Journal of Plant Physiology 294 (2024) 154202

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Impact of the TOR pathway on plant growth via cell wall remodeling

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ARTICLE INFO

Keywords:
Cell wall
Target of rapamycin
Plant growth
Expansion
Biomass

ABSTRACT

Plant growth is intimately linked to the availability of carbon and energy status. The Target of rapamycin (TOR) pathway is a highly relevant metabolic sensor and integrator of plant-assimilated C into development and growth. The cell wall accounts for around a third of the cell biomass, and the investment of C into this structure should be finely tuned for optimal growth. The plant C status plays a significant role in controlling the rate of cell wall synthesis. TOR signaling regulates cell growth and expansion, which are fundamental processes for plant development. The availability of nutrients and energy, sensed and integrated by TOR, influences cell division and elongation, ultimately impacting the synthesis and deposition of cell wall components. The plant cell wall is crucial in environmental adaptation and stress responses. TOR senses and internalizes various environmental cues, such as nutrient availability and stresses. These environmental factors influence TOR activity, which modulates cell wall remodeling to cope with changing conditions. Plant hormones, including auxins, gibberellins, and brassinosteroids, also regulate TOR signaling and cell wall-related processes. The connection between nutrients and cell wall pathways modulated by TOR are discussed.

1. Introduction

Organ elongation and expansion, the activity of meristems to generate new cells and organs, and the delicate equilibrium between C assimilation and losses resulting in net biomass accumulation contribute to plant growth. Briefly, these processes encompass cell expansion, proliferation, and biomass accumulation. Cell expansion can be defined by a permanent increase in size, influenced by the surrounding wall's stretchability property, plus the vacuole's water absorption potential to augment its size without diluting its nutrients. Cell division and elongation processes in plants are unique because of a structure that sets shape, resistance and mediates the exchange of molecules: the cell wall (CW) (Hilty et al., 2021).

Although the exact mechanisms involved in photosynthesis, i.e., how plants produce sugars from CO_2 and water, are well known, less is understood about how the cell partitions C into sugars and in the pool of nucleoside diphosphate sugars (NDP-sugars) used as building blocks for the CW. Moreover, information regarding the regulation of the enzymes involved in CW synthesis, including composition and deposition, still needs to be included. Sugars, products of photosynthesis, can be transiently stored into starch, fructans, or oligosaccharides, which are later converted into raffinose, sucrose, or stachyose to be transported to their destination and subsequently converted into hexose monophosphate and then usually into NDP-sugars. After activation, these NDP-sugars can be used by glycosyltransferases for the synthesis of CW glycoproteins and polysaccharides, such as cellulose, hemicellulose, and pectin. Plants need polymers made of sugars to construct CW structures, which are essential for plant growth (reviewed by Verbančič et al., 2017). Indeed, these sugars constitute the main C sink and, consequently, the portion of the plant's biomass that are useful for many industrial applications, such as fuels and bioproducts.

The "Target of Rapamycin" (TOR) pathway is a central hub that connects external signs to internal anabolic responses in various organisms. In plants, TOR forms only one complex (TORC) composed of the triad of proteins: TOR, Regulatory-Associated Protein of TOR (RAPTOR), and Lethal with SEC13 protein 8 (LST8) (Maegawa et al., 2015). TOR affects several developmental processes, including growth (Deprost et al., 2007; Moreau et al., 2012; Ren et al., 2012; Salem et al., 2018; da Silva et al., 2021), flowering, embryogenesis, photoautotrophic transition (Moreau et al., 2012), senescence (Moreau et al., 2012; Ren et al., 2012), and chloroplast development (Bakshi et al., 2017). TORC disruption leads to a severe plant growth arrest phenotype: reduced fresh and dry weights (affecting biomass), smaller cells (limiting expansion), smaller roots, and fewer and reduced leaves (DeProst et al.,

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https://doi.org/10.1016/j.jplph.2024.154202
Received 1 October 2023; Received in revised form 12 February 2024; Accepted 13 February 2024
Available online 22 February 2024

2007; Moreau et al., 2012; Ren et al., 2012; Caldana et al., 2013; Salem et al., 2018; da Silva et al., 2021). TOR impacts general growth and positively controls leaf expansion, root hair elongation, and cell division.

