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# Cellulose and callose synthesis and organization in focus, what's new?

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Plant growth and development are supported by plastic but strong cell walls. These walls consist largely of polysaccharides that vary in content and structure. Most of the polysaccharides are produced in the Golgi apparatus and are then secreted to the apoplast and built into the growing walls. However, the two glucan polymers cellulose and callose are synthesized at the plasma membrane by cellulose or callose synthase complexes, respectively. Cellulose is the most common cell wall polymer in land plants and provides strength to the walls to support directed cell expansion. In contrast, callose is integral to specialized cell walls, such as the cell plate that separates dividing cells and growing pollen tube walls, and maintains important functions during abiotic and biotic stress responses. The last years have seen a dramatic increase in our understanding of how cellulose and callose are manufactured, and new factors that regulate the synthases have been identified. Much of this knowledge has been amassed via various microscopy-based techniques, including various confocal techniques and super-resolution imaging. Here, we summarize and synthesize recent findings in the fields of cellulose and callose synthesis in plant biology.

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## The plant cell wall

All plant cells are encased by cell walls that provide protection of the plant against environmental conditions, dictate cell expansion needed to support plant morphology, and allow for solute transport between cells and from a plant's root to its shoot [1]. Hence, cell walls are essential for plants to grow and develop.

While cell wall composition and architecture change during development and in response to environmental stress, a range of polysaccharides provide the basic cell wall structure. The polysaccharides may be divided into two major classes based on their physio-chemical characteristics; that is, the homopolysaccharides cellulose and callose, and the heteropolysaccharides pectins and hemicelluloses [2,3]. The latter two are referred to as matrix polysaccharides and are typically produced in the Golgi apparatus and subsequently secreted to the apoplast where they may be modified and incorporated into the growing cell wall [2,3]. In contrast, the β-1,4-glucan cellulose and the β-1,3-glucan callose are made at the plasma membrane by large glucan synthase complexes that are referred to as cellulose synthases (CesAs) and callose synthases (CalS or GSL for GLUCAN SYNTHASE-LIKE), respectively [4,5]. While cellulose is found in virtually all cell walls in land plants, callose is typically made in specialized walls that support cell division, tip growth, pollen and pollen tube development, and plasmodesmata function, as well as during responses to environmental stress.

