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Review article

The function and biosynthesis of callose in high plants

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ABSTRACT

The two main glucan polymers cellulose and callose in plant cell wall are synthesized at the plasma membrane by cellulose or callose synthase complexes. Cellulose is the prevalent glucan in cell wall and provides strength to the walls to support directed cell expansion. By contrast, callose is mainly produced in special cell wall and exercises important functions during development and stress responses. However, the structure and precise regulatory mechanism of callose synthase complex is not very clear. This review therefore compares and analyzes the regulation of callose and cellulose synthesis, and further emphasize the future research direction of callose synthesis.

1. Introduction

The cell wall is essential for plant growth and development. All plant cells are wrapped in cell walls, which protect plants from environmental hazards, define the cell expansion supporting plant morphology, and allow the transport of substances between cells and from roots to stems [1, 2].

Although the composition and structure of the cell wall varied in response to environmental and developmental factors, the polysaccharides (including callose, cellulose, hemicellulose and pectin) provide the basic structure for the cell wall [2, 3, 4]. Callose and cellulose have a similar primary structure (Figure 1A). Callose mainly consists of repeating glucose units linked by β-1,3 glycosidic bonds, while cellulose is a polysaccharide of glucose mainly linked by β-1,4-glycosidic bonds [5, 6]. Different from hemicellulose and pectin that are synthesized and assembled in the Golgi apparatus, secreted into the apoplast, and modified and integrated into the cell wall, cellulose and callose are synthesized by plasma membrane-located glucan synthase complex, cellulose synthase (CesAs) and callose synthase (CalS also known as GSL for GLUCAN SYNTHASE-LIKE) [7, 8]. The two enzymes share UDP-glucose as the initial substrate [5]. Therefore, callose and cellulose may have similar synthesis mechanisms.

In this review, we summarized and analyzed the regulatory mechanism of callose biosynthesis and function in comparison to the cellulose. In addition, we especially focus on highlighting the unexplored areas and identifying new biological questions that need to be addressed to advance the understanding of callose synthesis regulation.

2. Callose synthase in higher plants

GSLs located on the plasma membrane directly catalyzes the synthesis of callose from UDP-glucose [5]. GSLs are widespread among various plant species and are present in special cell walls. Callose is synthesized by GSLs to respond to a wide range of environmental and physiological signals [9]. Like CesAs, the GSLs in plants often contains multiple members, forming a moderately sized gene family. In *Arabidopsis*, there are 12 GSL genes which were named as GSL1-GSL12 [9], while there are 10 predicted GSL genes in rice. Phylogenetic analysis revealed that the proteins are divided into two groups (Figure 1B). 4 rice GSLs (OsGSL1, OsGSL2, OsGSL3 and OsGSL8) and 4 *Arabidopsis* GSLs (AtGSL1, AtGSL5, AtGSL8 and AtGSL10) are grouped in a small clade. Other GSLs formed the neighboring subgroup. According to the functional characteristics of GSL genes, members of different subfamilies play partially redundant roles in regulation of multiple processes including plant growth,

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development and stress responses. A single GSL gene could be involved in multiple biological processes.

3. The function of callose in higher plants

The rigidity of cellulose supports the complete structure of plant cells, while also protecting plant cells from the influence of external stress [7, 10]. Callose also plays a role of support and barrier. However, callose is only distributed in specific cell wall, such as cell plates, outer wall of pollen wall and plasmodesmata [11, 12, 13, 14]. These all indicate a special function of callose in plants.

3.1. The role of callose in plant growth and development

During the process of cell division in higher plants, the cell plate determines correct assembly of cell wall layer. Callose forms a coat-like structure covering the surface of cell Plates [14, 15]. The changing process from the tubular network to a porous cell plate to the mature cell wall may be driven mainly by the synthesis of callose. Mutation of callose synthase gene *GSL8/MASSUE* delays callose deposition in the cell plates [16]. Moreover, *gsl8/massue* mutant displays a typical cytokinesis defect phenotype, such as bi- or multi-nucleate, with cell-wall stubs [16]. Therefore, callose regulates cell division through cell plates in plants.

