Cell Wall Integrity

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Cell wall biosynthesis is a complex biological process in plants. In the rapidly growing cells or in the plants that encounter a variety of environmental stresses, the compositions and the structure of cell wall can be dynamically changed.

cell wall integrity cell wall sensor salt stress

1. Introduction

High salinity is an adverse environmental stress that severely affects the growth and yield of crops. Excessive accumulation of sodium in plants confers both ion toxicity and osmotic stress, which in turn dramatically affect the morphological, physiological, biochemical, and metabolic status of plants [1]. Currently, more than 20% of the irrigated lands in the world are threatened by high salinity, and the area of saline soils is increasing gradually every year accompanied by the global climate change and poor irrigation practices [2][3][4]. It is expected the global population will reach to nearly 10 billion in 2050, and to meet the increasing food demand in future, the utilization of saline soils to grow major crops tends to be inevitable. Therefore, the cultivation of crops with increased salt tolerance is a major objective in salt stress community.

To avoid the damage caused by excessive salts in soil, plants have evolved various strategies to overcome the problems caused by high salinity. Ion homeostasis, osmotic adjustment, ROS balance, and metabolic adjustment are the major factors that are associated with the tolerance of plants to salt stress. Based on the capacity of plants to adapt to salt stress, plants can be classified into glycophytes and halophytes. Our major crops, such as rice, maize, and wheat, are glycophytes that are unable to complete their life cycle when they are being exposed to high salinity. Halophytes, however, have developed various strategies to adapt to the environments with a high concentration of sodium. For example, halophytes are able to extrude salts via glands or store excessive Na^+ in the vacuoles of epidermal bladder cells [5][6].

More and more studies point out that maintenance CWI is also critical for the adaptation of plants to high salinity. Plant cell walls, which mainly consist of polysaccharides and structural proteins, are essential for the establishment of plant morphology and protection of plants against adverse environmental changes [7]. During plant growth and development or in response to environmental stresses, the cell wall compositions and structures are dynamically modulated, allowing rapid cell elongation and increased stress tolerance [8]. To maintain CWI during the reorganization of cell wall, plants need to constantly monitor the chemical and mechanical properties of the cell walls and also need to process an ability to repair cell wall once they are seriously disrupted. It has been shown

that CWI maintenance mechanism exists in plants and is essential for the regulation of growth and development and in response to stress conditions [9][10]. The progresses about CWI sensing and maintenance system in plants have been summarized in several outstanding review papers [8][11][12].

2. Importance of Cell Wall Biosynthesis in Salt Tolerance

The plant cell wall is a dynamic network composed of cellulose, hemicellulose, pectin, lignin, and multiple types of structural proteins [13][14]. Moreover, cell wall-remodeling enzymes, various ions, and reactive oxygen species (ROS) also exist in the apoplast and are involved in the regulation of CWI. Upon exposure to high salinity, several changes in the cell wall have been identified, including the reduction of cellulose content [15][16], disruption of the cross-linking of pectins [9], and accumulation of lignin [17]. Studies have shown that the plants that are defective in cell wall biosynthesis are hypersensitive to salt stress, suggesting that maintenance of CWI is important for the adaptation of plants to high salinity.

2.1. Cellulose

Cellulose is the most abundant organic component in the cell wall of terrestrial vascular plants. Cellulose microfibrils are composed of β-1,4-linked glucan chains, which are synthesized at the cell surface by cellulose synthase (CesA) complexes (CSCs) [18][19]. Each CSC is assembled into a hexameric rosette structure, harboring CesA catalytic subunits and several accessory proteins. In *Arabidopsis*, there are ten CesA proteins [18]. It is well known that CesA1, CesA3, and CesA6 are assembled in a CSC to synthesize cellulose in the primary cell wall, while CesA4, CesA7, and CesA8 are mainly involved in the synthesis of cellulose in the secondary cell wall [20]. Experimental data have shown that the cellulose contents are significantly reduced after salt treatment and the plants with a loss of function of CESA1 and CESA6 gene display reduced root elongation and severe root tip swelling under salt stress, indicating that cellulose biosynthesis is important for salt tolerance in plants [21][22]. Clear evidences have indicated that the CSCs are dissociated from plasma membrane within 30 min after exposure to high salinity. However, during the growth recovery phase after salt treatment, the CSCs can be reassembled at the plasma membrane to synthesize new cellulose, and the capacity to reassemble CSCs during the growth recovery stage is critical for plants to maintain root and hypocotyl growth under salt stress [16].

