Accepted Article

Article type: Invited Expert Review

Received Dec. 3, 2019 Accepted Dec. 16, 2019

Edited by: Zhizhong Gong, China Agricultural University, China

Running title: Multiple functions of abscisic acid in plants

# Abscisic acid dynamics, signaling and functions in plants

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jipb.12899.

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**Abstract**

Abscisic acid (ABA) is an important phytohormone regulating plant growth, development and stress responses. It has an essential role in multiple physiological processes of plants, such as stomatal closure, cuticular wax accumulation, leaf senescence, bud dormancy, seed germination, osmotic regulation and growth inhibition among many others. ABA controls downstream responses to abiotic and biotic environmental changes through both transcriptional and posttranscriptional mechanisms. During the past twenty years, the ABA biosynthesis and many of its signaling pathways have been well characterized. Here we review the dynamics of ABA metabolic pools and signaling that affects many of its physiological functions.

## INTRODUCTION

ABA is the hormone that is usually associated with major plant responses to stress. Pioneering studies by Hemberg found a water and ether soluble growth-inhibiting substance that is critical for the maintenance of bud dormancy in potato and *Fraxinus* (Hemberg 1949a,1949b). This growth inhibitor was isolated in buds of *Acer pseudoplatanus* by Philip Wareing in 1963, and named dormin (Eagles and Wareing 1963). During the same period a substance that controlled abscission of cotton fruits was discovered by Frederick Addicott and named abscisin II (Ohkuma et al. 1963). The Addicott lab found that abscisin II also promotes leaf abscission in cotton seedlings and inhibits indoleacetic acid induced growth of *Avena* coleoptiles. Later, dormin and abscisin II were found to be the same chemical compound and named as abscisic acid (Cornforth et al. 1965; Addicott et al. 1968). Although the abscission-promotion role of ABA was considered by many to be an indirect effect of the elevated level of ethylene (Cracker and Abeles 1969), recent studies have

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demonstrated that ABA promotes leaf senescence and abscission independent of ethylene (Ogawa et al. 2009; Zhao et al. 2016).

Over the past 40 years, the core components of ABA biosynthesis and signaling have been identified through molecular-genetic, biochemical and pharmacological approaches. Genetic screens for *viviparous* mutants in maize and *Arabidopsis*, and for mutants that are insensitive to sugar, salt and ABA during germination lead to the identification of numerous components involved in ABA biosynthesis and signaling. Some of the first identified were the clade A PP2Cs such as ABA Insensitive (ABI) 1 and ABI2, and the core transcription factors ABI3, ABI4 and ABI5 (Koornneef et al. 1984; Giraudat et al. 1992; Finkelstein 1994; Leung et al. 1994; Meyer et al. 1994; McCarty 1995; Leung et al. 1997; Rodriguez et al. 1998; Finkelstein and Lynch 2000; Laby et al. 2000; Gonzalez-Guzman et al. 2002). Biochemical studies of the ABA activation of protein kinases resulted in the identification of AAPK, which is a homolog of the core protein kinases, SnRK2s in *Vicia faba* (Li and Assmann 1996). Due to its high functional redundancy, the ABA receptor Pyrabactin resistance 1 (PYR1) and PYR1-like (PYL) proteins (hereafter referred to as PYLs) were not revealed until 2009 by Sean Cutler and co-workers through chemical genetic screens for mutants that are insensitive to the ABA analog pyrabactin (Park et al. 2009). In the meantime, regulatory components of the ABA receptors (RCARs) were isolated through yeast two-hybrid screens in the Erwin Grill lab (Ma et al. 2009). The identity of the proteins of PYL/RCAR family was also demonstrated by *in vitro* reconstitution of the core ABA signaling pathway (Fujii et al. 2009), and later further confirmed by substantial genetic and structural evidence (Melcher et al. 2009; Miyazono et al. 2009; Nishimura et al. 2009; Santiago et al. 2009a, 2009b; Yin et al. 2009; Gonzalez-Guzman et al. 2012; Zhang et al. 2015; Miao et al. 2018; Zhao et al. 2018).

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Here, we will summarize latest updates on dynamics of ABA level, ABA signaling and its stringent regulation as well as versatile functions in physiological processes.

## METABOLIC CONTROL OF ABA LEVELS

Plants quickly accumulate ABA and in turn activate several stress responses when subjected to abiotic stresses including drought, salt, cold, osmosis and several others. When environments are optimal, ABA is reduced to basal levels which promotes optimal growth. Modulation of ABA levels in tissues and cells is critical for balancing defense and growth processes when plants experience non-optimal environments. ABA levels are controlled by synthesis and degradation, metabolism, (de)conjugation and transport.

### ABA biosynthesis

ABA is a sesquiterpenoid containing 15 carbon atoms. It is synthesized both in plants and some phytopathogenic fungi using two distinct pathways. Phytopathogenic fungi synthesize ABA through the mevalonate pathway with intermediates containing no more than 15 carbon atoms, which is also called the “direct pathway” (Hirai et al. 2000; Izquierdo-Bueno et al. 2018; Takino et al. 2018). Plants synthesize ABA using the carotenoid pathway also called the “indirect pathway”. This is initiated from the cleavage of a $C_{40}$ precursor known as β-carotene (Nambara and Marion-Poll 2005; Arc et al. 2013). It should be noted that β-carotene precursors including isopentenyl pyrophosphate (IPP), farnesyl diphosphate ($C_{15}$), geranylgeranyl diphosphate ($C_{20}$) are also precursors of the phytohormones cytokinins (CK), brassinosteroids (BR), and gibberellins (GA), respectively.

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Genetic screens of *viviparous* mutants in maize have identified several ABA auxotrophic mutants, named *vp2*, *vp5*, *vp7* and *vp9*, which are defective in zeaxanthin synthesis (James 1990). The conversion of zeaxanthin ($C_{40}$) to xanthoxin ($C_{15}$) is carried out in plastids (Figure 1). The *Arabidopsis* loss-of-function mutant, *aba1*, has defective gene for zeaxanthin epoxidase (ZEP) which catalyzes the conversion of zeaxanthin to all-*trans*-violaxanthin via antheraxanthin (Audran et al. 2001). This pathway then bifurcates into two pathways catalyzing all-*trans*-violaxanthin. One pathway requires neoxanthin synthase (NSY) encoded by the *Arabidopsis ABA4* gene and an unknown isomerase, which convert all-*trans*-violaxanthin to 9'-*cis*-neoxanthin through all-*trans*-neoxanthin; in another possible pathway an unknown isomerase catalyzes all-*trans*-neoxanthin to 9'-*cis*-violaxanthin directly (North et al. 2007). Then, 9'-*cis*-neoxanthin and 9'-*cis*-violaxanthin both can be oxidatively cleaved by the 9-*cis*-epoxycarotenoid dioxygenase (NCED) encoded by *VIVIPAROUS14 (VP14*) in maize, resulting in the production of the $C_{15}$ xanthoxin, which can also act as a growth inhibitor (Anstis et al. 1975; Schwartz et al. 1997). In *Arabidopsis*, based on analyzing the sequence and function of homologous genes of *VP14*, *NCED2*, *NCED3*, *NCED5*, *NCED6* and *NCED9* have been identified as participants in a rate-limiting step in ABA biosynthesis, where *NCED3* is perceived as the critical enzyme for ABA synthesis at this point (Iuchi et al. 2001; Tan et al. 2003).

These processes all take place in plastids, and in the cytoplasm, a short-chain alcohol dehydrogenase encoded by *AtABA2/AtGIN1* then converts xanthoxin into abscisic aldehyde which is eventually oxidized to abscisic acid (ABA) by AtABA3, which is an abscisic aldehyde oxidase (AAO3) (Bittner et al. 2001; Cheng et al. 2002). First mutant identified as defective in ABA synthesis were in tomato and called *flacca* and *sitiens*, which are impaired in the oxidation of ABA aldehyde to

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ABA (Tal 1966; TAYLOR et al. 1988). These data not only revealed an intact biosynthesis pathway of ABA, but also showed that ABA synthesis is via an indirect pathway in plants rather than a direct one based on $C_{15}$ isoprenoid synthesis in fungi (Nambara and Marion-Poll 2005).

