Short title: TOR signaling in response to plant stress

Target of Rapamycin Signaling in Plant Stress Responses

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One-sentence summary: Recent significant advances allow a more complete understanding of TOR's many functions in plant responses to different nutrient deficiencies and abiotic stresses.

Author contributions:

L.F. analyzed the phosphoproteomic data. L.F., P.W. and Y.X. wrote the manuscript.

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Abstract

Target of Rapamycin (TOR) is an atypical serine/threonine protein kinase that is evolutionally conserved among yeasts, plants, and mammals. In plants, TOR signaling functions as a central hub to integrate different kinds of nutrient, energy, hormone, and environmental signals. TOR thereby orchestrates every stage of plant life, from embryogenesis, meristem activation, root and leaf growth to flowering, senescence, and life span determination. Besides its essential role in the control of plant growth and development, recent research has also shed light on its multifaceted roles in plant environmental stress responses. Here, we review recent findings on the involvement of TOR signaling in plant adaptation to nutrient deficiency and various abiotic stresses. We also discuss the mechanisms underlying how plants cope with such unfavorable conditions via TOR-ABA crosstalk and TOR-mediated autophagy, both of which play crucial roles in plant stress responses. Until now, little was known about the upstream regulators and downstream effectors of TOR in plant stress responses. We propose that the SnRKs-TOR axis plays a role in sensing various stress signals, and predict the key downstream effectors based on recent high-throughput proteomic analyses.
Introduction

Plants are challenged throughout their life cycles by various types of environmental stresses, such as nutrient deficiencies, extreme temperatures, drought, and high salinity. To deal with such unfavorable growth conditions, plants have evolved elaborate and efficient stress perception and signal transduction systems. Furthermore, plant stress responses are always accompanied by extensive transcriptional, translational, and metabolic changes to redirect energy and nutrient resources for stress adaptation. Increasing evidence has revealed an essential role of TOR (target of rapamycin), a master regulator of energy maintenance and metabolic homeostasis in all eukaryotic organisms, in plant stress responses and stress adaptation.

TOR was first identified in budding yeast through genetic mutant screens for resistance to rapamycin, a chemical molecule produced by the bacterium *Streptomyces hygroscopicus* (Heitman et al., 1991). Subsequent studies identified TOR genes in almost all eukaryotes, including animals and plants (Kunz et al., 1993; Menand et al., 2002; Sabatini et al., 1994). TOR is an atypical serine/threonine protein kinase, resembling phosphatidylinositol lipid kinases, that is both structurally and functionally conserved among all eukaryotes (Xiong and Sheen, 2014). TOR exerts its function in complex forms. In mammals and yeasts, TOR forms at least two structurally and functionally distinct protein complexes (TORCs) with both shared (LST8) and distinct (Raptor in TORC1, and Rictor, mSIN1 in TORC2) TOR interacting partners. In plants, the precise compositions of the TOR kinase complexes have not been characterized. *TOR, Raptor,* and *LST8* (but neither *Rictor* nor *mSIN1*)
gene orthologues could be identified in all available plant genomes, indicating that only classical TORC1 exists in plants. One copy of $TOR$, two copies of $Raptor$ ($RaptorA$, $RaptorB$), and two copies of $LST8$ ($LST8-1$, $LST8-2$) exist in the Arabidopsis ($Arabidopsis thaliana$) genome, although $LST8-2$ might be a pseudogene due to its undetectable transcript level (Anderson et al., 2005; Deprost et al., 2005; Moreau et al., 2012). Gain of- and loss of- function analyses have revealed that $Arabidopsis$ TOR, Raptor, and LST8 are all essential for regulating multiple aspects of plant growth, development and stress adaptation (Anderson et al., 2005; Deprost et al., 2005; Moreau et al., 2012; Ren et al., 2011; Xiong et al., 2013). It is worth noting that, based on these functional analyses, TOR appears to regulate a much broader spectrum of biological functions than Raptor or LST8. For example, the null $tor$ mutant is embryo lethal, while the $raptora/b$ double mutant exhibits normal embryonic development but is arrested during seedling development, and the $lst8-1$ mutant only exhibits modest dwarf growth and early senescence phenotypes. Interestingly, although most eukaryotes have only one copy of the $TOR$ gene, two $TOR$ genes have been identified in three polyploids ($Glycine max$, $Populus trichocarpa$, and $Brassica rapa$) and 4 $TOR$ genes have been identified in allotetraploid cotton ($Gossypium hirsutum$; Song et al., 2018). Sessile plants might possess unique TOR complexes with plant-specific components that serve as a functional equivalent of TORC2 or may even have plant-specialized functions for adaptation to constant environmental challenges.

