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Review

Polysaccharide deposition during cytokinesis: Challenges and future perspectives

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ABSTRACT

De novo formation of a new cell wall partitions the cytoplasm of the dividing cell during plant cytokinesis. The development of the cell plate, a transient sheet-like structure, requires the accumulation of vesicles directed by the phragmoplast to the cell plate assembly matrix. Fusion and fission of the accumulated vesicles are accompanied by the deposition of polysaccharides and cell wall structural proteins; together, they are leading to the stabilization of the formed structure which after insertion into the parental wall lead to the maturation of the nascent cross wall. Callose is the most abundant polysaccharide during cell plate formation and during maturation is gradually replaced by cellulose. Matrix polysaccharides such as hemicellulose, and pectins presumably are present throughout all developmental stages, being delivered to the cell plate by secretory vesicles. The availability of novel chemical probes such as endosidin 7, which inhibits callose formation at the cell plate, has proved useful for dissecting the temporal accumulation of vesicles at the cell plate and establishing the critical role of callose during cytokinesis. The use of emerging approaches such as chemical genomics combined with live cell imaging; novel techniques of polysaccharide detection including tagged polysaccharide substrates, newly characterized polysaccharide antibodies and vesicle proteomics can be used to develop a comprehensive model of cell plate development.

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Abbreviations: SNARE, Soluble N-ethylmaleimide-sensitive factor protein attachment protein receptor; RABA, Rab GTPase A.

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1. Introduction

The formation of the cell plate and a new cell wall during plant cytokinesis separates two daughter cells. This process is fundamentally different from animal and fungal cytokinesis, in which a contractile actomyosin ring constricts the plasma membrane to separate the two daughter cells [1,2]. Formation of the cell plate is a complex and multifaceted process, relying on cytoskeleton-guided vesicular trafficking and the deposition of large amounts of polysaccharides [1,3]. In this review, we focus on polysaccharide deposition during cytokinesis in somatic plant cells. Regarding other aspects of cytokinesis and for additional background information, we direct the reader to several excellent studies and reviews [1–9].

The completion of nuclear division at the end of late anaphase is followed by vesicle trafficking directed to the center of the dividing cell, known as the cell plate assembly matrix. Vesicle delivery is directed by a plant-specific cytoskeletal array of antiparallel microtubules coaligned with the actin cytoskeleton (collectively described as the phragmoplast), positioned perpendicular to the division plane [5,10]. Fusion and fission of the accumulated vesicles at the center of the dividing cell promote the formation of the incipient cell plate [1]. The formation of the cell plate takes place in distinct stages, as previously elegantly described [3,5]. The first stage, known as fusion of Golgi-derived vesicles stage, encompasses vesicular fusion and fission events, leading to the second stage and formation of a tubulo-vesicular network. In the third stage, a tubular network is formed. During the fourth stage, a planar fenestrated sheet is formed. Plasmodesmata can develop through open fenestrae that contain strands of endoplasmic reticulum. Cell plate expansion is centrifugal, led by the accumulation and fusion of newly arriving vesicles at the leading edge (Fig. 1), thus all four stages can exist simultaneously. The accumulation of polysaccharides occurs throughout the cell plate formation, with callose featuring prominently at the maturing center. Finally, the cell plate fuses with the parental cell wall and the process com-