**ABA metabolism and (de)conjugation**

Plants accumulate ABA rapidly when exposed to many different environmental conditions. The maintenance of a basal level of free ABA consistent with different tissues in different environments is paramount to the appropriate growth and development states of the whole plant. Therefore, catabolism of ABA is also strictly controlled by both ABA conjugation and catalytic hydroxylation. ABA can be glucosylated by a UDP-glucosyltransferase (UGT) encoded by *UGT71C5.* The ABA-glucose ester, ABA-GE is an inactive form of ABA (Liu et al. 2015b). In contrast, *AtBG1* and *AtBG2* encode β-glucosidases that rapidly transform ABA-GE to active ABA which is released from the endoplasmic reticulum and vacuole respectively, when the environment changes (Lee et al. 2006; Xu et al. 2012). The conjugation cycle established by glucosyltransferase and β-glucosidase allows plants to phenotypically adapt to their environment through ABA-mediated responses by activating and inactivating ABA rapidly.

Catabolism of ABA occurs by the conversion from ABA to phaseic acid (PA) which is catalyzed by a cytochrome P450 monooxygenase (P450) encoded by *CYP707As* (Kushiro et al. 2004). PA is then catalyzed to dihydrophaseic acid (DPA) and DPA-4-O-β-D-glucoside (DPAG) by PA reductase (PAR) ABH2 and glycosyltransferase (GT) respectively (Weng et al. 2016). Interestingly, PA has been

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reported to selectively activate a subset of ABA receptor PYLs (Figure 1) (Weng et al. 2016).

**ABA transports**

In addition to ABA metabolism and (de)conjugation, the transports of ABA among cells and organs have global effects on plants. Keiichi Ikegami et al. found that isotope-labeled ABA moves from leaves to roots during water deficits and ABA can accumulate only in leaves when leaves and roots are separately exposed to limiting water (Ikegami et al. 2009). Other studies have confirmed that ABA is synthesized in leaves and then transported to other organs (Zhang et al. 2018a). Thus, transport of ABA between cells, tissues and organs is an important part of the role of ABA in systemic stress responses of the whole plant.

ABA exists naturally in plants as both an anionic form ($ABA^-$) and a protonated form (ABAH). ABAH can diffuse passively through the plasma membrane, and the diffusion of ABA largely declines with alkalization of the cytoplasm which increases during osmotic stresses (Wilkinson and Davies 1997; Karuppanapandian et al. 2017). The active transport of ABA relies on: a) ATP-binding cassette (ABCG) transporters; b) NRT1/PTR (NPF); c) multidrug and toxic compound extrusion (MATE)-type/DTX transporters (DTX50); d) AWPM-19 family proteins (OsPM1), which were originally identified in rice (Kuromori et al. 2010; Kuromori et al. 2011; Kanno et al. 2012; Zhang et al. 2014; Kang et al. 2015; Yao et al. 2018).

In eukaryotes, there are eight subfamilies of ABA transporters, namely ABCA to ABCH. Of the ABCG subfamily, several members have been identified in *Arabidopsis* and *Medicago truncatula*, including both ABA exporters such as

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AtABCG25, AtABCG31 and MtABCG20, and ABA importers such as AtABCG30 and AtABCG40 (Kuromori et al. 2010; Kang et al. 2011; Kuromori et al. 2011; Kang et al. 2015; Pawela et al. 2019). Among these transporters, AtABCG25 functions in exporting ABA from vascular tissues to multiple sites such as guard cells. This transporter together with AtABCG31 also exports ABA from the endosperm, whereas AtABCG30 and AtABCG40 import ABA into the embryo (Kuromori et al. 2010; Kang et al. 2015). Besides ABCG transporters, AtDTX50 also acts as an exporter of ABA, and both AtNPF4.6 and OsPM1 control ABA influx (Kanno et al. 2012; Zhang et al. 2014; Yao et al. 2018). The gene encoding AtABCG22 is similar in sequence to *AtABCG25*. However, AtABCG22 may not transport ABA directly, although it is possibly involved in ABA efflux (Kuromori et al. 2011). Functionally, ABA transporters have been increasingly shown to be involved in transpiration, root morphology, seed germination and other processes important to stress responses of ABA transporters that mediate ABA movement from cell to cell.

**Stress-mediated changes in ABA**

Visualization is a functional approach in studying ABA. With the introduction of FRET (fluorescence resonance energy transfer) marker/sensors, ABACUS and ABAleon, detection of ABA at a cell level become attainable (Jones et al. 2014; Waadt et al. 2014). Changes in ABA levels in individual guard cells and roots were detected after exposure to altered amounts of humidity and salinity (Waadt et al. 2014). The root derived CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED 25 (CLE25) peptide, together with BARELY ANY MERISTEM (BAM) receptors, promote ABA biosynthesis in leaves, in response to dehydration by upregulating *NCED3* expression (Takahashi et al. 2018). The

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flowering repressor SHORT VEGETATIVE PHASE (SVP), a central regulator of ABA catabolism, is able to decrease expression of *CYP707A1/3* while enhancing expression of *AtBG1* simultaneously in response to water deficit (Wang et al. 2018c). Also, NGATHAs (NGAs) proteins upregulate expression of *NCED3* via direct binding (Sato et al. 2018). The HD-ZIP transcription factor HAT1, a negative regulator in ABA biosynthesis, which suppresses the expression of both *ABA3* and *NCED3*, can be phosphorylated and inactivated by SnRK2.3 (Tan et al. 2018). These transcriptional changes lead to the rapid release and subsequently increased synthesis of ABA, while reducing ABA catabolism under drought stress, allowing the initiation of several ABA mediated responses that affect the growth and survival of plants.

Biotic stresses such as pathogen infection can also modulate ABA homeostasis in host plants. Some biotrophic pathogens such as wheat rust fungi can promote increases in ABA that lead to elevated apoplastic sugar accumulation by enhancing *TaSTP6* expression (Huai et al. 2019). Upon infection by the necrotrophic pathogen *Botrytis cinerea* the transcription factor WRKY33 promotes ABA biosynthesis by upregulating transcription of *NCED3* and *NCED5* in *Arabidopsis* (Liu et al. 2015a). The tomato NAC transcription factor LeJA2 (for jasmonic acid 2) upregulates expression of *LeNCED1* that also promotes ABA biosynthesis that can limit pathogen entry through stomata (Du et al. 2014).

Hormone crosstalk also participates in the homeostasis of ABA. For example, auxin and GA coordinate fruit growth and ripening via affecting the regulatory loops of *FveCYP707As* and *FveNCEDs* to control endogenous ABA levels in woodland strawberry (*Fragaria vesca*) (Liao et al. 2018). In addition, JA accumulation is

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required for ABA accumulation in roots of *Arabidopsis* after dehydration treatment (de Ollas et al. 2015).

More future efforts would shed a light on linking the global modulation of ABA content to multiple biological processes. Collectively, all these progresses fine-tune the level of ABA during different development stages and in response to various environmental changes, so that more elements acting upstream of ABA accumulation and the processes coordinating dynamic modulation of ABA content and biological activity remain to be discovered.

## CORE ABA SIGNALING

ABA functions in organs through the recognition by its intracellular receptors, PYLs (Ma et al. 2009; Park et al. 2009). The ABA bound PYLs form complexes with the clade A PP2Cs, allows the release of the inhibition of SnRK2 protein kinases by PP2Cs (Fujii et al. 2009; Ma et al. 2009; Park et al. 2009; Rubio et al. 2009). SnRK2s are then activated through autophosphorylation, or they can be activated by other protein kinases such as Raf-like MAPKKKs (Lee et al. 2015; Saruhashi et al. 2015; Nguyen et al. 2019). SnRK2s regulate multiple physiological responses through phosphorylating target substrates including ion channels, transcription factors, transporters amongst others (Umezawa et al. 2013; Wang et al. 2013). In the absence of ABA, PP2Cs interact with and repress SnRK2s to block ABA signaling.

The discovery of PYL/PP2C co-receptors has led to a substantial effort to unravel the complex signaling system that controls plant responses to ABA. We review here recent studies conserving the crosstalk regulation of core ABA stress signaling components including PYLs, PP2Cs and SnRK2s. Regulation of these

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components are critical to manage excessive and detrimental defense responses under abiotic stress conditions. They make up the core signaling system that maintains homeostatic optimal growth in non-optimal growth environments.