In plants, TOR functions as a central hub that integrates signals, including
nutrient, hormone, light, energy, and other environmental cues to orchestrate growth and development. TOR modulates a myriad of cellular activities, including cell division, cell expansion, transcription, mRNA translation, ribosome biogenesis, metabolism, nutrient assimilation and transport, and signaling via multiple partners and effectors in complex signaling networks, which have been extensively discussed in several excellent recent reviews (Jamsheer K et al., 2019; Ryabova et al., 2019; Shi et al., 2018; Wu et al., 2019). Besides its essential role in the control of plant growth and development, recent research also suggests an indispensable role for TOR in plant environmental stress responses. Plants with TOR dysfunctions behave as if they are stressed, even in the absence of a stressor. Transcriptome and metabolomics analyses in lst8-1 and the conditionally inducible tor-es, amiR-tor mutant revealed a broad regulation of plant stress- and autophagy-related genes, and diverse plant metabolic pathways modulating myo-inositol, raffinose, and galactinol, which usually accumulate under stress conditions such as high light, nutrient starvation, cold, drought, and high salt (Caldana et al., 2013; Moreau et al., 2012; Xiong et al., 2013). Down-regulated TOR signaling by chemical inhibitor AZD-8055 also activates genes involved in stress hormone (e.g., ethylene, jasmonic acid (JA), and abscisic acid (ABA)) signaling pathways (Dong et al., 2015). Intriguingly, modulating TOR expression can cause either stress-sensitive or stress-tolerant phenotypes depending on the type of stress encountered, further supporting the multifaceted roles of TOR in plant responses to abiotic stress (Bakshi et al., 2017; Deprost et al., 2007; Dong et al., 2019; and, Wang et al., 2017). Here, we focus on recent advances that enable a more
thorough understanding of TOR’s many functions in plant responses to different nutrient deficiencies and various abiotic stresses, and discuss potential upstream regulators and downstream effectors of TOR.

TOR Signaling in Nutrient Sensing and Deficiency

Plants obtain different kinds of nutrients from above-ground photosynthesis and below-ground soil nutrient assimilation. The ability to sense, assimilate, transport, and utilize various nutrients between sink and source organs is vital for plant survival and growth. TOR is a core component in plant nutrient sensing and communication networks.

In plants, glucose derived from photosynthesis in leaf sources provides carbon-based energy and building blocks (Li and Sheen, 2016; Sheen, 2014). Depletion of glucose completely blocks the kinase activity of TOR, and increases the expression of sets of autophagy- and protein degradation-related genes, indicating that recycling processes are activated to overcome the nutrient-deficient conditions (Xiong et al., 2013; Xiong and Sheen, 2012). Glucose can quickly reactivate TOR activity via the glycolysis-mitochondria-electron transport chain (ETC) energy relay, as chemical inhibitors targeting the first step of glycolysis and different steps of ETC completely prevent TOR activation by glucose. Thus, sugar-mediated TOR can sense the cellular metabolic and bioenergetic status to manipulate energy signaling in plants. Glucose-activated TOR then phosphorylates and activates transcription factor E2Fa/E2Fb to promote root growth and true leaf formation by enhancing cell division.
activity in the root meristem and shoot apex, respectively (Li et al., 2017; Xiong et al., 2013; Xiong and Sheen, 2012). Interestingly, in the shoot apex, glucose alone is not enough to activate cell proliferation; the Rho-like small GTPase ROP2 was shown to bind to and activate TOR in a synergistic action along with glucose and auxin signaling (Li et al., 2017; Xiong et al., 2013; Xiong and Sheen, 2012). TOR also mediates crosstalk between sugar signaling and brassinosteroid (BR) signaling. Glucose-activated TOR can inhibit autophagy to stabilize BZR1, which is a positive regulator in BR signaling, to promote cell growth in hypocotyls (Zhang et al., 2016).

Sulfur is another important nutrient for plants. Sulfur assimilation begins with \( \text{SO}_4^{2-} \) that is absorbed by sulfate transporters in the roots and transformed into adenosine 5'-phosphosulfate (APS), \( \text{SO}_3^{2-} \), and \( \text{S}^{2-} \), which are catalyzed by ATP sulfurylase (ATPS), APS reductase (APR), and sulfite reductase (SIR), respectively (Jobe et al., 2019). \( \text{S}^{2-} \) then reacts with O-acetylserine (OAS) to produce cysteine, which serves as the donor for either protein synthesis or sulfur-containing compounds including glutathione (GSH) and various glucosinolates. Recently, the relationship between TOR and sulfur signaling has become evident. In the \textit{sir1-1} mutant, which could not produce \( \text{S}^{2-} \), TOR activity is abolished, and glucose content is significantly lower than that in wild-type Arabidopsis (Dong et al., 2017). Interestingly, exogenous supply of glucose or grafting the wild-type shoot onto the \textit{sir1-1} root rescues TOR activity, cell division in root apical meristem, and the growth arrest phenotype in the \textit{sir1-1} mutant (Dong et al., 2017), suggesting that sulfur availability does not affect TOR signaling independently, but acts through glucose energy signaling. Moreover,
reducing glutathione synthesis by inhibiting glutamate-cysteine ligase activity partially restores the dwarf phenotype and increases TOR activity in the sir1-1 mutant, suggesting that reallocation of sulfur flux from GSH biosynthesis to protein translation can promote plant growth via the regulation of TOR (Speiser et al., 2018). In addition, Malinovsky et al (2017) reported that a distinct plant defense-related glucosinolate, 3-hydroxypropylglucosinolate, can function like a TOR inhibitor to block glucose-TOR- promoted root meristem activation and root elongation. Thus, the direction of sulfur flux and its derived metabolites appear to serve key roles in balancing plant growth and stress responses via TOR regulation in response to environmental cues.

