases MUR3 [130]. Overexpression of XT1 and MUR3 may lead to their being mislocalized in the cis and medial Golgi, but further research is needed to determine if xyloglucan side chain initiation occurs in early Golgi divisions.

Disorders in cell wall growth and the production of cytokinesis stubs have been found in mutants [131]. The cell plate accumulates CSLD5 in the form of punctate structures [132]. Mannans or xylans may be the cell wall substance that this enzyme generates [133]. However, the cytokinesis failure in Arabidopsis is exacerbated when the csld5 mutant is co-dominant in combination with the csld2 or csld3 mutants, which normally govern root-hair development [134]. We may get vital insight into these proteins functions by clearly distinguishing which cell wall components they make.

16. CELL PLATE

An area without overlapping between microtubules and the cell plate assembly matrix is where vesicles arrive. This is where the cell plate assembly matrix may be found [135]. During cell plate development, monomeric RAB-GTPases link vesicles and facilitate vesicle transportation [136]. In order to go from the Golgi and TGN to the cell plate, RABGTPases such as RAB-E1, RAB-A3, and RAB-A2are required [137]. RAB-A5c, which is a different kind of RAB-GTPase, tends to collect in its own distinct vesicles and rarely with the TGN. Cytokinesis and diffuse development are dependent on RAB-A5c, which is found on the cell plate [138]. Triple mutants of RAB-A1a-c are more susceptible to the cytokinesis-inducing drug Endosidin1 than single mutants [139]. STOMATAL CYTOKINESIS DEFECTIVE1 (SCD1), SCD2 and the Transport Protein Particle II (TRAPPII) complex components are also essential for cell plate formation [140]. Subsequently, the TRAPP-Interacting Plant Protein (TRIPP) was discovered to be a plant-specific component of the highly conserved complex of TRAFPI. TGN to cell plate trafficking of TRIPP is essential for cytokinesis [141]. A fascinating interaction between exocyst proteins and SCD2, SCD1, and TRAPPII members may help coordinate vesicle trafficking at early and late stages during the development of cell plates [142].

Comment [O13]: Lower case

17. CALLOSE: A MAJOR PRECURSOR OF CELL PLATE

Except in plasmodesmata and under circumstances that cause stress or injury, callose, a significant component of the cell plate, is seldom seen in primary cell walls [143]. Xyloglucans and cellulose both include beta-1,4-linked glucan chains, but cellulose is made up of beta-1,3-linked glucans. When it comes to plasmodesmata, wound healing, pathogen response, pollen surface patterning, and other aspects of symplastic transport, many callose synthases play a role that is both distinct and overlapping [144]. Cellulosic mixtures with high levels of callose, which may be crucial for cell plate development, are more elastic in vitro [145]. Callose polymerization may provide the disseminating power needed to compress the tubulo-vesicular network into a fenestrated film, according to biophysical modelling.

Calcium is required for the action of callose synthase [146]. The ER may provide calcium to callose synthases during the development of cell plates: In several plant species, ER–cell plate connection has been observed [147]. Researchers have used staining to show that *Tradescantia virginiana* experiences calcium sequestration, which causes problems with cell plate development [148]. Mutants of the P. patens species have ER connections with the cell plate that are defective in the sabre strain, and this leads to abnormal callose buildup and ultimately cytokinesis abnormalities [149]. ER connections that have been changed may be responsible for the sluggish buildup of calloses in the sabre mutant. This is an intriguing possibility.

18. CONCLUSION

Modification and building of the cell wall are dynamic processes that are carefully regulated dynamic processes that include secretion and endocytosis. There are still many unanswered questions, such as

how the addition of cellulose and non-cellulosic polymers is linked, how non-cellulosic polymers are transportation between the Golgi and the plasma membrane, and on which cytoskeletal tracks, and how the cytoskeleton and the activity of CSCs are significantly affected by environmental and mechanical gestures.

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Comment [O14]: Too many references
Maximum from 50 to 60

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