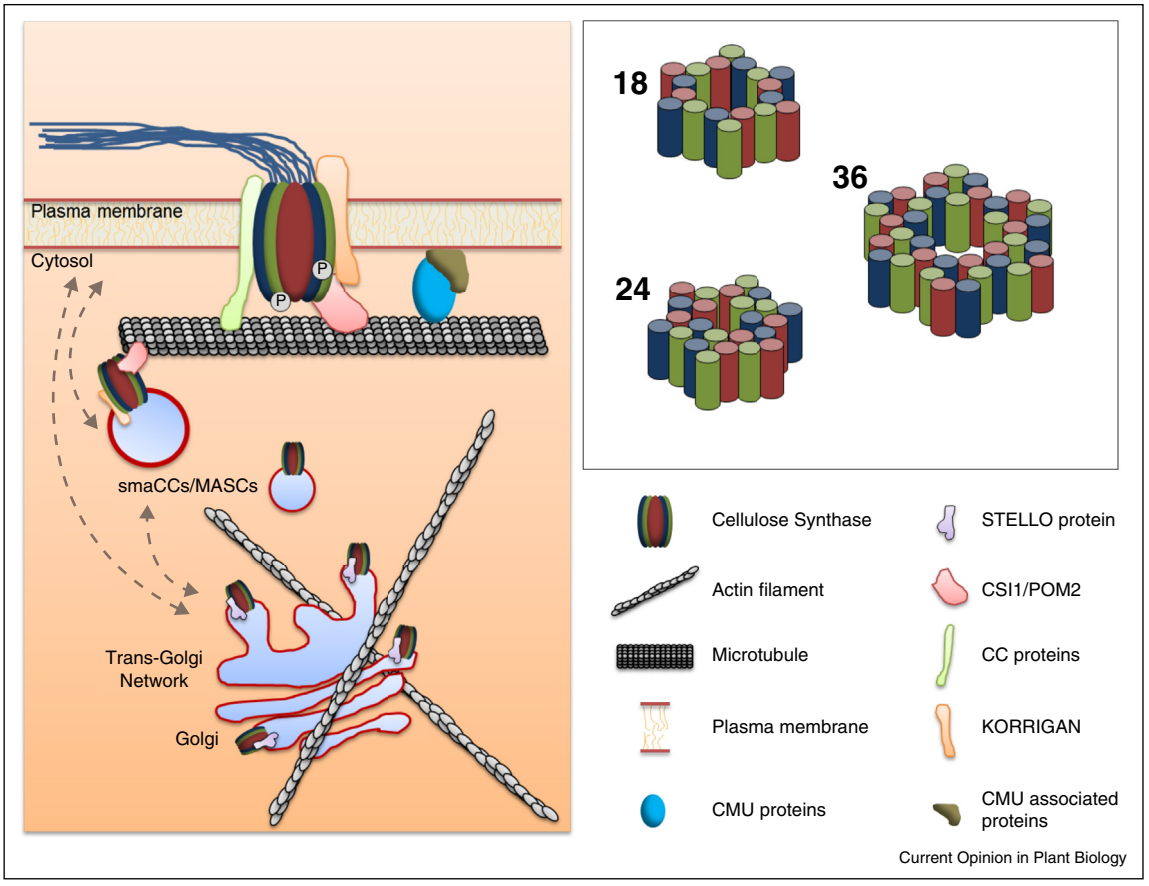
## Cellulose synthesis

Cellulose is synthesized by massive CesA protein complexes that are 40–60 nm in diameter [6] and that typically consist of a heterotrimeric CesA core, and associated proteins, at the plasma membrane [4] (Figure 1).

### Cellulose synthase assembly and secretion

The CesA complex is likely assembled in the Endoplasmic Reticulum (ER) or Golgi [4]. However, our understanding of what is regulating the assembly and the subsequent trafficking of the complex to the plasma membrane is very limited. Nevertheless, the recently identified STELLO (STL) proteins that interact with the CesAs in the Golgi have at least provided a first ingress on the assembly. Impaired STL function led to a redistribution of the CesAs in the Golgi, that is, from peripheral to central Golgi localization, and to a reduction in CesA secretion and thus reduction in cellulose production [7•]. Interestingly, less CesA subunits were incorporated into CesA complexes in *stl* mutants, indicating that the STLs work as assembly factors for the CesA complex [7•]. Based on point mutations it appears likely that the

**Figure 1**




Cellulose synthase and synthesis. Left panel: cellulose is produced by large cellulose synthase (CesA) complexes at the plasma membrane. The CesA complex is assembled in the Golgi, or possibly the Endoplasmic Reticulum, with the aid of the recently described STELLO proteins. The CesA complex is secreted/internalized to/from the plasma membrane via the Trans-Golgi Network and/or small CesA compartments that can interact with microtubules or the actin cytoskeleton (indicated by dashed lines). The CesA complex is inserted next to cortical microtubules and guided via CSI1/POM2 along the microtubules, which are stabilized by CMU proteins, during cellulose synthesis. The Companion of CesA (CC) proteins are part of the CesA complex and protect the cellulose producing capacity against environmental stress. The endo-glucanase KORRIGAN also partake in the CesA complex and may contribute to correct microfibril formation or in the severing of cellulose chains during or after synthesis. Several CesA subunits may be phosphorylated, which regulates the behaviour of the CesA complex. Right panel: The CesA complex has traditionally been anticipated to contain 36 CesA subunits; however, recent estimates of cellulose fibril width have suggested that the complexes may contain only 18 or possibly 24 CesA subunits. Alternatively, the CesA complex still holds 36 subunits, but not all of them are active.

STLs are glycosyltransferases, though the substrate of the STLs remains elusive.

Once the CesAs are assembled, they may be trafficked to the plasma membrane, possibly via the trans-Golgi network (TGN) and small vesicle compartments named Microtubule-Associated Cellulose Synthase Compartments (MASCs; [8])/Small CesA Compartments (SmaCCs; [9]; Figure 1), where they typically are inserted in close vicinity to cortical microtubules [9]. Apart from the STLs, several factors influence the rate of CesA secretion, including the actin cytoskeleton [10], the kinesin FRA1 [11] and the acidification of the TGN [12]. Nevertheless, regulatory components that specifically impact CesA trafficking remain ill defined.

## Cellulose synthase at the plasma membrane

As alluded to above, the CesAs are typically delivered to the plasma membrane in close proximity of cortical microtubules [9]. Here, the CesAs are presumably activated by a currently unknown mechanism, and begin to track along the microtubules. It is plausible that phosphorylation of the CesAs could play a role in the activation. Indeed, mutations of several phosphorylation sites of different CesAs affect the tracking behaviour and the speed of the complexes [13–15]. The CesAs use UDP-glucose as substrate, and the catalytic activity of them is likely the driving force behind the motility of the complexes [16••]. Here, individual glucan chains crystallize into cellulose fibrils that are entangled by other cell wall polymers. Hence, further synthesis will push the CesA