Apart from the CesAs, several cellulose biosynthesis-related proteins have also been reported involved in salt tolerance. For example, KORRIGAN1 (KOR1), a putative endo-1,4-β-D-glucanase, is an integral part of the primary cell wall CSC and is required for root elongation under salt stress [22][23]. Cellulose synthase interacting protein 1 (CSI1) and companion of cellulose synthase 1 (CC1 and CC2) proteins, acting as companions of CesAs, are both required for cellulose biosynthesis [16][21]. Mutations in *CSI1* or *CC1* and *CC2* lead to reduced root or hypocotyl elongation under salt stress. *CTL1* encodes a chitinase-like protein that participates in the deposition of the ordered cellulose, and mutation of this gene results in increased sensitivity to high salinity [24] (Table 1).

Table 1. List of the cell wall biosynthesis-related genes that are involved in salt stress response.

Name	Gene ID	Annotation	Function	Reference(s)
AtCesA1/RSW1	At4g32410	Cellulose synthase catalytic subunit	Cellulose synthesis in the primary cell wall	[22]
AtCesA8/IRX1	At4g18780		Cellulose synthesis in the secondary cell wall	[25]
AtCC1	At1g45688	Cellulose synthase companion protein	Cortical microtubules assembly and cellulose biosynthesis under salt stress	[16]
AtCC2	At5g42860			
AtCTL/POM1	At1g05850	Chitinase-like protein 1	Involved in the assembly of glucan chains	[24][26]
AtCSI1/POM2	At2g22125	Cellulose synthase-interactive protein 1	Companion of CesAs; required for cell elongation in root	[21]
AtCCoAOMT1	At4g34050	Caffeoyl-CoA 3-*O*-methyltransferase	Involved in lignin synthesis	[17]
AtKOR/RSW2	At5g49720	Endo-β-1,4-glucanase	Integral component of CSC; required for cell elongation in root	[23]
AtHSR8/MUR4	At1g30620	Golgi-localized UDP-D-xylose 4-epimerase	Arabinose biosynthesis; related to the modification of polysaccharides and glycoproteins	[27]
AtGALS1	At2g33570	β-1,4-galactan synthase	Transfer of galactose from UDP-α-d-Gal or arabinopyranose from UDP-β-l-Ara*p* to growing β-1,4-galactan chains	[28][29]
AtXTH30	At1g32170	Xyloglucan endotrans glucosylase-hydrolase	Cleave or rejoin the xyloglucan; *xth30* mutation decreases crystalline cellulose content and affects the depolymerization of microtubules under salt stress	[30]
AtPMEI13	At5g62360	Pectin methyl-esterase inhibitor 13	Inhibits the activity of PMEs	[31]
AtBPC1	At2g01930	BPC-type transcription factor	Regulation of the expression of *AtGALS1*	[28]
AtBPC2	At1g14685			
AtGCN5	At3g54610	Histone acetyltransferase	Epigenetic regulation of cell wall-related genes	[32]
OsTSD2	Os02g51860	Pectin methyltransferase	Regulation of pectin metabolism	[33]

Name	Gene ID	Annotation	Function	Reference(s)
OsBURP16	Os10g26940	β subunit precursor of polygalacturonase 1	Involved in cell wall pectin degradation	[34]

2.2. Hemicellulose

Hemicelluloses are grouped into xyloglucans (XyG), xylans, mannans, and β-(1,3;1,4)-glucans, and the abundance and structure of these polysaccharides vary greatly in different plants species [35]. Xylan is considered as a cross-linking polysaccharide in the establishment of cell wall architecture [35][36]. XyG contributes to the strengthening of cell wall during cell elongation by binding to cellulose micro-fibrils with hydrogen bonds [37][38]. XyG can be cleaved by the cell wall remodeling enzymes xyloglucan endotransglucosylase/hydrolases (XTHs) [39]. After cleavage, the reducing end of the XyG is attached to the non-reducing end of another XyG oligomer or polymer to produce chimeric XyG molecules [39]. The XTHs-mediated modification of XyG is considered to be important for controlling cell wall extensibility. Studies have reported that XTHs are involved in salt stress response in plants. *Arabidopsis XTH30*, encoding a xyloglucan endotransglucosylase/hydrolase 30, is strongly upregulated under salt stress [30]. Loss of function of the *XTH30* gene leads to increased salt tolerance, which is mainly caused by the slower reduction of crystalline cellulose content and alleviated depolymerization of microtubules in response to salt stress [30]. This result suggests that XTH30 plays a negative role in salt tolerance. However, the positive roles of XTHs in salt tolerance have also been reported. Constitutive expression of *CaXTH3* in hot pepper [40][41] and *PeXTH* in *Populus euphratica* [42] enhance tolerance to salt stress, and disruption of *XTH19* and *XHT23* genes in *Arabidopsis* results in decreased salt tolerance [43].