**ABA receptors**

In *Arabidopsis*, the PYL ABA receptor family consists of 13 ABA receptors, and one non-responsive PP2C regulator PYL13 (Fujii et al. 2009; Li et al. 2013; Zhao et al. 2013). PYLs have differing binding properties with ABA, and selectively interact with PP2Cs (Szostkiewicz et al. 2010; Hao et al. 2011; Antoni et al. 2012; Li et al. 2013; Zhao et al. 2013; Tischer et al. 2017). PYLs bind with PP2Cs in both ABA-dependent and ABA-enhanced manners. Generally, monomeric PYLs such as AtPYL4-6 and AtPYL8-10 have higher ABA binding affinity and interact with PP2Cs in an ABA-enhanced manner; while dimeric PYLs such as AtPYR1 and AtPYL1-2 have lower ABA binding affinity and interact with PP2Cs in an ABA-dependent manner (Hao et al. 2011). In contrast, AtPYL13 and OsPYL12 interact with and inhibit several PP2Cs in an ABA-independent manner (Li et al. 2013; Zhao et al. 2013; He et al. 2014; Nemoto et al. 2018), indicating that they are not straightforward ABA receptors. Orthologous of PYLs have been identified in subaerial algae *Zygnematophyceae* (de Vries et al. 2018; Cheng et al. 2019). Albeit to the emergence before landing, the ancient ZcPYL8 encoded by *Zygnema circumcarinatum* cannot bind with ABA and possess the ABA-independent inhibition of PP2C (Sun et al. 2019). The ABA receptors have been reported only in land plants, suggesting that ABA signaling has been critical for plants during the transiting from an aquatic to a terrestrial environment (Lind et al. 2015; Wang et al. 2015a; Bowman et al. 2017; Jahan et al. 2019).

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Although these PYLs function redundantly in regulating ABA coreceptor PP2Cs, some of them function separately in regulating distinct downstream factors. For example, AtPYL6 interacts with and regulates the central JA signaling regulator MYC2 in an ABA-enhanced manner, which may control the synergistic effect of ABA and JA on the inhibition of seed germination (Aleman et al. 2016). AtPYL8 and AtPYL9 interact with the auxin signaling regulator AtMYB77, which promotes lateral root growth recovery from inhibition by core ABA signaling (Zhao et al. 2014; Xing et al. 2016). *PYLs* are differentially expressed in multiple organs, cells, and different growth stages (Gonzalez-Guzman et al. 2012; Antoni et al. 2013). For example, *AtPYL8* is specifically expressed in the root epidermis and in the lateral root cap, which is consistent with its functions in regulating growth of primary and lateral roots (Antoni et al. 2013; Zhao et al. 2014). AtPYL9 is highly expressed in senescent leaves, and promotes ABA-induced leaf senescence. Among the six *PYLs* expressed in guard cells, PYL2 mainly contributes to ABA-induced stomatal closure, whereas PYL4 and PYL5 are essential for stomatal responses to $CO_2$ (Dittrich et al. 2019).

The PYL ABA receptors are redundant but essential for ABA perception, signal transduction and response to stress in plants. This is demonstrated by the "stratospheric" order of *PYL* mutants, including the *pyl* quattuordecuple mutant in *Arabidopsis*, and the *ospyl* septuple mutant in rice (Miao et al. 2018; Tena 2018; Zhao et al. 2018). The growth of the *pyl* quattuordecuple mutant is severely impaired in soil and it fails to produce seeds. Another high order *pyl* duodecuple mutant, with all *PYL* ABA receptors mutated except *AtPYL6*, is extremely insensitive to ABA with respect to several physiological processes including seed germination, seedling growth, stomatal movement, leaf senescence and gene response expression (Zhao et al. 2018). The *ospyl* septuple mutant in rice, with all group I (*OsPYL1-6* and *OsPYL12*) *PYLs*

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mutated, is insensitive to ABA during seed germination and stomatal movement, and shows a strong preharvest sprouting phenotype in field conditions (Miao et al. 2018). In contrast to the severe growth defects of *PYL* mutants in *Arabidopsis*, mutations of group I *OsPYLs* promote rice growth in the field (Miao et al. 2018; Zhao et al. 2018). Overexpression of *PYL* ABA receptors enhances ABA responses and water use efficiency that impact abiotic stress tolerance in model plants such as liverworts, *Arabidopsis* and poplar, in addition to major crops such as rice and wheat (Santiago et al. 2009b; Saavedra et al. 2010; Kim et al. 2012; Pizzio et al. 2013; Kim et al. 2014; Tian et al. 2015; Yang et al. 2016; Zhao et al. 2016; Han et al. 2017; Mega et al. 2019).

**Regulation of ABA receptors**

PYLs undergo posttranscriptional modifications such as phosphorylation, nitration and ubiquitination in plants. These decorations control the fine regulation of responses to environmental changes (Figure 2). PYLs are phosphorylated by multiple protein kinases including TOR, *Arabidopsis* Early flowering 1 (EL1)-like casein kinase (AEL), C-terminally encoded peptide receptor 2 (CEPR2), and Cytosolic ABA receptor kinase 1 (CARK1). TOR kinase phosphorylates PYLs at a conserved site corresponding to PYL4 Ser114 that inactivates PYLs (Wang et al. 2018b). The AEL casein kinases phosphorylate PYLs at partially conserved sites corresponding to PYR1 Ser109 and PYR1 Ser152 and promotes ubiquitination and degradation of PYLs (Chen et al. 2018). The plasma membrane localized leucine-rich receptor-like kinase CEPR2 phosphorylates PYLs at a conserved site corresponding to PYL4 Ser54 and promotes degradation of PYLs (Yu et al. 2019). A putative receptor-like cytoplasmic kinase (RLCK) VIII subfamily kinase CARK1 phosphorylates PYR1 and

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PYL1/2/3/8 at a less conserved site corresponding to PYR1 Thr78 which enhances ABA responses, whereas the *cark1* mutant is less sensitive to ABA (Zhang et al. 2018b; Li et al. 2019b). CARK1 is activated by ABA, but the ability of CARK1 to be activated by environmental changes or other hormones is still unknown (Zhang et al. 2018b). The degradation of PYLs is regulated both by ubiquitin ligase substrate adaptor DDA1 and RING-type E3 ligase RSL1 via the ubiquitin-proteasome system, and by the ESCRT-I components VPS23A and ALIX through the endosomal-vacuole pathways (Bueso et al. 2014; Irigoyen et al. 2014; Yu et al. 2016; García-León et al. 2019). Consistent with their known functions, the triple knockout mutant of *CEPR2* and its homologs *Phloem intercalated with xylem* (*PXY*) and *PXY-Like 2* (*PXL2*) are hypersensitive to ABA. This is similar to the mutants of TORC, including *tor* and *raptor1b*, triple mutants of *AELs*, and mutants of members of ESCRT-I Component, such as *vps23a*, *alix-1* and *fyve* (Yu et al. 2016; Chen et al. 2018; Wang et al. 2018b; García-León et al. 2019; Li et al. 2019a; Yu et al. 2019). Besides posttranscriptional regulation of PYLs, expression of *PYR1*, *PYL1-6* and *PYL8* is also down-regulated by osmotic stress (Bhaskara et al. 2012), which could be important in the establishment of homeostatic ABA responses.

Signaling crosstalk between ABA receptors and growth promoting signaling networks is crucial to the balance between growth and ABA-dependent stress responses which generally inhibit growth. It is well known that TOR is activated by glucose and other components that participate in energy homeostasis (Xiong and Sheen 2012). Besides energy signaling components, nitric oxide (NO) also inactivates PYLs by tyrosine nitration (Castillo et al. 2015). Although it is still not clear how CEPR2 and AEL responded to environmental changes or other hormones, phosphorylation of PYLs by CEPR2 and TOR is diminished after ABA treatment,

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suggesting that the activity and abundance of PYLs are tightly controlled under unstressed conditions, to prevent ABA-mediated suppression of growth (Wang et al. 2018b; Yu et al. 2019).