Organic nitrogen-containing molecules (amino acids) are key upstream signals for mTOR activation. A very recent study showed that the accumulation of branched-chain amino acids could also up-regulate TOR activity in Arabidopsis, causing reorganization of the actin cytoskeleton and actin-associated endomembranes (Cao et al., 2019). Although amino acid sensors for leucine, arginine, and glutamine have been discovered in mammalian systems in the past decades (Saxton and Sabatini, 2017), no orthologues have been identified in plant genomes. Plants obtain organic nitrogen through nitrogen assimilation. Plants take in nitrate/ammonium from the soil and convert these compounds to glutamine, and then into other amino acids via the glutamine synthetase (GS)/glutamine-2-oxoglutarate aminotransferase (GOGAT) cycle (Krapp, 2015). It has been reported that Arabidopsis seedlings overexpressing TOR are hypersensitive to high nitrate inhibition of root growth (Deprost et al., 2007).
Recent studies showed that TOR is inhibited in nitrogen-deprived seedlings, and that re-supply of either nitrate, ammonium, or amino acids quickly reactivates TOR (Liu et al., 2018). However, nitrogen starvation is often associated with higher level of sugars. It remains to be examined whether inhibition of TOR by nitrogen starvation, like sulfur deprivation, is related to metabolic and energy generation processes, or whether plants have evolved unique nitrogen-sensing systems for TOR activation.

A direct link between other essential inorganic nutrients and TOR is also being established. Couso et al. (2019) reported that in *Chlamydomonas reinhardtii*, phosphorus deprivation negatively affected LST8 protein stability, resulting in a down-regulation of TORC1 activity. Interestingly, in addition to the direct influence of carbon, nitrogen, sulfur, and phosphorus availability on TOR kinase activity, genome-wide transcriptional profiling has revealed that glucose-TOR signaling activates transcription of genes involved in sulfur assimilation and transport including *APS1/3, APK1/2, APR1/2/3, SIR, SULTR1.2/2.2/3.5/4.2*, as well as genes involved in nitrogen assimilation and transport, including *NIA1/2, NIR1, NRT1.1/1.2/1.5/2.2/3.1* (Xiong et al., 2013). Therefore, there is a reciprocal positive feedback regulation loop between glucose, sulfur, and nitrogen signaling, and TOR may function as a central hub that orchestrates nutrient acquisition, shuttling, and communication between above-ground and below-ground tissues (Figure 1).

**TOR Signaling in Abiotic Stresses**

Advancing research has shown that TOR plays multifaceted roles in the plant
response to various kinds of abiotic stress, and may function as either a positive or a negative regulator depending on the type and duration of stress encountered.

Temperature is a major factor in plant metabolism and growth. Wang and coworkers showed that Arabidopsis TOR activity is quickly abolished by cold treatment at time points as early as 10 min, but recovers after 2 hours of treatment (Wang et al., 2017). Furthermore, cold treatment compromises enhanced anthocyanin accumulation in the inducible tor-es mutant under normal temperature, indicating that TOR is likely to be a negative regulator in cold acclimation. Because inhibition of translation is essential for cold tolerance, inactive TOR might decrease translation in plants to prepare them for unfavorable cold conditions (Wang et al., 2017). However, another independent study suggested that TOR seems to positively regulate the plant cold response (Dong et al., 2019). Depletion of AtTHADA (which codes for AtTHADA, the plant protein orthologue of the cold response regulator HsTHADA in human) lowers energy status, decreases TOR activity, and causes growth arrest in Arabidopsis (Dong et al., 2019). Meanwhile, the Atthada mutant and TOR-RNAi (35-7) lines are hypersensitive to cold conditions (Dong et al., 2019). The differences between these studies might be caused by different silencing efficiencies in different TOR-RNAi lines or by different growth conditions, further indicating the complexity and dynamic nature of the TOR-regulated cold response.

In addition to cold stress, TOR is involved in high temperature tolerance. Exogenous application of glucose, overexpression of TOR, and overexpression of \textit{E2Fa} all result in higher heat shock gene expression and seedling survival rates after
recovery from heat stress treatment. Down-regulation of TOR, down-regulation of E2Fa, and treatment with the TOR inhibitor AZD-8055 or Torin1 lead to decreased seedling survival (Sharma et al., 2019). HIKESHI-LIKE PROTEIN1 (AtHLP1) is an orthologue of HsHikeshi, which imports HSP70 into the nucleus to promote thermo-tolerance in human (Koizumi et al., 2014; Kose et al., 2012; Sharma et al., 2019). Glucose-TOR-activated E2Fa directly binds to the promoter of AtHLP1 to activate AtHLP1. AtHLP1 binds directly to the promoters of many heat shock genes, which in turn leads to histone acetylation and H3K4me3 accumulation to activate and maintain thermo-memory, eventually enhancing thermo-tolerance (Sharma et al., 2019). Interestingly, proHLP1::GUS exhibits strong GUS induction in the proliferation zone of the shoot apex after 24 hours of heat stress recovery in the presence of glucose. These results suggest that cell proliferation in the shoot apex must be coordinated with internal and external cues to maintain growth and survival, and is mediated by glucose-TOR energy signaling.