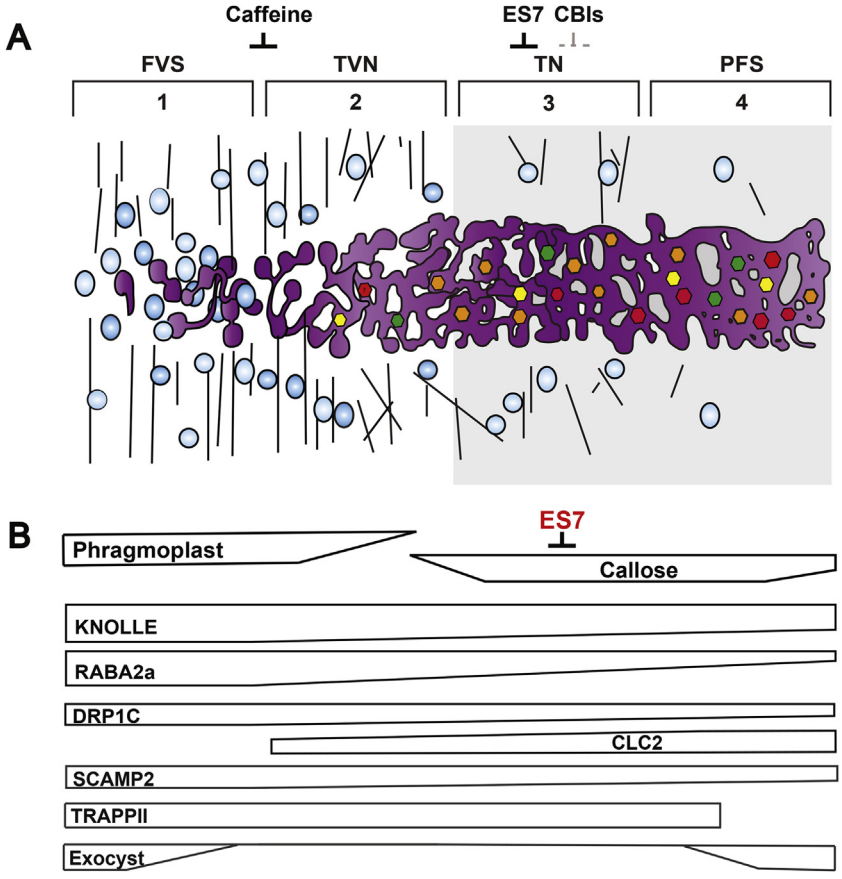

Fig. 1. Proposed model of cell plate formation and its inhibition by endosidin 7. (A) Cell plate formation stages and its temporal inhibition by endosidin 7. At the early stage of cell plate formation, vesicles guided by the phragmoplast array are gathering at the cell plate assembly matrix. Accumulated vesicles undergo fusion and fission and change their structure to form a membrane network (purple tubular membrane structures). There is abundant callose accumulation (orange hexagons) at the tubular network stage (TN, Stage 3) which transitions to a planar fenestrated sheet (PFS, stage 4). Endosidin 7 specifically inhibits callose synthase activity at this stage, preventing cell plate maturation, while caffeine affects the stage between the transition of fusion of Golgi-derived vesicles to a tubulo-vesicular network (stages 1 and 2, respectively). Cellulose accumulation is shown by red hexagons; its inhibition by cellulose biosynthesis inhibitors (CBIs) leads to cytokinesis defects. Hemicellulose and pectins (green and yellow hexagons) accumulate presumably from early stages onwards at the cell plate. Detection of all different polysaccharides during the developing stages of cell plate formation in the same experimental system awaits verification. (B) Differential accumulation of cellular components during cell plate maturation, callose deposition and response to endosidin 7. The RAB GTPase RABA2a association with the membrane is significantly reduced, while KNOLLE levels remain relatively higher compared to RABA2a. Endosidin 7 does have a unique mode of action preventing maturation steps after stage 2 by inhibiting callose accumulation at the cell plate. Dynamin related protein1C (DRP1C) accumulates both in early and late cell plate stages, while clathrin light chain 2 (CLC2) is only observed during mature stages, concurrent with callose localization. The Secretory Carrier Membrane Protein 2 (SCAMP2) accumulates at the cell plate from the early stages onwards. The tethering complex Transport Protein Particle II (TRAPPII) and exocyst complexes are present during initiation of cytokinesis. Thereafter, the Transport Protein Particle II complex is present during cell plate expansion, while the exocyst is required mainly for cell plate maturation. Temporal accumulation of the bottom 3 proteins requires further confirmation in the proposed model, in context of callose deposition and response to endosidin 7. Many proteins involved in vesicle trafficking during cytokinesis are not described due to a lack of information about their relationship to polysaccharide deposition or response to endosidin 7.