In the process of plant reproduction development, callose is deposited between the primary cell wall and the plasma membrane, which can be used to maintain the morphology of the microspore mother cell and prevent the fusion and aggregation of the tetrad cells [17, 18]. AtGSL1 and AtGSL5 are responsible for forming the callose wall that separates the tetrad cells, and *atgsl1* and *atgsl5* mutants can cause abnormal microspore development [19]. In addition, callose seem to participate in the formation of primexine by providing mold for the construction of the outer wall of pollen during microspore formation. Mutation of *AtGSL2* affects the deposition of callose in the primary cell wall of microspores and cannot form a proper sculpted outer wall, leading to the production of abortive pollen grains and male sterility [17, 20]. *OsGSL5,* homologous gene of *AtGSL2* in rice, played a similar function [21]. Thus, callose is essential to plant reproductive development.

In higher plants, plasmodesmata between cells regulates the transport of nutrients and signal molecules between cells [22]. The callose is often found to be deposited in the plasmodesmata. The deposition of callose determines the size exclusion limit (SEL) of the plasmodesmata, which affects their permeability [22]. The change in permeability of plasmodesmata affects the development of stomata and sieve, the phototropism, and the transportation of phloem [23, 24, 25, 26]. *Arabidopsis gsl8/chor* mutant also showed reduced callose deposition in plasmodesmata, and increased SEL in leaf epidermal cells. Increased SEL affected stomatal development and phototropic response through regulating the distribution of stomatal's developmental regulator SPCH and auxin, respectively [24]. *CANNOT REACH THE ROOF 1* (*CRR1*) in rice encodes a homologous protein of *Arabidopsis* GSL8 [23]. The *crr1* mutant shows delayed ovary expansion and defective vascular cell pattern. It indicates that the increase in plasmodesmata permeability may induce the diffusion of cell fate determinants from the sieve element precursor cells to the adjacent dedifferentiated parenchyma cells, leading to the formation of clusters of sieve elements [23]. The *Arabidopsis GSL7* gene regulates the deposition of callose at plasmodesmata in early-stage sieve plates, which results in sieve elements with fewer PD pores and affects phloem transport [25, 26]. In short, by controlling the developmental signals and the symplast transport mechanism of different solutes, callose in plasmodesmata is essential for plant development.

3.2. Callose deposition in response to stress

It is generally believed that callose positively regulates the stress response of plants [27, 28, 29, 30]. Under abiotic and biotic stress, plants often trigger the accumulation of callose. This process happens in a few seconds [29]. Callose deposition in cell wall, plasmodesmata, and sieve pore controls the cell wall permeability, which prevents the further penetration of the pathogen and deleterious metals into the tissue, and the loss of cellular water and solute to maintain the internal stabilities of cells [31].

Among the various abiotic stresses, chilling stress [32], water stress [33], heat [34], and heavy metals [35] are the major abiotic stresses challenging overall plant growth. These abiotic stresses could induce callose deposition. Action potentials arose in the phloem of maize leaf tips after chilling, and phloem transport of photoassimilates is inhibited [32]. This process is closely associated with callose deposition in leaf, which may be caused by the occlusion of plasmodesmata and phloem sieve pores. Tocopherol prevents abnormal callose deposition in phloem tissue, maintaining the transport of photoassimilates in cold conditions [36, 37]. Knockdown or knockdown of tocopherol cyclase in maize and potato resulted in vascular-specific callose deposition in leaves and defective sucrose export. Heavy metal ions such as Al^{3+} and Cd^{2+} are also involved in regulating callose deposition in plants [38]. Depolarization of the plasma membrane caused by aluminum induces callose deposition in tobacco cells [39]. In addition, increase of calcium concentration in the