When TOR is down-regulated, plants accumulate starch, which influences C fluxes and biomass accumulation. The impaired growth phenotype derived from TOR down-regulation partially results from adverse effects on CW-related mechanisms (Ren et al., 2012; Caldana et al., 2013). In animals, emerging data indicates that TOR control over cell size is related to its interaction with cytoskeletal elements and vesicle trafficking (Gonzalez and Rallis, 2017). In Arabidopsis (reviewed by Pottier et al., 2023) and other plants (Bakshi et al., 2017; De Vleschauwer et al., 2018; Choi et al., 2022), the impact of the TOR pathway on the CW machinery takes place through transcriptional modulation, conditional translation, and protein-protein interaction. Although plant TOR research has been evolving rapidly in the last decade, the limited available information on TOR subcellular localization might hinder establishing a tighter link between TOR and the CW. So far, TOR has only been identified in the plant cytosol (Ren et al., 2011; Schepetilnikov et al., 2017; Dai et al., 2022), around the mitochondria (Dai et al., 2022), endosome (Schepetilnikov et al., 2017) and nucleus (Ren et al., 2011). Investigating the upstream signals and the CW-related TOR downstream targets contributes to establishing a stronger correlation between nutrient partitioning and CW building. Such a cell structure is one of the most relevant impacting growth, providing a better understanding of how TOR conveys environmental cues into plant growth and development.

2. The TOR pathway mediates the interplay between C status and CW investment

Carbon assimilation through photosynthesis is primarily directed towards the CW, where it is incorporated into biomass (Wang et al., 2013; Boex-Fontvieille et al., 2014; Haigler et al., 2001). Although dry-matter accumulation has been intensively studied, the exact mechanisms by which external and internal signals link growth with CW building must be thoroughly understood (Bischoff et al., 2011; Boex--Fontvieille et al., 2014).

Following photosynthesis, C is stored as transitory starch during the day to be remobilized and provide energy during the night (Smith and Stitt, 2007; Stitt and Zeeman, 2012; Sulpice et al., 2014). General plant growth depends on energy, C, and water status (Apelt et al., 2017). While the circadian clock drives cell expansion, CW synthesis is influenced by the C status of the plant (Ivakov et al., 2017). The TOR pathway is one of the leading actors regulating plant sugar metabolism performing a twofold interaction with sugars: this complex is induced by sugars and controls sugar levels in plants (Dobrenel et al., 2013). TORC senses sugar signals to control growth and cell division, as plants with inhibited TOR have reduced fresh and dry weight (biomass, C accumulation), besides cell length (Deprost et al., 2007; Moreau et al., 2012; Ren et al., 2012; Salem et al., 2018; da Silva et al., 2021). CW biogenesis impacts cell size, form, and function (Burton et al., 2010), but CW remodeling properties limit growth. Given the relevance of the link between sugars and TOR, this kinase is expected to play a preponderant part in biomass accumulation through CW synthesis.

Plant CWs are intricate structures formed by polysaccharides, such as cellulose, hemicellulose, and pectin, besides structural proteins (SPs). Cellulose is the primary CW component in the form of microfibrils that provide strength and stand as the scaffold for the other polymers (reviewed by Verbančič et al., 2017), while SPs provide form and structure to the CW framework. TORC impacts the CW-dedicated expression machinery. The expression of CW SPs, such as extensins, Pro-rich proteins, arabinogalactan- (Xiong et al., 2013; Dong et al., 2015), and Hyp-rich glycoproteins (Ren et al., 2012; da Silva et al., 2021; De Vleesschauwer et al., 2018; Scarpin et al., 2020) are positively-regulated by the TOR pathway. Extensins are involved in CW reinforcement and required for proper wall assembly (Cannon et al., 2008), which shows the essential role of TOR in this cell structure. Moreover, the visible growth arrest phenotype displayed by TOR-inhibited plants (Deprost et al., 2007; Moreau et al., 2012; Ren et al., 2012; Salem et al., 2018; da Silva et al., 2021) resonates with the decreased expression of CW SP genes, as dry matter accumulation and CW reinforcement are two correlated processes (Wai et al., 2017).