TOR positively regulates the plant response to drought and osmotic stresses. In Arabidopsis, TOR overexpression lines have a longer primary root than control lines exposed to a high concentration of potassium chloride (Deprost et al., 2007). Ectopic expression of Arabidopsis TOR gene in Oryza indica rice enhances water-use efficiency (WUE), growth, and yield under water-limiting conditions (Bakshi et al., 2017). These transgenic rice lines also show seed germination insensitivity to ABA treatment (Bakshi et al., 2017, 2018). These observations suggest that constitutive TOR expression might alleviate the effect of drought or osmotic stress on plant
In contrast, TOR negatively regulates the plant response to oxidative stress and DNA/RNA damage. Maf1 is a conserved repressor of RNA polymerase III (Pol III), which is responsible for synthesizing small RNAs, 5S rRNA, and tRNAs. Maf1’s activity is mediated by phosphorylation/dephosphorylation, and dephosphorylation of Maf1 promotes its repressor activity. Both oxidative stress or DNA/RNA damage and TOR silencing stimulate Maf1 dephosphorylation (Ahn et al., 2018). It is very likely that these stresses inhibit TOR activity to enhance the dephosphorylation of Maf1 and activate its repressor function. In this way, plants may slow down protein synthesis and cell growth or division to overcome these environmental stresses.

Crosstalk between TOR Signaling and ABA Signaling

The phytohormone ABA plays a key role in integrating a wide range of stress signals and controlling downstream stress responses. Upon stress, ABA accumulates rapidly and binds to its intracellular PYR/PYL/RCAR receptors. The ABA-receptor complex binds to and inhibits the clade A PP2C protein phosphatases. PP2C inhibition releases the activity of Snf1-related protein kinase 2s (SnRK2s), which phosphorylate downstream targets to mediate protective responses such as stomatal closure and the expression of ABA-responsive genes (Chen et al., 2019).

TOR signaling has been found to regulate ABA biosynthesis and distribution. ABA content is decreased in raptorb seedlings, lst8-1 seedlings, and seedlings treated with the TOR inhibitor AZD-8055 (Kravchenko et al., 2015). Some genes that encode
critical enzymes in ABA biosynthesis, such as \textit{NEDC3} and \textit{AOO3}, show decreased expression in the \textit{raptorb} mutant (Kravchenko et al., 2015). However, the ABA content of \textit{raptorb} mutant seeds is elevated (Salem et al., 2017), suggesting that TOR may also be involved in the distribution of ABA.

TOR signaling and ABA signaling converge on two Protein Phosphatase 2A (PP2A)-associated proteins, TAP46 and TIP41 (Ahn et al., 2011; Hu et al., 2014; Punzo et al., 2018a; Punzo et al., 2018b). TAP46 is directly phosphorylated by TOR kinase, and functions as a positive effector in TOR signaling (Ahn et al., 2011). Meanwhile, TAP46 negatively regulates the phosphatase activity of PP2A, prevents it from dephosphorylating ABI5 (thereby stabilizes ABI5), and finally enhances ABA sensitivity in plants (Hu et al., 2014). TIP41 interacts with the catalytic subunit of PP2A and negatively regulates ABA sensitivity (Punzo et al., 2018a; Punzo et al., 2018b). TIP41 is also involved in TOR signaling. \textit{tip41} mutants display growth retardation, similar to the phenotype caused by \textit{TOR} silencing, and are hypersensitive to the TOR inhibitor AZD-8055 (Punzo et al., 2018a; Punzo et al., 2018b). Recent large-scale genetic screens for insensitivity to the TOR inhibitor AZD-8055 identified two important mediators of ABA signaling, \textit{YAK1} and \textit{ABI4}, as the key downstream regulators of TOR signaling to control root growth, meristem activation, and seed germination (Barrada et al., 2019; Kim et al., 2016; Li et al., 2015).