**Regulators of ABA co-receptors**

Protein phosphorylation and dephosphorylation control is crucial for maintaining the appropriate balance of ABA-mediated growth control depending on the environmental status of the plant (Zhu 2016; Shi et al. 2018; Yang and Guo 2018). Protein phosphatases can interact with and inhibit SnRK2, SnRK1, SnRK3 and even mammalian AMPKs, which are also core components in abiotic stress, ABA and energy signaling (Sanders et al. 2007; Zhu 2016). Among 80 PP2Cs in *Arabidopsis*, nine clade A PP2Cs including ABI1/2, HYPERSENSITIVE TO ABA (HAB) 1/2, ABA-HYPERSENSITIVE GERMINATION1 (AHG1), AHG3/PP2CA, HIGHLY ABA-INDUCED (HAI) 1/2/3, and 3 clade E PP2Cs E-Growth-Regulating PP2C (EGR) 1/2/3 function as negative regulators of stress responses. Clade A PP2Cs are core negative regulators of ABA signaling, and have important functions for suppressing stress signaling and allowing the appropriate degree of plant growth suppression, especially under unstressed or mild stress conditions (Fujii et al. 2009; Rubio et al. 2009; Umezawa et al. 2009; Komatsu et al. 2013). Under stressed conditions, the ABA-bound PYLs interact with the conserved C-terminal catalytic domains of clade A PP2Cs, which in turn releases the inhibition of SnRK2s by PP2Cs and allows activation of stress responses (Ma et al. 2009; Park et al. 2009).

Besides clade A PP2Cs, EGR1/2/3 suppress plant growth partially through dephosphorylating microtubule associated protein MASP1 Ser670 and destabilizing microtubules which are required for appropriate levels of growth under osmotic stress

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(Bhaskara et al. 2017). They also inhibit proline accumulation and suppress resistance responses to drought and cold stresses through suppressing SnRK2 activation (Bhaskara et al. 2017; Ding et al. 2019). Up to now, ancient PYL without ABA binding affinity has been reported in algae, while PP2Cs and SnRK2s from algae have conserved function compared with that from higher plants (Lind et al. 2015; de Vries et al. 2018; Cheng et al. 2019; Sun et al. 2019).

Plant growth and stress responses are carefully controlled by both activity and abundance of PP2Cs. Although ABA and abiotic stresses inactivate PP2Cs to induce stress responses, the expression levels of PP2Cs are actually upregulated by abiotic stresses and ABA through ABRE-BINDING FACTORS (ABFs), creating a counteractive control loop to maintain new homeostatic levels (Bhaskara et al. 2012; Bhaskara et al. 2017; Wang et al. 2019). Also, under unstressed conditions or transition from stressed to unstressed conditions, ABA and abiotic stress signalings need to be suppressed to appropriately promote plant growth. Indeed, several studies have indicated that activities of PP2Cs can be enhanced by several PP2C binding proteins. For example, ENHANCER OF ABA CO-RECEPTOR1 (EAR1) interacts with the non-conserved N-terminal regulatory domains of PP2Cs, including ABI1/2, HAB1/2, AHG1/3, to enhance their activities (Wang et al. 2018a). The PR5 receptor-like kinase 2 (PR5K2) also may repress ABA and stress signaling through phosphorylating ABI1/2 and enhancing their protein phosphatase activities (Baek et al. 2019). Moreover, function of the clade E PP2C, EGR2 requires myristoylation by NMT1, which is suppressed by cold stress (Ding et al. 2019).

By contrast, under stressed conditions or ABA treatment, activities of PP2Cs can be reduced by ABA receptor PYLs and several other regulators, such as the putative

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leucine-rich repeat-RLK, RECEPTOR DEAD KINASE1 (RDK1) that can promote ABA responses by interacting with ABI1 (Kumar et al. 2017). PP2Cs also are degraded by the 26S proteasome pathway through the PUB12/13 U-box, RGLG1/5 RING-type and multimeric cullinc3 (CUL3)-RING-based E3 ligases by interacting with the adaptor BTB/POZ AND MATH DOMAIN proteins (BPMs), that are promoted by ABA (Figure 2) (Kong et al. 2015; Wu et al. 2016; Belda-Palazon et al. 2019; Julian et al. 2019).

**Regulators of core protein kinases**

Abiotic stresses and ABA induce the activation of several protein kinases including SnRK2s, CPK3, SOS2/CIPK24/SnRK3.11 and CIPK23 in *Arabidopsis* and MdCIPK22 in apple, affecting phosphorylation changes of multiple downstream regulators (Guo et al. 2001; Boudsocq et al. 2007; Ho et al. 2009; Lin et al. 2009; Mehlmer et al. 2010; Umezawa et al. 2013; Wang et al. 2013; Ding et al. 2015; Ding et al. 2018; Ma et al. 2018). Among these, the SnRK2.2/3/6 core protein kinases that are activated by osmotic, salt, cold, and ABA treatment. It is well known that ABA-bound PYLs interact with clade A PP2Cs, which in turn release SnRK2.2/3/6 from inhibition. SnRK2s may then be activated by autophosphorylation and/or transphosphorylation by several other kinases, such as the Raf-like MAKKKs, RAF10 and ARK (for ABA and abiotic stress-responsive Raf-like kinases) (Figure 2). These kinases appear to be critical for the activation of SnRK2s and subsequent responses to ABA and abiotic stresses in *Arabidopsis* and *Physcomitrella patens* (Huang et al. 2014; Lee et al. 2015; Saruhashi et al. 2015; Stevenson et al. 2016; Hwang et al. 2018; Nguyen et al. 2019; Shinozawa et al. 2019).
BRASSINOSTEROID INSENSITIVE 2 (BIN2), the Glycogen synthase kinase 3s

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(GSK3s)/Shaggy-like kinases (ASKs) repress brassinosteroid (BR) signaling, whereas they enhance ABA signaling through phosphorylation specifically of SnRK2.2/3 at Thr180 on SnRK2.3, but not SnRK2.6 (Cai et al. 2014). Moreover, NO signaling also represses ABA signaling through S-nitrosylation of SnRK2.6 at Cys137 that inactivates SnRK2s (Wang et al. 2015b). Although PYLs are essential for ABA mediated activation of SnRK2s, they are also involved in antagonistic regulation of activation of SnRK2s during osmotic stress (Zhao et al. 2018). Together, SnRK2s can be activated by abiotic stresses, and repressed by growth promoting signals such as NO and BR.

## ABA-INDUCED STOMATAL CLOSURE

Stomata is pivotal for gas exchange and transpiration of plants, and the closure of it can be induced by numerous environmental factors such as drought, pathogen attack, dark, low humidity, high $CO_2$ concentrations and so on (Bauer et al. 2013; Assmann and Jegla 2016; Martin-StPaul et al. 2017; Su et al. 2017). ABA plays an important role in the closure of stomata by regulating guard cell ion fluxes. Stomatal closure is the major process controlling transpirational water loss of plant. ABA affects stomatal pore size by both $Ca^{2+}$-dependent and $Ca^{2+}$-independent pathways (Figure 3).