The synthesis of CW components starts with converting assimilated C from remobilized starch or free sugars as sucrose, to NDP-sugars by several routes. In growing tissues, these nucleotide sugars are ultimately converted to CW polysaccharides as cellulose microfibrils (reviewed by Verbančič et al., 2017). However, it is not completely clear how the TOR signaling is interconnected with the C supply and the sugars pool for the interconversion to CW polysaccharides (see Pottier et al., 2023). Cellulose synthases (CesAs) are responsible for cellulose synthesis, and the rate of these enzymes migration from the Golgi complex to the plasma membrane (PM) is a proxy for CW growth. Moreover, it has been proposed that TOR could be one of the candidates to regulate the transport of the CesAs to the membrane (Ivakov et al., 2017). Once placed at the PM, CesAs are displayed as rosettes to synthesize cellulose, whose microfibrils indicate the direction of cell elongation, mediated by the microtubules. LST8 is a positive CELLULOSE SYNTHASE-LIKE G3 gene regulator under sugar abundance (Moreau et al., 2012). However, the expression of CesAs showed increased and decreased levels under TORC suppression (Xiong et al., 2013; Dong et al., 2015; da Silva et al., 2021). Moreover, COBL2 transcript levels, assigned to act on cellulose deposition, architecture, and the solubility of pectic components (Ben-Tov et al., 2015; Ben-Tov et al., 2018), were augmented in TORC-inhibited plants (Caldana et al., 2013; Dong et al., 2015). TORC-deficient tomato pericarp presented reduced cellulose deposition (Choi et al., 2022), showing that the effect of the TOR pathway on this polysaccharide might be tissue- or organ-specific, depending also on the wall type.

Cellulose microfibrils are embedded in a matrix of hemicellulose and pectins linked by glycosidic linkages. The CW precursor myo-inositol decreased upon TOR inhibition, while its product, d-galacturonate, besides 3-Deoxyoctulosonate, increased (da Silva et al., 2021). The accumulation of D-glucuronate and 3-Deoxyoctulosonate suggests that TOR mediates the incorporation of these compounds into pectin, which is required for proper cell elongation (Ren et al., 2012). Indeed, the most vital target link between the CW and TOR was established by Leiber et al. (2010). The *A. thaliana lrx1* mutant lines present aberrant root hairs, while its suppressor, *rol5*, reverts the phenotype similarly to the wild type. Inhibition of TOR by rapamycin treatment led to the suppression of *lrx1* aberrant root hairs and induced CW changes similar to *rol5* mutants. Arabidopsis plants with reduced TOR activity led to a lowered Rhamnogalacturonan I (RGI)-galactan side chain and an increase in arabinogalactan protein (Leiber et al., 2010). RGI is the major Arabidopsis component of pectin, and its activity is linked to CW strengthening and pectin matrix porosity. Pectins are structural polysaccharides accounting for one-third of the CW dry mass (Philippe et al., 2017). They regulate the wall porosity and hydration, which influences wall thickness and mobility of CW-modifying enzymes, allowing polysaccharides to slide through the wall. Moreover, pectins adjust the wall expansion by impacting the alignment of cellulose microfibrils. Due to impaired RGI, disrupted TOR plants presented reduced CW strengthening or porosity, precluding the mobility and activity of CW proteins (Leiber et al., 2010).