Upon sensing environmental stresses, plants usually transiently sacrifice growth and activate protective stress responses. Recently, a reciprocal negative crosstalk between TOR and ABA signaling has been shown to regulate such a trade-off between
plant growth and stress adaptation (Figure 2) (Wang et al., 2018). In unstressed Arabidopsis, TOR phosphorylates ABA receptors at a highly conserved serine, corresponding to Ser119 in PYL1, to compromise ABA signaling by abolishing PYL binding activity to ABA, thereby inhibiting PP2C phosphatase. Expression of phosphor-mimicking PYL1^{S119D} in multiple ABA receptor mutants does not complement the ABA-insensitive phenotype (Wang et al., 2018). raptorB and lst8-1 mutants display hypersensitivity to exogenous ABA application (Wang et al., 2018; Salem et al., 2017). On the other hand, ABA also antagonizes TOR signaling. ABA-activated SnRK2s directly interact and phosphorylate RaptorB. This phosphorylation triggers the disassociation of RaptorB from the TOR complex, and thereby inhibits TOR’s kinase activity (Wang et al., 2018). Therefore, under nutrient-rich conditions, active TOR inhibits ABA signaling to direct resources to growth, whereas under stress conditions, ABA signaling is activated, and ABA-activated SnRK2 inhibits TOR activity to sacrifice growth for survival during stress. Importantly, the serine residue corresponding to Ser119 in PYL1 is highly conserved across all 121 PYLs from 12 different plant species, suggesting that this phosphor-regulatory feedback loop is a conserved mechanism that land plants utilize to optimize the balance of growth and stress responses. Strikingly, several PYLs (PYL5 to PYL12) in Arabidopsis can bind to and inhibit PP2Cs even in the absence of ABA (Fujii and Zhu, 2012; Hao et al., 2011), while phosphor-mimicking mutation of TOR phosphorylation site within PYL10 abolishes this ABA-independent interaction with PP2Cs (Wang et al., 2018). Therefore, TOR might also inhibit the
activation of the ABA-independent PYLs under non-stress conditions to promote
growth and development.

**TOR Negatively Regulates Autophagy**

Autophagy is a process in which harmful or unwanted cellular components are
delivered into lytic vacuoles to be recycled (Signorelli et al., 2019; Zhuang et al.,
2018). Autophagy promotes plant resistance to nutrient deficiency, salt stress, drought
stress, oxidative stress, and endoplasmic reticulum (ER) stress (Pu et al., 2017a). TOR
is one of the key negative regulators of autophagy. Down-regulation of TOR
expression or kinase activity leads to constitutive activation of autophagy (Liu and
Bassham, 2010). However, TOR antagonizes some, but not all, of the abiotic
stress-triggered autophagy process (Liu and Bassham, 2010; Pu et al., 2017a; Pu et al.,
2017b; Soto-burgos and Bassham, 2017). Nutrient deficiency, salt stress, and drought
stress all induce autophagy through TOR kinase, as overexpression of TOR under
these condition significantly reduces the autophagy caused by these stresses (Pu et al.,
2017a; Pu et al., 2017b; Soto-burgos and Bassham, 2017). However, oxidative stress
and ER stress trigger autophagy in a TOR-independent manner (Pu et al., 2017a; Pu et
al., 2017b; Soto-burgos and Bassham, 2017).

The autophagy related 1 (ATG1)/ATG13/ATG17 kinase complex plays an
essential role in the onset of autophagy, and is the direct TORC1 substrate in
mammals and yeast. In Arabidopsis, there are three ATG1 and two ATG13
homologues; their roles in the regulation of autophagy in response to nutrient
starvation have been uncovered (Suttangkakul et al., 2011). Son et al. (2018) found that ATG13 contains a motif that could be phosphorylated by TOR kinase, and that deletion of this TOR-recognized motif in ATG13 enhances autophagy in Arabidopsis protoplasts. Recent high-throughput phosphoproteomics analysis using Arabidopsis suspension cell culture also revealed that ATG1s and ATG13s are direct TOR substrates. These studies reinforce that TOR-regulated phosphorylation of the ATG1/ATG13/ATG17 complex is essential for inhibiting autophagy in plants.

The upstream signals of TOR signaling also regulate autophagy. As a growth hormone, auxin stimulates TOR activity through a physical interaction between TOR and auxin-activated ROP2 to promote the activation of shoot apex cell proliferation (Li et al., 2017; Schepetilnikov et al., 2013). Interestingly, auxin also acts upstream of TOR in the regulation of autophagy. As mentioned above, nutrient deficiency, salt stress, and drought stress induce autophagy via TOR signaling, but the addition of auxin prevents the autophagy phenomenon induced by these stress conditions (Pu et al., 2017a). Meanwhile, auxin has no effect on oxidative or ER stress-induced autophagy, indicating that auxin specifically affects TOR-dependent autophagy (Pu et al., 2017a).

Upstream Regulators of Plant TOR-Stress Signaling

In contrast with the significant progress made in discovering the various molecular functions of TOR signaling in plant stress responses, the upstream regulators of TOR remain poorly understood. Plants possess a family of unique Rho-like small GTPases
with 11 members that function as central hubs in signaling networks (Nagawa et al., 2010). As mentioned above, ROP2/3/6 has been shown to bind to and activate TOR stimulated by auxin signaling (Li et al., 2017; Schepetilnikov et al., 2013). Whether other ROPs are involved in stress sensing and regulation in TOR signaling remains a worthwhile question to be studied.

SnRKs are a group of kinases that play vital roles in a wide range of plant stress responses. Plants contain three SnRK families: SnRK1s, SnRK2s, and SnRK3s (Halford and Hey, 2009). Increasing evidence suggests that part of the SnRK-regulated stress response is achieved by the SnRKs-TOR module.