### $Ca^{2+}$-dependent pathway

ABA can induce opening of $Ca^{2+}$ channels which allows calcium ions to mediate the closure of stomata pores (Mcainsh et al. 1990, 1992; Hamilton et al. 2000; Pei et al. 2000). The increase in cytosolic $Ca^{2+}$ in guard cells in response to ABA likely involves the induction of reactive oxygen species (ROS) and

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inositol-1-4-5-triphosphate ($IP_3$) (Gilroy et al. 1990; Lee et al. 1996; Pei et al. 2000; Murata et al. 2001; Mustilli et al. 2002). $Ca^{2+}$ mediated signals could be decoded by several $Ca^{2+}$ sensors, including Calcium Dependent Protein Kinase (CPK) 3/4/6/10/11, which may phosphorylate and activate the Slow-type (S-type) anion efflux channels including SLOW ANION CHANNEL1 (SLAC1) and SLOW ANION CHANNEL-ASSOCIATED (SLAH3), which are involved in stomatal closure and reduction of leaf water loss (Mori et al. 2006; Zhu et al. 2007; Zou et al. 2010; Brandt et al. 2012). Although CPK21 and CPK23 also phosphorylate and activate SLAC1 and SLAH3, *cpk21* and *cpk23* knockout mutants have enhanced drought tolerance, which is inconsistent with the general role of CPK21/23 and other CPKs in regulating anion channels (Ma and Wu 2007; Geiger et al. 2010; Franz et al. 2011; Geiger et al. 2011; Brandt et al. 2012; Demir et al. 2013). CPK8 was also reported to regulate stomatal closure that is induced by ABA, ROS and $Ca^{2+}$ through the direct phosphorylation of CATALASE3 (CAT3) (Zou et al. 2015). The CPK11-Di19-PR1/2/5 pathway also contributes to drought tolerance probably by affecting stomatal movement (Liu et al. 2013). Besides CPKs, CBL-interacting protein kinase 23 (CIPK23) has also been implicated through genetic analyses in ABA-induced stomata closure (Cheong et al. 2007). In addition to the modulation of anion channel efflux, other ion channels can be regulated in a $Ca^{2+}$ dependent manner. GOAK, a $K^+$ outward rectifying channel, is phosphorylated and activated by CPK21 (Hosy et al. 2003; van Kleeff et al. 2018). Moreover, CPK13 also inactivates KAT1 and KAT2, two $K^+$ influx channels, and affects stomatal behavior through specific phosphorylation events (Ronzier et al. 2014). The activity of the $H^+$-ATPase of guard cells of fava bean guard cells was shown to be inhibited by $Ca^{2+}$ in isolated microsomal membranes (Kinoshita et al. 1995).

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**$Ca^{2+}$-independent pathway**

The ABA activated SnRK2.6/Open Stomata1 (OST1) is a key regulator of stomata closure (Li et al. 2000). ABA can also activate the malate transporter Rapid-type (R-type) anion channel, QUAC1 (also called ALMT12), which is independent of $Ca^{2+}$ and is controlled by OST1 in guard cells (Meyer et al. 2010; Imes et al. 2013). OST1 can also up-regulate the activity of SLAC1 and KUP6, a KUP/HAK/KT family potassium efflux transporter, and inhibit KAT1 through phosphorylation, also affecting stomatal movement (Kwak et al. 2001; Geiger et al. 2009; Sato et al. 2009; Osakabe et al. 2013). Significantly, OST1 also can phosphorylate and negatively regulate the bHLH transcription factor, ABA-responsive kinase substrates (AKS1), which subsequently binds to the promoter of *KAT1* directly, leading to reduced expression of *KAT1* (Takahashi et al. 2013). In *Arabidopsis* guard cells, NRGA1, a putative mitochondrial pyruvate carrier can negatively regulate the inhibition of inward $K^+$ currents through ABA (Li et al. 2014). A plasma membrane receptor kinase GHR1, also controls ABA- and $H_2O_2$-regulated stomatal closure by controlling SLAC1 activity, and contributes to systemic stomatal responses (Hua et al. 2012; Devireddy et al. 2018).

Both $Ca^{2+}$-dependent and $Ca^{2+}$-independent pathways mediate the decline of turgor of guard cells through membrane depolarization during water deficits, leading to reductions in stomatal aperture. It has been thought that OST1 and CPKs converge at the level of PP2Cs so that $Ca^{2+}$ and CPKs have an effect on stomatal movement downstream of ABA receptors in guard cells. For example, ABI1 can dephosphorylate and inactivate CPK6 and OST1 in guard cells (Geiger et al. 2011; Brandt et al. 2012). It has been argued that ABA may function upstream of $Ca^{2+}$

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signaling because ABA accumulates slower than $Ca^{2+}$ under osmotic stress. Recent studies have also suggested that salicylic acid (SA) may induce stomatal closure independent of OST1 but dependent on CPK3/6 (Prodhan et al. 2018). There is a possibility that osmotic stresses may also induce $Ca^{2+}$ elevation and regulate stomatal movement through $Ca^{2+}$ sensors directly.

**$CO_2$, pathogen and ABA signaling**

The involvement of several environmental factors together with ABA on stomatal closure has been studied as well. An increase in $CO_2$ concentration is able to reduce the number and size of stomata (Woodward 1987; Gray et al. 2000). Stomatal movement also is triggered by high concentrations of $CO_2$ and this is impaired in *ost1* mutants but not in ABA biosynthesis mutants such as *nced3/nced5* and *aba2-1*, and in the ABA signaling mutant *pyl112458*. These results suggest that the role of $CO_2$ in stomatal closure is independent of ABA but not OST1 (Xue et al. 2011; Hsu et al. 2018). However, another research has shown that the effects of $CO_2$ on stomatal closure are dependent on ABA signaling, and therefore, the relationship between $CO_2$ and ABA needs further clarification (Chater et al. 2015). Recently, Dittrich et al. has shown that the ABA receptor PYLs integrate several environmental factors such as $CO_2$, dark and relative air humidity under long-term change of environment (Dittrich et al. 2019).

Plants also mediate stomatal behavior to counter the ability of some pathogens to control stomatal functions (stomatal immunity). Two receptors that recognize Pep1 peptide of damage/danger-associated molecular patterns (DAMPs), PEPR1/2, have been recognized to function in stomatal guard cells to control stomatal pore size through SLAC1/SLAH3, independent of OST1 (Zheng et al. 2018). However, a

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flagellin peptide from *P. syringae* (flg22), a member of the pathogen-associated molecular pattern (PAMP), induces stomatal closure by stimulating SLAC1/SLAH3 in an OST1-dependent manner in guard cells (Guzel Deger et al. 2015). Su et al. also revealed that the MKK4/5-MPK3/6-organic acid metabolism cascade inter-dependently functions with ABA to mediate stomatal immunity (Su et al. 2017). Also, the phytotoxin produced by *P. syringae*, coronatine (COR), is able to block ABA-induced stomatal closure but not block the MPK3/6-mediated pathway (Melotto et al. 2006).

**ABA IN SEED DEVELOPMENT**

In *planta*, when male and female gametes combine to form a fertilized egg, the zygote will further develop through embryogenesis and endosperm proliferation. After that, subsequent division of embryo cells is arrested at the mature embryo stage and storage products accumulate. In the final stages of seed development dehydration occurs spontaneously and the embryo enters a desiccation-tolerant and dormant state. Upon re-hydration, the embryo radicle enlarges by cell elongation breaking through the seed coat (germination) and the embryo enters the next generation (Mansfield and Briarty 1996; Raz et al. 2001). ABA is involved in many phases of embryo development during transformation of generations (sporophyte to gametophyte to sporophyte). Here we will introduce the roles of ABA in storage product accumulation, desiccation tolerance, dormancy, germination and post-germination growth arrest.

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**Central regulation in embryo development**

The continuous growth of the embryo is arrested during the transition from the embryogenesis phase to the early maturation phase, which is primarily regulated through control of cell division (Raz et al. 2001). Embryo growth arrest in mature seeds is controlled by FUSCA3 (FUS3), Leafy cotyledon 1 (LEC1) and LEC2, which is evidenced by the fact that *fus3*, *lec1* and *lec2* mutants all fail to fully suspend embryo growth and exhibit premature germination. Mutants impaired in ABA signaling, such as *ospyl* septuple, *snrk2.2/3/6* triple and *abi3*/*vp1* double mutant also show premature germination in *Arabidopsis*, rice and maize (Robichaud et al. 1979; Finkelstein and Somerville 1990; Nakashima et al. 2009; Miao et al. 2018). However, ABA biosynthesis and signaling mutants *aba1* and *abi3* display normal embryo growth, indicating that FUS3, LEC1 and LEC2 control embryo growth arrest independent of ABA signaling (Raz et al. 2001).