Additionally, gene expression data shows that TOR regulates pectin deposition and degradation. Pectate lyases-like (PLL) (Ren et al., 2012) and pectinesterases/pectin methylesterases (PMEs) followed TOR down-regulation, reducing their transcripts levels (Caldana et al., 2013; Xiong et al., 2013; Dong et al., 2015). PLLs are proposed to be part of pectin and other CW polysaccharides digestion (Wieczorek et al., 2014) and PMEs cleave methyl groups of pectins, increasing the CW rigidity. After the transport from Golgi to the CW, pectin is partially deesterified

by PMEs, which exposes a carboxyl group on galacturonosyl residues and allows the pectin to be stiffened by cross-binding with calcium ions (Guan and Nothnagel, 2004). PMEs act with polygalacturonase (ADGP) into homogalacturonan disassembly (Lashbrook, 2005), and PLs use homogalacturonan de-esterified by PMEs as a substrate. Moreover, ADPGs (Ren et al., 2012; Caldana et al., 2013) displayed increased transcript levels in plants under TOR suppression. Such results are expected to contribute to the impaired cell phenotype observed when TOR is down-regulated (Caldana et al., 2013) and could be involved in the abnormal cell-to-cell adhesion and inhibited growth phenotype observed in the down-regulated TORC *A. thaliana* plants (Deprost et al., 2007; Moreau et al., 2012; Ren et al., 2012; Salem et al., 2018). Interestingly, many of the mentioned CW genes are under the trithorax homolog ATX1 regulation (Alvarez-Venegas et al., 2006). Both the TOR pathway (Dong et al., 2023) and ATX1 (Saleh et al., 2008) are inducers of histone H3 methylation, which suggests that ATX1 can be one of the TOR targets (Sharma et al., 2022), being controlled by epigenetic factors, and coordinating part of the changes in CW machinery.

Expression (Caldana et al., 2013; Xiong et al., 2013; da Silva et al., 2021) and metabolic (Ren et al., 2012; Caldana et al., 2013) data show that TOR inhibition increases the levels of lignin precursors. After cellulose, lignin accounts for 30% of the existing organic C (Qualley et al., 2012), largely impacting plant growth. Lignin is a phenolic compound usually found in the secondary CW that confers resistance to the whole plant (Liu et al., 2018). Lignin content is often augmented when plants face several stresses (Zhao et al., 2022; Han et al., 2022), pointing that the absence of a functional TORC can be perceived as a stress to redirect part of the C budget to lignin synthesis rather than other polysaccharides that contribute to primary wall synthesis and growth.

Given that cell growth is dependent on cell expansion through CW remodeling and integration of cellulose microfibrils, hemicelluloses, and the pectin matrix (Chebli and Geitmann, 2017), TOR seems to be required to mediate C incorporation to biomass altering C allocation under sugar availability.

3. Cell elongation is promoted by expansins that are transcriptionally induced by TOR

The synthesis and rearrangement of CW components is only one aspect of cell growth, as expansion needs to take place to incorporate the newly synthesized wall polysaccharides. Not only the biomass accumulation is affected through CW synthesis, but also the expansive growth, which albeit interconnected processes, can be distinctively regulated (Voxeur and Hofte, 2016; Ivakov et al., 2017). Cell elongation follows a rhythmically oscillating pattern with circadian regulation (Dornbusch et al., 2014), with the highest rates near the transition from dark to light (dawn). The TOR pathway controls growth by integrating and coordinating external signals, sugar status, and the circadian clock into plant metabolic responses. Although increasing evidence points to a determinant role of TORC connecting the diel cycle and the circadian information in plant growth and development (Urrea-Castellanos et al., 2022), a clear link between the TOR hub and the circadian regulation of the CW expansion needs further exploration.