SnRK1 complex functions as a conserved energy sensor, which is activated under low energy conditions and is repressed under energy-rich conditions. In yeast and animal cells, nutrient starvations stimulate SNF1/AMPK, which repress TOR activity by phosphorylating Raptor proteins to suppresses cell growth and biosynthetic processes (Gwinn et al. 2008). In Arabidopsis, KIN10/11 protein kinases provide catalytic activities in the SnRK1 complex, and act antagonistically to TOR in the regulation of convergent primary sugar responsive genes (Baena-gonzalez et al., 2007; Li et al., 2016; Xiong et al., 2013), indicating that KIN10/11 functions upstream of TOR to regulate energy starvation processes. Furthermore, it was reported that KIN10 interacts with and phosphorylates Raptor in the TOR complex, providing a biochemical basis for the SnRK1-TOR regulation module (Nukarinen et al., 2016). Notably, KIN10 also functions upstream of TOR to activate autophagy (Pu et al., 2017b; Soto-burgos and Bassham, 2017).
The SnRK2s are a group of plant-specific serine/threonine kinases with 10 members. SnRK2.2, 2.3, and 2.6 are key regulator in ABA signaling, where all the 10 members are essential for osmotic stress responses (Zhu, 2016). As discussed above, ABA-dependent SnRK2.6 phosphorylates RaptorB and dissociates it from the TOR complex (Figure 2). In this way, SnRK2s shut down TOR-promoted growth and enhance stress adaptation responses (Wang et al., 2018). Osmotic stresses also repress TOR activity (Wang et al., 2018), and PYR1/PYLs/RCARs could interact with SnRK2s to inhibit activation of SnRK2s upon osmotic stress condition (Zhao et al., 2018). Whether TOR phosphorylation of PYLs regulates osmotic stress-induced SnRK2 activation or vice versa is not known yet.

SnRK3 is also known as CIPK [CBL (Calcineurin B-like protein)-interacting protein kinase] (Manik et al., 2015). Arabidopsis has 26 CIPKs in total (Kolukisaoglu et al., 2004). The majority of stresses trigger rapid, transient Ca\textsuperscript{2+} signatures; and consequently, as a Ca\textsuperscript{2+} sensor, the CBL-CIPK module participates broadly in various kinds of stress responses, especially in ion homeostasis (Liu et al., 2000; Sardar et al., 2017; Zhu, 2016). Interestingly, the expression of SnRK3.24 (CIPK5) is down-regulated after long-term TOR inhibition (Dong et al., 2015), and the cipk5 mutant exhibits decreased TOR activity (Meteignier et al., 2017), suggesting that SnRK3s might, like KIN10 and SnRK2s, phosphorylate Raptor to regulate TOR activity and signaling.

### Downstream Effectors of Plant TOR-Stress Signaling
TOR is a core merging point in the plant stress signaling network. However, until now, only a very limited number of TOR substrates or TOR-regulated proteins have been identified. Very recently, Van Leene et al. (2019) performed quantitative phosphoproteomics and interactome analysis using Arabidopsis cell cultures with or without AZD8055 treatment. A total of 83 TOR-regulated phosphoproteins and 215 proteins interacting with the TOR complex (TOR, LST8-1, RaptorA, or RaptorB) were identified (Van Leene et al., 2019). Some of these proteins may be direct TOR substrates. We performed a literature search to examine the biological functions of these proteins, and found that 19% of TOR-regulated phosphoproteins and 20% of TOR complex interacting proteins participate in various stress responses (Table 1). These TOR signaling-related targets include VIP1 (VirE2-Interacting Protein1) involved in osmotic and sulphate deprivation response, GCN5 (General Control Nonderepressible5) affecting histone acetylation under cold and salt stress, ATG1/13 for autophagy induction, and LARPI (La-related protein1) involved in the heat stress-triggered mRNA degradation process (Andrea et al., 2009; Merret et al., 2013; Qi et al. 2017; Son et al., 2018; Zheng et al., 2018). These putative TOR substrates provide valuable directions for future studies of TOR-regulated stress responses.

Conclusion

In the last decade, our knowledge of plant TOR signaling has increased significantly. It is now clear that TOR acts as a master regulator to sense and transduce nutrient, energetic, hormonal, metabolic, and environmental stress inputs into physiological,
molecular, and developmental responses for growth and stress adaptation. Despite the
great wealth of information that has become available, several questions still remain
to be answered, and many others are emerging (see Outstanding Questions). In
addition to its well known roles in regulation of protein translation, it will be fruitful to
dissect how TOR signaling represses a vast spectrum of primary target gene pathways
in stress and immune responses. As a protein kinase, the phosphorylation of Thr449 in
the TOR-substrate protein ribosomal S6 kinase 1 (S6K1) is used as a conserved
indicator of endogenous TOR activity. Developing tissue-specific and
fluorescence-visualized TOR kinase activity markers will help to quantitatively
measure TOR activity and specific signaling output in different organs, e.g. sink and
source tissues, thereby facilitating a more accurate interpretation of the different or
even opposite phenotypes when TOR signaling is perturbed under various
environmental conditions.