During seed maturation, the ABI3/FUS3/LEC2 (AFL), subfamily of B3 transcription factors, together with LEC1 and LEC1-LIKE (L1L) compose of a transcription control network called LAFL (Figure 4) (Kwong et al. 2003; Jia et al. 2014). Hormone signaling, some metabolic pathways and other transcriptional control networks are targeted by LAFL and mediate the embryogenesis process but have distinct temporal patterns of development (Jia et al. 2013). The core LAFL network functions upstream of several genes that modulate seed development including Zinc finger factor *PEI1*, *APETALA2 (AP2)*, *BABY BOOM* (*BBM*), *FLOWERING LOCUS C* (*FLC*), and two genes encoding seed storage proteins (SSP) including 2S albumin storage protein 1 (At2S1) and CRUCIFERIN C (CRC) (Jia et al. 2014). Moreover, BBM has been also reported to regulate expression of most members of the LAFL

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network during somatic embryogenesis (Horstman et al. 2017). The LAFL network, can also be regulated by the sister subgroup of AFL type B3 transcription factors such as VIVIPAROUS1/ABI3-LIKE1/2/3 (VAL1/2/3), which repress the LAFL network during germination but not affect seed maturation (Figure 4) (Jia et al. 2013; Zhou et al. 2013; Jia et al. 2014).

**Last phase of seed maturation**

After the interruption of cell division during embryogenesis, plant seeds begin to accumulate storage components and begin to desiccate. This final stage results in a metabolically quiescent or dormant state, enabling seeds to survive several stressful environments. ABA also functions in this final developmental stage and affects several important traits of the dormant seed.

*Reserve product accumulation*

Seed maturates by metabolically producing and then accumulating several reserve components need for germination and initial seedling growth and development. The initiation of reserve accumulation is mediated by several processes such as gene expression, posttranslational modulation, strengthening the activity of enzymes and ATP production (Bewley et al. 2013a).

Before storage product accumulation, there is often a period of de-greening that is important for seed maturation and some commercial traits such as storability, essential for seed oil quality (Delmas et al. 2013). SnRK2s that are activated by ABA and the downstream transcription factor ABI3 are often required for this de-greening process, which can be observed by the presence of a greenish-brown seed coat evidenced by *snrk2.2/3/6* and *abi3-6* (Nakashima et al. 2009; Delmas et al. 2013).

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ABI3 interacts with the SnRK2 activated transcription factor ABI5, and these components may function together in transcriptional regulation of ABA-responsive genes (Nakamura et al. 2001). Indeed, two stay-green genes, *SGR1* and *SGR2*, are targets of ABI3 and function redundantly in regulating de-greening of seed (Delmas et al. 2013).

ABA functions in the storage of lipids, proteins and carbohydrates in seeds. Consistent with the role of ABA in promoting accumulation of seed storage, products, often seedlings impaired in ABA signaling such as *pyl* duodecuple and *snrk2.2/3/6* triple mutants exhibit reduced accumulation of seed products, whereas overexpression of *SnRK2.6* increases overall seed production (Zheng et al. 2010; Gonzalez-Guzman et al. 2012; Zhao et al. 2018). Inactivation of SnRK2.6, which mediates ABA signaling, but not ABA-irresponsive SnRK2.4, results in a 7% to 25% reduction in oil content of seed (Zheng et al. 2010). According to microarray data, the expression of some genes encoding seed reserve products such as the 12S globulin storage protein is impaired in the *snrk2.2/3/6* triple mutant, confirming that ABA can promote seed storage accumulation through transcriptional regulation (Nakashima et al. 2009). Indeed, two ABF transcription factors ABI5 and bZIP67, together with ABI3, and the AP2/ERF transcription factor ABI4, control expression of genes related to numerous events involved in seed storage processes downstream of ABA (Nambara et al. 1992; Parcy et al. 1994; Soderman et al. 2000; Mendes et al. 2013; Zinsmeister et al. 2016). The transcription factor, bZIP67, together with two other LEC1 inducible transcription factors, L1L and NUCLEAR FACTOR-YC2 (NF-YC2), activate *FATTY ACID DESATURASE 3* (*FAD3*) to affect omega-3 fatty acid accumulation in seeds (Mendes et al. 2013). ZmbZIP22 has also been reported to regulate seed storage events. For example, ZmbZIP22 is required for the transcription of a 27-kD γ-zein

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gene (Li et al. 2018; Dong et al. 2019). ABA highly induces the expression of the *DELAY OF GERMINATION 1* (*DOG1*)*-LIKE 4 (DOGL4)*, which encodes a major inducer of reserve accumulation during seed maturation (Figure 4) (Sall et al. 2019). Ectopic expression of *DOGL4* enables the expression of seed maturation- specific genes even during the germination process, including the major seed reserve proteins *ALBUMIN*s, *CRUCIFERIN*s and *OLEOSIN*s (Sall et al. 2019). Altogether, the classic PYLs-SnRK2s-ABFs signal cascade plays an essential role in the assimilation and deposition of storage nutrients in plant seeds.

In the LAFL network, LEC1 is a key modulator in fatty acid (oil) biosynthesis through the global elevation of the expression of several related genes. For example, *Arabidopsis 2S storage protein 3* (*At2S3*), a representative seed storage protein gene, is dependent on FUS3 and partially dependent on both ABI3 and the AP2/EREBP type transcription factor WRINKLED1 (WRI1) (Kagaya et al. 2005b; Mu et al. 2008). FUS3 modulates the expressions of storage protein genes in an indirect but still ABA dependent manner, by requiring the ABA-induced synthesis of several ectopically intermediate regulatory factor(s) (Kagaya et al. 2005a). A *LEC2-GR* inducible line, in which *LEC2* was fused with the *glucocorticoid receptor* (*GR*) promoter, is activated by the gulcocorticoid dexamethasone (DEX), accumulates seed specific mRNA and storage oil in leaves. This suggests that LEC2 harbors a synergistic activity with ABI3, FUS3 and LEC1 to affect reserve product accumulation (Santos Mendoza et al. 2005). The AP2/EREBP domain protein, WRI1 also functions in multiple processes involving the accumulation of oil and sugars in seeds. The wrinkled-like seed mutant *wri1* that disables the conversion by sucrose and glucose into triacylglycerols (TAGs), has an 80% reduction of seed oil content, and an elevation of soluble sugar (Focks and Benning 1998; Cernac and Benning

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2004; Mu et al. 2008; To et al. 2012). WRI1 is regulated by LEC1, LEC2 and GmDREBL at the transcriptional level. WRI1 is also regulated by 14-3-3, KIN10 and perhaps by OST1 at the protein level (Baud et al. 2007; Mu et al. 2008; Baud et al. 2009; Sirichandra et al. 2010; Ma et al. 2016; Zhang et al. 2016; Zhai et al. 2017; Kong and Ma 2018). To date, we still have an incomplete understanding of the roles of ABA in regulating seed storage-related proteins and genes. The role of ABA in controlling the activity of transporters for nutrients such as sugar and nitrogen in seed storage processes is very likely but remain obscure (Baud et al. 2005; Chen et al. 2015). For instance, the mutant *suc5* was also found to have diminished levels of seed oil (Baud et al. 2005). Altogether, members of LAFL network together with other factors have crucial roles in the orchestration of the accumulation of storage products during the maturation of seeds. However, we need further research on the effects of ABA on several nutrients-specific transporters and importance of these transporters in both seed storage and maturation.

*Desiccation tolerance*

In the early periods of histodifferentiation and cell expansion, the water content of seeds is gradually increased followed by a significant decrease in water during accumulation of storage components and overall maturation (Bewley et al. 2013b). Simultaneously, with the final stages of maturation, seeds acquire severe desiccation tolerance and dormancy. The attainment of this tolerance is associated with the accumulation of a series of protectants such as antioxidants, sugar and late embryogenesis abundant (LEA) proteins (Koornneef et al. 2002; Finch-Savage and Leubner-Metzger 2006). Interactions between LEAs and sugars contribute to the formation of a glassy state that suspends metabolic activities and protects seed tissues

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and cells from many survival threatening events such as membrane damage (Buitink and Leprince 2008). Core elements of ABA signaling, like SnRK2s, PYR/PYL/RCARs and ABFs, have been found to control the regulation of gene expression that controls key protection from seed desiccation such as *LEAs* and *HSPs* that are modulated by the LAFL network (Wehmeyer and Vierling 2000; Nakashima et al. 2009; Maia et al. 2014; Zhao et al. 2018). Besides, being an important component in light signaling, HY5, is also able to induce the expressions of *LEAs* probably through binding with the promoter of *ABI5* directly (Chen et al. 2008). DOG1 was also demonstrated to increase the expressions of *LEA* and *HSP*, via ABI5/ABI3, and may accelerate the accumulation of N-rich compounds, which promote the dormancy and storability of seed (Dekkers et al. 2016).