The rearrangement of plant CW components has a fundamental and driving role in cell expansion. TOR is a positive regulator of expansins (EXPs) (Moreau et al., 2012; Ren et al., 2012; Caldana et al., 2013; Dong et al., 2015; Scarpin et al., 2020; da Silva et al., 2021). As the name speaks for itself, EXPs facilitate CW loosening and extension by disrupting non-covalent bonds between cellulose microfibrils and other CW components without cell lysis, thereby allowing cells to expand and grow (Cosgrove et al., 2015). The acid cell growth hypothesis states that the plant hormone auxin activates PM H + -ATPases to send H+ outside the cell, which acidifies the apoplast. The acid pH activates EXPs and other enzymes, such as Xyloglucanendotransglucosylase/Hydrolases (XTH), PMEs and cellulases. These enzymes break the links between the CW polymers and reduce the turgor pressure, allowing water to enter the cell due to osmotic differences. Once the water enters the plant vacuole, it increases the cell volume, and CW loosening induces hydration and swelling. CW porosity enhances the creation of space for the newly synthesized polysaccharides and proteins delivered through vesicle transport. The CW surface area rises by integrating these new polysaccharides (reviewed by Majda and Robert, 2018). The expression of CW proteins, including EXPs, increased following glucose-TOR signaling (Xiong et al., 2013). Indeed, reduced cell length is a well-characterized phenotype of plants under TOR repression (Deprost et al., 2007; Ren et al., 2012; Caldana et al., 2013; da Silva et al., 2021). This established a link between sugar sensing and TOR-mediated cell elongation control through EXPs expression. However, sugar status solely did not seem decisive in cell expansion, which is under circadian control (Ivakov et al., 2017). Interestingly, the TOR antagonist Sucrose non-fermenting-related kinase 1 (SnRK1) interfered with EXP induction when sucrose was exogenously supplied (Simon et al., 2018). Whether this interplay involves TOR signaling is a matter to be explored.

Plant cell wall polymers undergo continuous changes during plant growth and development. CW modification and remodeling are carried out by enzymes, such as glycosyl hydrolases (GH), including XTH. Transcriptomic data suggests that several GH are downregulated , while XTH shows increased expression (Dong et al., 2015; Caldana et al., 2013). Interestingly, by silencing TORC in tomato fruits, Choi et al. (2022) observed an early ripening phenotype at least partially linked to increased transcript levels of β-mannosidase, β-galactosidase, β-N-acetyl-D-hexosaminidase, EXP, polygalacturonase 2A and cellulase 2. These enzymes restructure CW polysaccharides by disrupting chemical bonds and degrading sugar-enriched molecules to promote cell development, fruit ripening, and environmental responses, contributing to the dynamically complex and extensible nature of the plant CW. Whether TORC mediates CW remodeling by regulating the expression of these enzymes in other organs and conditions remains an intriguing open question to be answered. In *Saccharomyces cerevisiae*, there are two TOR Complexes. While TORC1 targets cell volume and anabolic processes (e.g., protein and macromolecule synthesis), TORC2 is related with cell surface homeostasis (related to PM tension control, endocytosis, lipid synthesis, and CW integrity pathway). The TORC2 activator Elm1 is induced by glucose and C availability. Elm1 is one of the candidates to promote cell growth and expansion integration, but the exact link with TORC2 is still missing (summarized by Riggi et al., 2020). As only one TORC has been identified in plants, and considering plants and yeasts CWs specificities, we can only speculate that such a TOR-mediated matched control between wall synthesis and expansion occurs in plants.

4. Active TOR is needed for CWs to recover from environmental stresses

Plant metabolism is influenced by different factors such as photoperiod, circadian clock, temperature, and cultivation. Phenotypic plasticity allows plants to adapt to environmental cues, performing better and advancing on the transitional changes needed for plant development. TORC is a vital controller that integrates nutrients and energy into metabolism for growth and developmental transitions. TOR activity usually increases when plants face several abiotic stresses (Pereyra et al., 2020). Indeed, rice plants transformed with *At*TOR, showing enhanced TOR activity, had their biomass increased under water limitation (Bakshi et al., 2017).