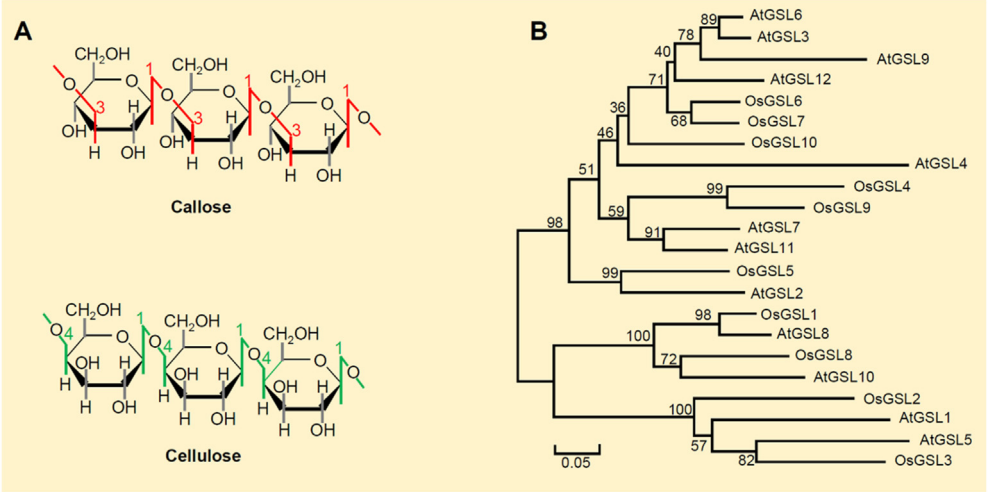

Figure 1. Callose structure, and phylogenetic tree analysis of callose synthases. (A) Comparison of the structure of callose and cellulose. (B) Phylogenetic tree analysis of callose synthases (GSLs) in rice and *Arabidopsis*.

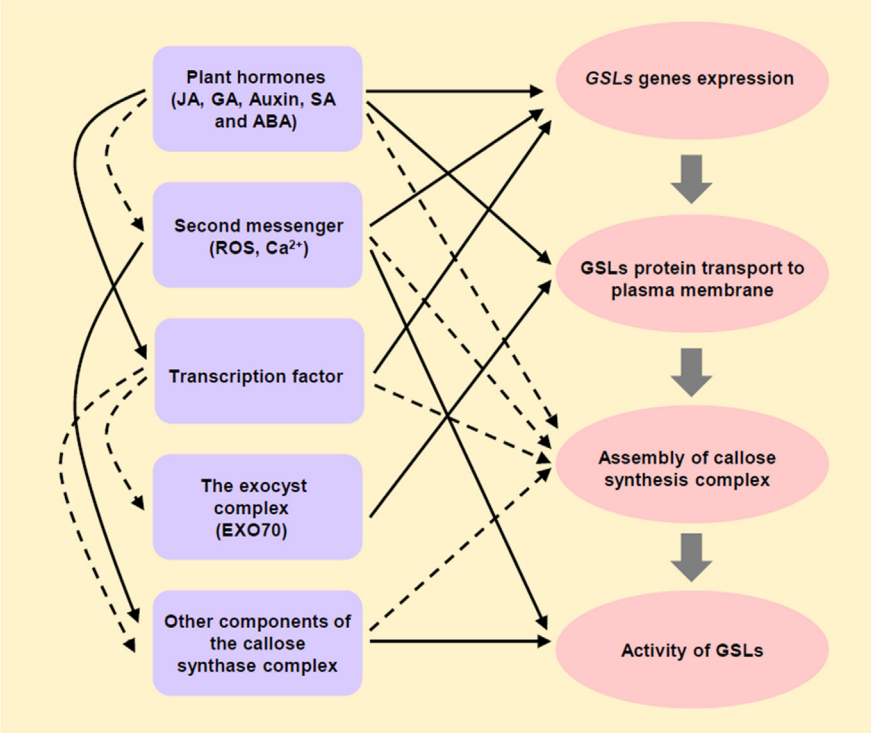

Figure 2. Regulation of callose biosynthesis.

cytoplasm is required for aluminum-induced callose deposition [40]. These studies suggest that callose is involved in the regulation of plant resistance to abiotic stress.