*Dormancy and germination*

After dehydration, metabolism ceases dramatically and the seed begins to enter into a quiescent state, which in most species, continues into various degrees and types of dormancy. ABA is a core regulator in this process and, it is noteworthy, that only the embryo produces ABA, not the maternal tissues. In this sense dormancy is a trait of the embryo and its associated tissues (Karssen et al. 1983; Frey et al. 2004). Genetic screening of mutants deficient in seed dormancy has led to the identification of several regulators of hormone metabolism and action signaling network that controls seed maturation and dormancy. Several regulators including HISTONE MONOUBIQUTINATION1 (HUB1), REDUCED DORMANCY 2 (RDO2), and DOG1 are involved in seed dormancy directly (Liu et al. 2007; Liu et al. 2011; Nakabayashi et al. 2012). In rice, SEED DORMANCY 4 (OsSDR4) is considered to be a regulator that is involved in seed dormancy with an unknown function. In

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*Arabidopsis*, SDR4-LIKE (AtSDR4L) regulates dormancy release and germination through both gibberellin (GA) synthesis and activities (Sugimoto et al. 2010; Cao et al. 2019).

Many mutations that affect ABA biosynthesis or sensing and responding to ABA such as *aba1*, *aba2/3*, *nced6/9*, *snrk2.2/3/6* and *pyl112458379101112*, all show reduced seed dormancy and early germination (Koornneef et al. 1982; Leon-Kloosterziel et al. 1996; Lefebvre et al. 2006; Nakashima et al. 2009; Zhao et al. 2018). Recently two raf-like MAPKKKs, Raf10/11 can phosphorylate SnRK2s and ABFs and affect seed dormancy (Lee et al. 2015; Nguyen et al. 2019). DOG1 also modulates seed dormancy as the mutant *dog1* is completely nondormant. However, *dog1* has nearly WT sensitivity to external application of ABA, indicating that the nondormant phenotype of *dog1* does not result from impairment of ABA signaling (Bentsink et al. 2006). Based on genetic analysis, DOG1 and ABA are both required for normal seed dormancy (Alonso-Blanco et al. 2003; Bentsink et al. 2006; Nakabayashi et al. 2012). Other research has revealed that DOG1 is characterized as an α-helical heme-binding protein that functions in the inhibition of AHG1/AHG3 downstream of heme (Nee et al. 2017; Nishimura et al. 2018). Although DOG1 also interacts with another PP2C protein REDUCED DORMANCY5 (RDO5), RDO5 also seems to function in seed dormancy independent of both ABA and DOG1 (Xiang et al. 2014).

GA is essential for the seed germination, which is evidenced by the defects in seed germination of several mutants with disrupted GA synthesis such as *ga1*, *ga2* and *ga3* (Debeaujon and Koornneef 2000; Ogawa et al. 2003). DELLA proteins, RGA-LIKE 2 (RGL2) and RGL3, are central repressors of seed germination

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indicating the important role of GA signaling in seed germination (Lee et al. 2010). The GA-insensitive mutant, *sleepy1* (*sly1*), exhibits attenuated seed germination due to enhanced accumulation of RGL2 (Ariizumi and Steber 2007). There are several other factors involved in GA signaling that function in seed germination, such as F-box proteins SNEEZY (SNE) and SPINDLY (SPY) (Silverstone et al. 2007; Ariizumi et al. 2011).

The opposing roles of ABA and GA in seed dormancy and germination result in a balanced control mechanism. As a negative regulator in GA signaling, the loss-of-function mutant *rgl2* has a reduced ABA concentration after imbibition, leading to the release from dormancy and acceleration of germination (Piskurewicz et al. 2008; Lee et al. 2010). NF-YC, together with RGL2, promotes *ABI5* expression to promote ABA-mediated repression of seed germination (Liu et al. 2016). The COP9 Signalosome 1 (CSN1), which is recognized as a modulator of ubiquitin E3 ligase, facilitates the degradation of RGL2, and CSN5A and may inhibit ABI5, possibly through a physical interaction, therefore promoting seed germination (Jin et al. 2018). Expression of both *RGL2* and *ABI5* also are activated by exogenous ABA (Piskurewicz et al. 2008). Together, the balancing roles of GA and ABA on germination is mainly achieved through effects on RGL2. Other signaling components of hormone metabolism and synthesis also contributes to this balance.

During cold stratification, expression of *CYP707As* that participate in ABA metabolism, and *AtGA3ox1* that is involved in GA synthesis are elevated, leading to a high GA/ABA ratio, which promotes seed germination (Okamoto et al. 2006; Su et al. 2016; Chen et al. 2019). The same expression control pattern was found with the *atper1* mutant that has a dysfunctional seed-specific peroxiredoxin (Chen et al. 2019).

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In imbibed seed, DELLA protein is degraded by the elevated GA to attenuate transcriptional activities of DELLA-ABI3-ABI5 module that accelerate germination. When exposed to high temperature, increased transcriptional activity of the DELLA-ABI3-ABI5 complex inhibits germination (Lim et al. 2013). This balance between ABA and GA control also involves interactions with other hormones like ethylene (ET), BR, strigolactone (SL), auxin, ROS, NO, and with the environmental cues i.e. temperature and light (Chen et al. 2009; Xiang et al. 2014; Dekkers and Bentsink 2015; Shu et al. 2016; Chen et al. 2019).

**Post-germination growth arrest**

ABA also functions in the process of post-germination growth (PGG) arrest. PGG arrest protects embryos from stressful surroundings that may threaten seedling survival. For example, germinated seed maybe subjected to an increasingly stressful osmotic environment. Seedling growth will cease under such conditions and reenter the quiescent state. This will protect the seedling until its surroundings become feasible for further growth and development needed to establish a photoautotrophy system (Hwang et al. 2018). Exogenous ABA is also able to induce PGG arrest. ABA-deficient and ABA-insensitive mutants are not able to normally transition to PGG arrest, suggesting that ABA plays an essential role in the establishment of PGG arrest (Barrero et al. 2005). There may also be multiple other participants in this process. For example, JMJ30, a histone demethylase, is able to block the inhibition mediated by the H3 lysine 27 trimethylation epi mark (H3K27me3) at the promoter of *SnRK2.8* and hence release the suppression of ABI3 to promote PGG arrest (Wu et al. 2019). Recently, it was reported that RAF22 in *Arabidopsis* acts as a negative

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regulator of PGG arrest that is, independent of the canonical ABI5-mediated ABA cascade (Hwang et al. 2018).

We continue to reveal the multiple roles of ABA in several stages of seed development. Besides the processes mentioned above, ABA also functions in seed testa pigmentation, capsule dehiscence and radicle emergence and in earlier aspects of seed maturation (Finkelstein and Lynch 2000; Frey et al. 2004). Seed are the guarantors of the survival of future generations. Their successful entry into and emergence from dormancy is critical to species survival in a constantly changing environment that can abruptly become hostile to several life processes. Therefore, further understanding the seed guides us to recognize plants better.

## THE ROLE OF ABA IN PLANTS DURING SEVERAL DEVELOPMENTAL STAGES

The biological regulations of ABA are ubiquitous during multiple developmental stages of plants, and many of them are implemented through ABF-mediated transcriptional processes. There are nine members in the ABF family including ABF1, ABF2/ABA–RESPONSIVE ELEMENT BINDING PROTEIN1 (AREB1), ABF3, ABF4/AREB2, AREB3, ABI5, bZIP15, bZIP67 and EEL, all belonging to the bZIP subfamily. These factors function redundantly in transcriptional regulation mediated by ABA (Fujita et al. 2005). ABI3 and ABI4 are two other important transcription factors that regulate ABA responses, through transcriptional reprogramming. Here we conclude distinct biological roles of ABA during different developmental phases.