The kinase receptor FERONIA (FER) impacts several cellular processes, such as sensing for CW recovery after high salinity exposure (Feng et al., 2018). FER is required for TOR activity to repress autophagy (Wang et al., 2022), although it has not been explored the role of these two proteins together in CW modifications to couple with abiotic stresses. The scarcity of N in soil downregulates the expression of several CW genes in TOR-inhibited *Mallus hupehensis* plants (Li et al., 2022), placing a role for TOR mediating N metabolism and plant CW building. CW modulation is also a category found to be upregulated in plants

recovering from heat stress under glucose supplementation. Given that the TOR pathway is needed for plant recovery after heat stress, it is possible that by targeting histone methylation through ATX1, TOR influences CW responses to enable cell recovery to high temperatures (Sharma et al., 2022). Coinciding with sugar deprivation responses, KIN10, a member of the SnRK1 group, triggers reprograming of CW machinery, especially loosening and disassembly (Baena-González et al., 2007). CW hydrolysis is stimulated under dark or sugar starvation, a condition opposite of an active TOR pathway, providing an alternative energy source for the deprived cell (Baena-González and Sheen, 2008).

The plant primary CW has a compensatory mechanism; when disturbed by genetic manipulation of its components, the cell can overcome this disturbance and accomplish close-to-normal growth, despite biochemical and structural alterations (Voxeur and Hofte, 2016). This mechanism is named the CW integrity system in plant primary CWs and leaves little space for the primary CW genetic manipulation or the discovery of regulatory components. However, secondary CWs do not seem to possess such a mechanism (Faria-Blanc et al., 2018). In *S. cerevisiae*, the TORC2 impacts the CW signaling by upstream regulating the Slt2 MAPK pathway, which controls Rho1, a small G protein (Levin, 2005). In another eukaryote, the human pathogenic fungus *Candida albicans*, the TOR pathway was also correlated with the small G protein Rhb1. Rhb1 is involved with Mkc1 MAP kinase linked to the CW integrity signaling (Tsao et al., 2009), possibly acting upstream from the TORC2 (Uritani et al., 2006). In plants, evidence is lacking to connect the TOR signaling with sensing the CW disturbances and integrating responses associated with the CW integrity pathway.

5. The connection between TOR and hormonal pathways modulates cell elongation

In addition to environmental influence, plant growth relies on internal cues that control gene expression. These endogenous signals involve hormonal regulation, conducted majorly by the plant phytohormones, such as auxin, cytokinin, gibberellins abscisic acid, ethylene, brassinosteroids, and jasmonic acid (Gray, 2004). Genes that were differentially methylated under TOR inhibition were assigned to distinct plant hormonal pathways (Zhu et al., 2020). Auxin is the plant hormone with the most crucial link with the TOR signaling pathway. Besides being a TORC activator (Schepetilnikov et al., 2013), this hormone promotes the phosphorylation of the TOR target ribosomal protein S6 (S6) (Turck et al., 2004), while TOR contributes to auxin signaling (Schepetilnikov et al., 2013; Deng et al., 2016; Pu et al., 2017). Cell elongation can be modulated by the joint activity of TOR and auxin in the expression and activation of EXPs. In *raptorb* Arabidopsis, reduced cell size is suggested to be due to FER-mediated induction of Rho-related GTPase of Plants2 (ROP2) (Salem et al., 2018), a target for TOR activation and signaling through auxin (Li et al., 2017; Schepetilnikov et al., 2017). Raptor is the TORC regulatory component responsible for stabilizing the complex and substrate requirement. Besides cell elongation, ROP2 is thought to impact TORC-induced cell proliferation, as it phosphorylates the transcription factors E2Fa and b (Li et al., 2017). It remains to be explored how both cell elongation and proliferation processes are integrated in TORC-mediated pathways and if they are environment- or substrate(glucose)- dependent. Moreover, the auxin efflux facilitator PIN2 is phosphorylated by TOR in plants supplemented with glucose, contributing to the distribution of this hormone and enabling cell elongation (Yuan et al., 2020).

Cytokinins can increase (Turck et al., 2004) or decrease (Marash et al., 2023) TOR activity depending on the condition. TOR is repressed by cytokinin to promote immunity, while gibberellin activates TORC and balances plant growth and defense (Marash et al., 2023). *Triticum aestivum* TOR is promoted by gibberellin (Alybayev et al., 2023), and the cell elongation induction by the improved wall extensibility caused by this hormone (Keyes et al., 1990) establishes a second link between hormonal pathways and TOR-mediated cell expansion.