Diverse biotic stresses also cause callose deposition in plants. Viruses and the blast fungus infection triggers plasmodesmata callose deposition that limit cell-to-cell spread of viruses and the blast fungus [41]. Different *Chrysanthemum* species exhibited the different abilities to tolerate the chrysanthemum stunt viroid (CSVd) infection [42]. The level of plasmodesmata callose was much higher in the tolerant cultivars than the sensitive ones. Callose deposition may be an early defense mechanism in plants against pathogen attack. In contrast, studies have reported that callose also negatively regulates the disease resistance of plants. The loss-of-function mutants of *GSL5/PMR4/CalS12* cannot synthesize callose in papillae, a physical barrier to slow pathogen invasion [43]. Unexpectedly, the reduction of callose in the *gsl5* mutant makes plants more resistant to powdery mildew [44]. Further study found that the lack of callose in *pmr4* mutants can enhance salicylic acid signaling, leading to increased resistance to pathogens [44]. These studies have shown that the response of plant pathogens involves multiple mechanisms in addition to callose. How to balance these two effects of callose in the stress response process, and the regulatory relationship between callose and other anti-stress factors remains to be studied.

4. Regulation of callose biosynthesis

4.1. Transcriptional regulation of callose synthase gene

Unlike cellulose, the production of callose in plants is relatively rare, ranging from about 0.3% (total cell wall content) in *Arabidopsis* to about 5% in the energy crop *Miscanthus x giganteus* [45]. In fact, callose induced by diverse development and stress responses is only deposited in a special cell wall, which may explain the specific expression of *GSL* gene family members cell or tissue types [9]. For instance, *OsGSL5* specifically highly expressed in the anther has been proved to participate in callose deposition during rice anther development [21]. However, precise regulation mechanism of specific expression of callose synthase gene has not been demonstrated unequivocally. Plant hormones are believed to play a key role in this process. The plant hormones auxin, abscisic acid (ABA), gibberellin (GA), and salicylic acid (SA) regulate the expression of GSLs [24, 46, 47, 48, 49]. Auxin induces *AtGSL8* expression through the auxin-responsive transcription factor ARF7 [24]. Then the asymmetric deposition of callose at plasmodesmata cause the auxin gradient in the *Arabidopsis* hypocotyl, which forms a feedback regulation loop and affects the phototropic of *Arabidopsis* [24]. High levels of ABA in poplar buds induces the expression of *callose synthase 1* under short-day conditions, resulting in a large amount of callose accumulated at plasmodesmata [49]. Jasmonic acid (JA) and salicylic acid (SA) play crucial roles in the defense signaling pathways. During the flg22-triggered innate immune response, SA induces callose deposition in plasmodesmata, but JA plays an opposite role [33, 50]. Interestingly, JA was reported to be required for proper callose deposition during necrotrophic pathogens-triggered basal defense response [51]. SA enhances callose deposition in plasmodesmata through the action of GSL6/CalS1 and PDLP5 (plasmodesmal protein 5). PDLP5-mediated callose deposition are dependent on the EDS1/ICS/NPR1-associated SA signaling pathway. Future research might uncover details of how transcription factors regulate the expression pattern of GSLs in response to plant hormones.