**Figure legends**

**Figure 1.** TOR signaling networks mediate nutrient inter-organ dialogues to
drive plant growth. Plant obtain carbon, nitrogen, sulfur, phosphate, and other
micronutrients from above-ground photosynthesis and below-ground soil nutrient
assimilation. There is a reciprocal positive feedback regulation loop between glucose,
sulfur, and nitrogen signaling, and TOR functions as a central hub that orchestrates
nutrient acquisition, shuttling, and communication between inter-organ coordination.
APS: adenosine 5'-phosphosulfate; APR: APS reductase; SIR: sulfite reductase; NIA: nitrate reductase; NIR: nitrite reductase; NRT: nitrate transporter; TPS: trehalose-6-phosphate synthase; SWEET: sucrose transporter.

Figure 2. A Tai-Chi model of the phospho-reciprocal regulation of the TOR kinase and ABA signaling to balance plant growth and stress response. Under growth-promoting conditions, active TOR phosphorylates ABA receptors PYR/PYLs to inhibit ABA signaling, and directs resources toward growth; under stress conditions, ABA-activated SnRK2s phosphorylate Raptor to decrease TOR activity, and sacrifice growth for survival during stress.

Table 1. TOR-regulated stress-related proteins

| Protein | AGI No. | Related plant stress responses                                                                 | Methods             |
|---------|---------|-------------------------------------------------------------------------------------------------|---------------------|
| VIP1    | At1g43700 | Wound, cold, heavy metal, salt, osmotic, oxidative and mechanical stress, sulfur deficiency (Andrea et al., 2009; Tsugama et al., 2012; Tsugama et al., 2018; Wu et al., 2010) | Phosphoproteomics  |
| OZF1    | At2g19810 | Sugar and nitrogen deficiency, oxidative, drought, salt and osmotic stress (Contento et al., 2004; Ding et al., 2013; Lee et al., 2012; Ping et al., 2011; Peng et al., 2007) | Phosphoproteomics  |
| ATG1c   | At2g37840 | Autophagy-related (Qi et al., 2017)                                                              | Phosphoproteomics  |
| BAM1    | At3g23920 | Drought, osmotic, salt and heat stress (Liu et al., 2019; Monroe et al., 2014; Prasch et al., 2015; Simpson et al., 2003) | Phosphoproteomics  |
| At3g26730 | At3g26730 | ABA-related (Bang et al., 2008)                                                                | Phosphoproteomics  |
| ATG13   | At3g49590 | Autophagy-related (Son et al., 2018)                                                            | Phosphoproteomics  |
| Gene   | Accession | Description                                                                 | Method       |
|--------|-----------|------------------------------------------------------------------------------|--------------|
| ATG1b  | At3g53930 | Autophagy-related (Qi et al., 2017)                                          | Phosphoproteomics |
| GCN5   | At3g54610 | Cold, salt stress (Pavangadkar et al., 2010; Zheng et al., 2018)             | Phosphoproteomics |
| EIF4G  | At3g60240 | Heat stress (Wu et al., 2013)                                                | Phosphoproteomics |
| ATG1a  | At3g61960 | Autophagy-related (Qi et al., 2017)                                          | Phosphoproteomics |
| ATHD1  | At4g38130 | Salt, drought, heat stress (Ueda et al., 2018)                               | Phosphoproteomics |
| LARP1a | At5g21160 | Heat stress (Merret et al., 2013)                                            | Phosphoproteomics |
| SGS3   | At5g23570 | Heat stress (Liu et al., 2019);                                               | Phosphoproteomics |
| YAK1   | At5g35980 | ABA-related, drought stress (Kim et al., 2016)                               | Phosphoproteomics |
| PLDRP1 | At5g39570 | Drought stress, salt stress (Ufer et al., 2017)                              | Phosphoproteomics |
| PAH2   | At5g42870 | Phosphorus depletion (Nakamura et al., 2009)                                 | Phosphoproteomics |
| AKS2   | At1g05805 | ABA-related (Takahashi et al., 2013)                                         | Interactome   |
| PFD4   | At1g08780 | ABA-related, cold stress (Perearesa et al., 2017; Kurup et al., 2000)        | Interactome   |
| KINβγ  | At1g09020 | Sugar deficiency (Emanuelle et al., 2015)                                    | Interactome   |
| FHY2   | At1g09570 | UV stress, cold stress (Rusaczonek et al., 2015)                             | Interactome   |
| HOP1   | At1g12270 | Heat stress (Fernandez-bautista et al., 2018)                               | Interactome   |
| HSP70B | At1g16030 | Heat stress (Sung et al., 2001)                                              | Interactome   |
| CAT1   | At1g20630 | Drought (Hsieh et al., 2002; Xing et al., 2008)                             | Interactome   |
| CPK11  | At1g35670 | ABA-related (Zhu et al., 2007)                                               | Interactome   |
| TUA2   | At1g50010 | Wounding, osmotic stress, cold stress (Testerink et al., 2004)               | Interactome   |
| FYPP1  | At1g50370 | ABA-related (Dai et al., 2013)                                               | Interactome   |
| MKK4   | At1g51660 | Wounding, osmotic stress (Li et al., 2018)                                   | Interactome   |
| CPN60B | At1g55490 | Cold stress (Goulas et al., 2006)                                            | Interactome   |
| PP2A-1 | At1g59830 | ABA-related (Punzo et al., 2018b)                                            | Interactome   |
| HOP2   | At1g62740 | Heat stress (Fernandez-bautista et al., 2018)                               | Interactome   |
| PP2A   | At1g69960 | ABA-related, salt stress (Hu et al., 2017)                                   | Interactome   |
| PP5    | At2g42810 | Heat stress (Park et al., 2011)                                              | Interactome   |
| KIN10  | At3g01090 | Autophagy-related, ABA-related, low energy, carbon and phosphorus deficiency (Hamasaki et al., 2019) | Interactome   |
| Gene/Protein | Accession Number | Stress/Condition | Reference(s) |
|-------------|------------------|------------------|--------------|
| S6K1        | At3g08730        | Cold, salt and osmotic stress (Mahfouz et al., 2006) | Interactome |
| HSP70       | At3g09440        | Cold, heat stress (Sharma et al., 2006) | Interactome |
| 2CPA        | At3g11630        | Cold, oxidative stress (Goulas et al., 2006; Juszczak et al., 2016; Pulido et al., 2010) | Interactome |
| HSC70-4     | At3g12580        | Heat, salt, osmotic and oxidative stress (Monterobarrientos et al., 2010) | Interactome |
| KIN11       | At3g29160        | Sugar deficiency (Baena-gonzalez et al., 2007; Sheen, 2014) | Interactome |
| ATJ3        | At3g44110        | Salt, osmotic stress (Salasmunoz et al., 2016) | Interactome |
| ATG13       | At3g49590        | Autophagy-related (Son et al., 2018) | Interactome |
| ATG1b       | At3g53930        | Autophagy-related (Qi et al., 2017) | Interactome |
| FER3        | At3g56090        | Oxidative stress (Ravet et al., 2009) | Interactome |
| MPK4        | At4g01370        | Salt, heat stress (Andrasi et al., 2019) | Interactome |
| GRXS17      | At4g04950        | Cold, heat, drought stress (Wu et al., 2017) | Interactome |
| TUA6        | At4g14960        | Salt stress (Dinneny et al., 2008) | Interactome |
| ATPDX1      | At5g01410        | Chilling, drought, salt, osmotic and ozone stresses (Denslow et al., 2007) | Interactome |
| HSP70-1     | At5g02500        | Cold, heat, salt, osmotic, heavy metal stress (Lee and Schoffl, 1996; Leng et al., 2017; Zhang et al., 2003) | Interactome |
| UBP12       | At5g06600        | UV stress (Khatheb et al., 2019) | Interactome |
| TSN1        | At5g07350        | Heat, salt stress (Gutierrezbeltran et al., 2015); | Interactome |
| GDH2        | At5g07440        | Salt stress (Jiang et al., 2007) | Interactome |
| ASN3        | At5g10240        | Nitrogen deficiency (Bi et al., 2007) | Interactome |
| GDH1        | At5g18170        | Low oxygen stress (Sarry et al., 2006) | Interactome |
| ATJ2        | At5g22060        | Heat, cold stress (Li et al., 2005) | Interactome |
| PFD5        | At5g23290        | Salt stress (Rodriguez-milla and Salinas, 2009) | Interactome |
| YAK1        | At5g35980        | ABA-related, drought stress (Kim et al., 2016) | Interactome |
| PFD3        | At5g49510        | Salt stress (Rodriguez-milla and Interactome |
Salinas, 2009)