2.3. Pectin

Pectin is a group of acidic polysaccharides that are enriched with α-(1, 4)-linked galacturonic acids in the backbone [44]. Pectin accounts for up to 40% of the dry weight of higher plant cell walls [44] and plays critical roles in plant growth and development [45], leaf senescence [46], biotic [47] and abiotic stress responses [48]. Pectin is composed of three major types: homogalacturonan (HG), rhamnogalacturonan-I (RG-I), and rhamnogalacturonan-II (RG-II) [7][44]. HG is synthesized in the Golgi apparatus and secreted to the apoplast in a highly methy-esterified form and later it is selectively de-esterified by pectin methyl esterases (PMEs) during cell growth and in response to environmental stimuli [7][44]. The degree and pattern of the methyl-esterification of pectin in some extent determines the stiffness of cell walls [49]. In *Arabidopsis*, there are around 66 members of PME family protein, and for most of PMEs, their activities can be inhibited by endogenous PME inhibitors (PMEIs) or a natural inhibitor epigallocatechin gallate (EGCG) [50][51]. High salinity triggers the demethyl-esterification of loosely bound pectins to inhibit cell swelling [52] and previous studies showed that the activity of PMEs is either positively or negatively associated with salt tolerance in plants [53]. For instance, null *Arabidopsis* function mutant *pme13* is hypersensitive to Na^+ toxicity in seed germination and seedling growth [53]. In contrast, overexpression of *Chorispora bungeana PMEI1* or *AtPMEI13* in *Arabidopsis* causes decreased PMEs activity and enhanced methyl-esterification level of pectins, which subsequently improves seeds germination and survival rate under salt stress [31]. The de-esterified HG

molecules can be cross-linked to form the so called egg-box structure, the process of which is mediated by divalent cations, such as Ca^{2+}, and the formation of egg-box structure promotes cell wall stiffening [54]. In the presence of high concentration of Na^+, the ratio of Na^+/Ca^{2+} in the apoplast is increased, and Na^+ is supposed to replace Ca^{2+} to bind pectins and thus disturbs the cross-linking of pectins, leading to reduced cell elongation [55]. Besides, the borate-mediated cross-linking of RG-II contributes to the strength of cell wall and is required for the regulation of growth recovery after exposure to high salinity [56][57].

The roles of pectin in salt tolerance have also been reported in rice. Polygalacturonase 1 (PG1) is a cell wall hydrolase that is responsible for the degradation of cell wall pectin. Overexpression of *OsBURP16*, which encodes a non-catalytic β subunit of PG1, results in an increased pectin degradation and increased salt-hypersensitivity in rice [34]. *OsTSD2* encodes a pectin methyltransferase in rice, and mutation in *OsTSD2* leads to a higher content of Na^+ and a lower level of K^+ in rice shoot under high salinity, which is mainly caused by the reduced expression of genes that are responsible for the maintenance of ion homeostasis, such as *OsHKT1;5*, *OsSOS1*, and *OsKAT1* [33] (Table 1).

2.4. Lignin

As one of the most abundant organic compound in plants, lignin is composed of phenylalanine-derived [58] or tyrosine-derived [59] aromatic monomer substances and is important for the secondary cell wall formation and the responses to a variety of environmental stresses [60]. High salinity induces the accumulation of lignin content and cell wall thickening via the activation of lignin biosynthesis pathway [60]. The accumulation of lignin contributes to the mechanical strengthening of cell wall and protection of membrane integrity under salt stress [61]. The effects of lignin accumulation on salt tolerance have been reported in different crops, including soybean [62], wheat [63], and tomato [64]. *CCoAOMT* encodes a caffeoyl CoA *O*-methyltransferase (CCoAOMT), which catalyzes caffeoyl CoA to feruloyl CoA in lignin biosynthesis pathway. The expression of *CCoAOMT* is induced in salt-adapted cell, and the plants with a loss-of-function of *CCoAOMT* are hypersensitive to salt stress [17]. *BpMYB46* and *BpNAC012*, encoding two transcription factors in white birch (*Betula platyphylla*), are required for the up-regulation of lignin biosynthetic genes and salt stress-responsive genes, and overexpression of these two genes enhances salt tolerance in *B. platyphylla* [65][66]. AgNAC1, a nuclear-localized protein in celery, acts as a positive regulator in inducing the expression of lignin-related and salt stress-responsive genes, and overexpression of *AgNAC1* enhances the formation of secondary walls and plant salt tolerance [67].

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