When grown in the dark, seedlings develop etiolated hypocotyls derived from the overstimulated cell elongation. This skotomorphogenesis process is mediated by sugar and TOR signaling that target the brassinosteroid pathway to induce cell expansion enzymes, such as EXPs (Zhang et al., 2016). Overlapping pathways in Arabidopsis mutants with impaired synthesis of brassinosteroid and *raptor1b* are reduced callose-related transcripts, besides lower protein abundance of expansins B and other few enzymes for CW biosynthesis and remodeling (Montes et al., 2022). CW deposition, strengthening, and hydrolysis could be points of convergence of the plant TORC and this hormone, which needs further investigation.

Both TOR (Kravchenko et al., 2015) and its antagonist, SnRK1 (Jossier et al., 2009), can interfere with abscisic acid (ABA) signaling in plants. ABA controls normal lignification and secondary CW deposition (Liu et al., 2020), a suggested strategy to couple with drought stress. The plant hormones salicylic acid (SA) and jasmonic acid (JA) act primarily on plant immunity. The tradeoff displayed by plant growth and defense has been extensively studied, and TOR research seems to corroborate this connection. While promoting growth, endogenous rice TOR antagonizes SA and JA signaling pathways (De Vleesschauwer et al., 2018). As JA reduces lignin deposition and secondary CW thickening (Zhao et al., 2023), SA up-regulates CW polysaccharide synthesis (Jia et al., 2021), TOR inhibition increases the content of lignin precursors (Ren et al., 2012; Caldana et al., 2013; Xiong et al., 2013; da Silva et al., 2021), and reduces ABA levels (Kravchenko et al., 2015), it remains to be explored how this kinase and the hormones SA, JA and ABA may act synergistically to affect secondary CW formation in normal and stressed conditions.

TOR negatively regulates ethylene biosynthesis by interacting with a downstream target, TAP46, and 1-aminocy-clopropane-1-carboxylate synthases (Zhuo et al., 2020). Likewise, the ethylene signaling pathway component, EIN2, is phosphorylated by glucose-TOR, which prevents its nuclear localization. In the nucleus, EIN2 suppresses several genes commonly induced by glucose-TOR, including a myriad of CW genes (Fu et al., 2021). This strong interplay between the TOR signaling and hormonal pathways can lead to cell elongation through direct or indirect transcriptional, translational, and post-translational control.

6. Conclusion and prospects

The TOR pathway impacts all aspects of plant growth: cell division, expansion, and biomass incorporation. Fig. 1 illustrates and summarizes the leading players mentioned to be involved in TOR-mediated CW regulation. The influence of TOR in both C status (Xiong et al., 2013) and the biological clock (Urrea-Castellanos et al., 2022) places this metabolic hub as a relevant candidate that could explain the mechanistic behind how the CW extensibility and carbohydrates incorporation impacts the adjustments in growth under different conditions. TOR repression largely influences a plethora of CW genes and proteins. So far, we cannot attribute these changes to a single controller or transcription factor downstream of the Complex.

As a kinase, TOR-mediated CW modulation is expected to be performed mainly by protein-protein interaction via phosphorylation of protein targets. However, we could not find CW-related proteins in LST8 and Raptor1B interactome and dedicated phosphoproteome (van Leene et al., 2019). Immunoprecipitation and identification of the TORC proteins by mass spectrometry are not performed by trivial protocols. Moreover, proteins localized at the CW or around this structure are not commonly recovered by total protein extraction because the CW and organelles membranes are soon discarded (Feiz et al., 2006). In addition, besides TORC2 localization near the PM (Sturgill et al., 2008), plants TORC has not been localized near the CW. It is more probable that the TOR control over the CW is mediated by cytosolic or nuclear upstream modulators.