| Gene 1  | Gene 2  | Function                          | Source                                |
|--------|--------|-----------------------------------|---------------------------------------|
| TAP46_2A | At5g53000 | Cold stress (Harris et al., 1999) | Interactome                           |
| ATG101 | At5g66930 | Autophagy-related (Li et al., 2014) | Interactome                           |

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• Glucose-TOR energy signaling regulates cell proliferation in the root and shoot apexes via global transcriptome reprogramming by phosphorylating transcription factors E2Fa,b.
• The direction of sulfur flux and its derived metabolites play a key role in balancing plant growth and stress responses via TOR regulation.
• TOR signaling pathway plays multifaceted roles in response to various abiotic stresses, e.g. temperature, drought, osmotic, oxidative stresses.
• The negative phosphorylation loop between ABA and TOR core signaling precisely balances stress and growth responses to adapt to changing environments.
• Phosphorylation of Raptor by stress-activated protein kinases is a conserved mechanism for the regulation of TOR.
• A systematic phosphoproteomics screen with a targeted protein complex analysis provides a rich dataset to discover TOR signaling components.
OUTSTANDING QUESTIONS

- Do plants possess functional TORC2, or even unique TORC involved in plant stress adaptation or plant specific biological processes, e.g. photosynthesis or nutrient assimilation?
- How are glucose, sulfur, and nitrogen signals sensed by plants to activate TOR? Is nitrogen regulation of TOR independent from energy-related pathways influenced by glucose or sulfur starvation?
- In addition to ABA, auxin, and BR, what other hormones, especially stress hormones (e.g. salicylic acid, jasmonic acid, and ethylene) regulate TOR signaling and how?
- How is TOR able to sense and distinguish diverse upstream signals?
- How is TOR able to specifically control special targets when facing different environments and requirements?
- How is TOR kinase regulated spatiotemporally in different cell or tissue types?
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