4.2. Post-transcriptional regulation of callose synthesis

Cellulose is synthesized from CesA complexes with a diameter of 40–60 nm [52], which usually consists of a heterotrimeric CesAs and related proteins on the plasma membrane [7]. It is generally believed that GSLs will also form a complex similar to CesAs [9]. In *Arabidopsis*, GSL6 can be purified together with the cell-wall associated proteins, phragmoplastin, and UGT1 [53], so it is speculated that the GSL complexes may contain monomeric GTPase, UDP-glucose transferase (UGT), annexin and sucrose synthase. The proteins of these complexes may regulate the activity of GSLs to a certain extent.

The CesA complexes localized to the plasma membrane are assembled in the Golgi apparatus [7], and then transported to the plasma membrane through the trans-Golgi network (TGN) and small vesicle compartments

[54, 55]. GSLs do not contain the signal peptides required for conventional secretory pathways, and their subcellular localization seems to require EXO70 family-mediated exocysts [56]. Whether the transport of GSL complexes is mediated by TGN still needs further corroboration.

Considering relatively slow callose deposition by transcriptionally regulated GSLs, it seems likely that rapid accumulation of callose in plants might require modulation by faster post-translational modification regulation. GSLs are predicted to have multiple phosphorylation sites. Various abiotic and biotic stresses may induce the phosphorylation of multiple GSLs in *Arabidopsis* [57, 58, 59, 60, 61, 62, 63, 64]. The additional study from yeast indicated that phosphorylation status of GSLs regulates their activity [65, 66, 67]. For CesAs, phosphorylation is an important regulatory player [68]. A subset of phosphorylation sites mutation reveals different functions of phosphorylation for CesAs [69].

Secondary messengers such as Ca^{2+} and ROS are involved in callose deposition induced by stress [70]. the plasma membrane NADPH oxidases (RBOHs) are activated by stress to produce apoplastic ROS [71]. However, the mechanism by which stress-induced ROS controls callose deposition remains to be identified. CalS8/GSL4 has been identified as the key enzyme synthesizing plasmodesmal callose in response to ROS [33]. As the expression of *GSL4* was not affected by H_2O_2 treatment, ROS-induced GSL4 activation may be subjected to post-transcriptional regulation. How GSL4 activity is controlled remains to be elucidated. Signaling players such as receptor-like proteins (RLPs) or receptor-like kinases (RLKs) possessing a ROS sensor ectodomain may link the signaling between ROS and GSL4 activation. Ca^{2+} sensed by CML (CALMODULIN-LIKE) proteins may act as the downstream of ROS [72]. One possibility is that CML member can bind to GSLs, which may directly activate GSLs. GSL5 might be a targeted regulation enzyme of CML41 during flg22-triggered immune response [29, 73]. The relationship between post-translational modification and GSL complex assembly and enzyme activity, as well as other post-translational protein modifications remains to be studied.

5. Future perspectives

In the context of climate change and environmental pollution, we are facing drought, high temperature, and heavy metal pollution, which are bringing about negative effects on many agricultural ecosystems around the world [74]. As an important plant glucan polymer, callose is involved in not only plant development but also response to various stresses. Genetic manipulation of enzyme activity and gene expression of GSLs therefore may contribute to improving the ecosystem function and agricultural productivity.

Like cellulose, callose is an important part of cell walls in plants. Both have similar primary structures, synthases, and common substrates. However, the difference is that callose only exists in special cell walls, and callose plays a different role from cellulose in the process of plant growth and development. Therefore, we give a general overview and brief summarization of the current understandings of function and the regulatory mechanism of callose biosynthesis (see Figure 2) in higher plants. Additionally, several critical questions remain unanswered: (i) What are the components of the callose synthase complex? (ii) how the callose synthase complex is assembled? (iii)How plants precisely regulate the function of the callose synthase complex? Although the assembly and regulation of callose synthase complex lack detailed potential molecular mechanisms, the comparative study of callose and cellulose should provide profound enlightenment and valuable insights for understanding their special functions and regulatory mechanisms in plants.

Declarations

Author contribution statement

All authors listed have significantly contributed to the development and the writing of this article.

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Data included in article/supplementary material/referenced in article.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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