There are missing links among nutrients and energy inputs, C assimilation, and partition into the cell organic compounds. The TOR-

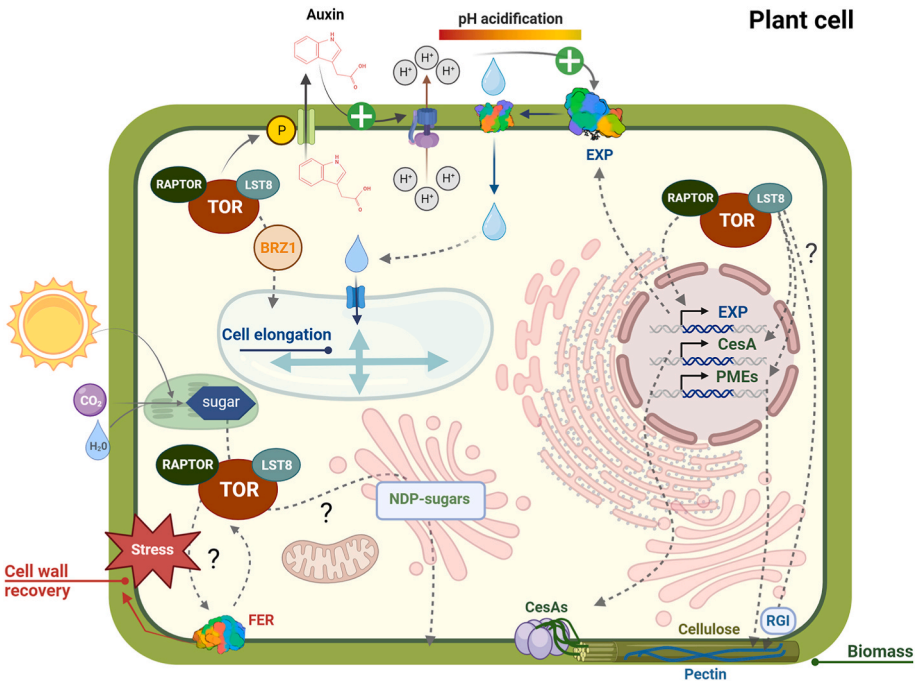

Fig. 1. Illustration of the leading players discussed to be involved in TOR interplay with cell wall elongation and biosynthesis. By increasing the expression of EXPs or via the plant hormone brassinosteroid, TOR is suggested to facilitate water entrance mediated by auxin, activating cell expansion. Photosynthesis produces sugars sensed by TOR, possibly impacting the NDP-sugars that are CW polysaccharide precursors. TOR can also influence CW recovery from stresses by processes mediated by FER. Lastly, TOR can also induce the expression of CesAs and PMEs acting on cellulose and pectin deposition, respectively, and resulting in biomass accumulation. + indicates activation, arrows indicate consecutive events and dotted arrows suggest indirect or unclear events. The cell, organelles, and molecules are not on scale. Created with BioRender.com.

mediated sensing and integration of these signals into expansive growth and biomass involve gene programs, protein, and metabolite signaling. The investigation of the mechanisms behind the C partition into cellulose and other polymers that constitute the CW can establish how the TOR pathway conveys external signals into plant growth.

CRediT authorship contribution statement

Maria Juliana Calderan-Rodrigues: Writing – review & editing, Writing – original draft, Supervision, Data curation, Conceptualization. **Camila Caldana:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

This work was supported by the Max Planck Society.

List of abbreviations

ADGP polygalacturonase
CW cell walls
CesA cellulose synthase
EXP expansin
FER FERONIA
GH glycosyl hydrolases
JA jasmonic acid
LST8 Lethal with SEC13 protein 8
NDP-sugar nucleoside-diphosphate sugars
PLL pectate lyases-like
PM plasma membrane
PME pectinesterases/pectin methylesterases
RAPTOR Regulatory-Associated Protein of TOR
RGI Rhamnogalacturonan I
ROP2 Rho-related GTPase of Plants2
SnRK1 Sucrose non-fermenting-related kinase 1
SP structural Protein
TOR Target of rapamycin
TORC TOR Complex
XTH Xyloglucanendotransglucosylase/Hydrolases

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