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**ABA in seed and seedling**

ABA has important function during several stages of the alteration of generations through gamete generation, subsequent fertilization and embryo development. Alteration of generations (sexual reproduction) conveys two major adaptive mechanisms. First, gamete formation by meiosis is the basis of most genetic variation through which natural selection works. Second, the meiotic process occurs by the passage into and out of a period of dormancy. During the dormant period, plant embryos can survive extreme environmental changes. As we have described, ABA mediates several developmental processes that affect the successful entry into dormancy as well as maintenance of and emergence from the dormant stage (Schopfer et al. 1979; Perkins et al. 2019). After germination, high-concentration ABA attenuates the growth of primary root, and in contrary, low-dosed ABA maintains the growth may through restricting the ethylene production controlled by expression of *ACS2/5*, under water stress (Figure 5) (Spollen et al. 2000; Xu et al. 2010; Li et al. 2011). Exogenous ABA can also promote the elongation of the seedling primary root in the *pyl112458* and *pyl* duodecuple mutants (Gonzalez-Guzman et al. 2012; Zhao et al. 2018). Genes in clade A *PP2Cs* family are intensively induced by ABA in the root and this may lead to decreased inhibition of primary root growth (Wang et al. 2019). In addition to root growth, ABA inhibits the emergence of vegetative leaves under non-stress conditions (Yoshida et al. 2019).

Quite interestingly, ABA promotes the quiescence and repression of stem cell differentiation in the primary root meristem, which is dependent on WUSCHEL RELATED HOMEOBOX5 (WOX5), a target of auxin signaling that is essential for Quiescence Center (QC) function (Han et al. 2010; Zhang et al. 2010; Wu et al.

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2018). Moreover, Yeast-One-Hybrid (Y1H) results have revealed that both WOX5 and NAC DOMAIN PROTEIN13 TFs may bind directly to the *ABRE* promoter element, which may also function in DNA damage responses and stem cell identity (Wu et al. 2018). Controlling stem cell development may be a critical strategy to adapt to stress environments through re-development of tissues and organs with more appropriate phenotypes.

**ABA in adult plant**

ABA also has several effects on adult plants. Under conditions of limited water, ABA transcriptionally regulates many genes. ABA induces several *LEA* class genes including *AIL1*, *RD29B*, *RAB18*, *EM1* and *EM6* which are the classic ABA-responsive marker genes thought to protect plants from water loss (Wang et al. 2018d). Mutants defective in multiple ABFs display wilted phenotypes under limiting water conditions. However, many details of ABFs regulation of water loss remain unclear (Yoshida et al. 2010; Yoshida et al. 2015). ABA also activates the expression of genes controlling wax synthesis helping to block water loss from leaves (Cui et al. 2016; Zhao et al. 2016; Zhao et al. 2017). The expression of wax-synthesis-related genes, *KCS2*, *CER1*, *LTP3* and *WSD1*, are strongly decreased in *snrk2.2/3/6* and *abi1-1* but are increased in *pRD29A-PYL9* mutants (Zhao et al. 2016). ABA effects on stomatal movement also require OST1-phosphorylation of AKS1. ABA also accelerates the degradation of starch to sugar during osmotic stress through transcriptionally controlling the expressions of *β-AMYLASE1 (BAM1)* and *α-AMYLASE3 (AMY3)* through several ABFs. The *amy3bam1* mutant displays dysfunctional translocation of carbon sources from leaves to roots under osmotic stress, suggesting that ABA may function to promote the export of sugars from source

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leaf tissues to sink tissues in the root (Thalmann et al. 2016). Through transcriptional modulation of ABFs, ABA controls chlorophyll degradation and starch biosynthesis and uptake of toxic cadmium (Cd) through an interaction between ABI5 and MYB49 (Figure 5) (Zhu et al. 2011; Gao et al. 2016; Zhang et al. 2019).

Under appropriate environmental conditions, the adult plant will begin to transition to flowering, which restarts the alteration of generations at the point of meiosis and pollination (gamete fusion). ABA is involved in several developmental processes associated with flowering and transition of generations. ABA functions in coordination of fruit growth and ripening (Rogler and Hackett 1975; Rusconi et al. 2013; Liao et al. 2018). And ABA also promotes capsule dehiscence and flower organ abscission (Zhao et al. 2018). However, as described, the major function of ABA in flowering involves its role in embryo dormancy which is the ultimate response to survive extreme environments.

**ABA in senescent plant**

An important aspect of the transition to flower and the successful production of dormant structures (seeds) is the senescence process. Senescence is the last step of development and can be induced by multiple factors. ABA plays critical roles in accelerating leaf senescence through transcriptional mechanism (Gao et al. 2016; Zhao et al. 2016). The expressions of *ORESARA1* (*ORE1*) and *SENESCENCE-ASSOCIATED GENE12* (*SAG12*), two marker genes induced during senescence, are transcriptionally activated by ABA signaling involving both ABFs and RAV1 (for ABA-insensitive/VP1) transcription factors (Figure 5) (Gao et al. 2016; Zhao et al. 2016). ABFs, such as ABI5 and EEL, also participate in dark induced senescence (Sakuraba et al. 2014). ABA systematically controls energy flow

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from source tissues (senescent leaves) to sink tissues (dormant seeds and floral meristem) (Zhao et al. 2016; Zhao et al. 2017). The floral meristems, under appropriate conditions, develop into dormant embryos. Senescence, in both processes, redistributes resources to dormant structures.

**PERSPECTIVES**

ABA has versatile roles in regulating plant growth, development and response to various environmental stresses. From 1960s when it was discovered till now, functions of ABA have been extensively studied, which was focused on the major metabolism and signaling pathway, and the regulatory mechanism of seed dormancy and stomatal movement. Due to the technology limitation of ABA visualization and the difficulty in illustrating stress signaling, the regulation of ABA metabolism has not been well studied, especially in cellular and tissue levels. Future efforts should be directed on how environmental changes modulate dynamics of ABA metabolism, and on how ABA regulates stress responses beyond functions in seeds and stomata.

Understanding how plants modulate ABA accumulation in response to environmental stresses is an important and challenging work, which would be facilitated by the identification of stress sensors. Although several putative sensors of salt, cold and osmotic stresses that affect $Ca^{2+}$ signals have been identified, the regulatory mechanism of ABA accumulation by these components is still unknown (Yuan et al. 2014; Ma et al. 2015; Jiang et al. 2019). Therefore, addressing the regulation of ABA dynamics requires investment on the upstream signaling of stresses together with innovative technologies for ABA visualization. The first challenge is to understand how stress induced $Ca^{2+}$ signal regulates SnRK2s activation and ABA accumulation that rapidly response to stresses. $Ca^{2+}$ signal may

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function together with ROS in regulating systemic signal that controls ABA accumulation in distal leaves, and ROS can inhibit core negative regulator PP2Cs (Sridharamurthy et al. 2014; Devireddy et al. 2018), indicating the role of transient $Ca^{2+}$ signal in regulating stress induced ABA accumulation. The next challenge is to clarify the spatiotemporal regulation of ABA accumulation and signaling including: 1) long-distance transport of stress signaling or ABA; 2) ABA dynamics in cellular, tissue or organ level. The recently developed excellent markers and reporters can facilitate these analysis (Duan et al. 2013; Jones et al. 2014; Waadt et al. 2014; Wu et al. 2018). Beside $Ca^{2+}$ and ROS signals, the small peptide CLE25 may also participate in the long distance delivery of stress signal to promote ABA biosynthesis in leaves (Ren et al. 2019).

The diverse function of ABA in regulating physiological processes is mainly attributed to the multiple downstream substrates regulated by SnRK2s. During past 20 years, excessive efforts have been focused on the regulation of seed germination and stomatal movement based on the well-established molecular-genetic and electrophysiological systems. However, recent biochemical and genetic studies have suggested that ABA also modulates multiple processes including senescence, abscission, vegetative dormancy, plant growth, carbon allocation, stem cell maintenance and differentiation and so on, probably through phosphorylation regulation by SnRK2 protein kinases (Fujii and Zhu 2009; Fujita et al. 2009; Nakashima et al. 2009; Yoshida et al. 2010; Gonzalez-Guzman et al. 2012; Umezawa et al. 2013; Wang et al. 2013; Yoshida et al. 2014; Miao et al. 2018; Zhao et al. 2018; Shinozawa et al. 2019). However, it is still not clear how ABA regulates these processes. Future efforts should also be directed to the regulation mechanism of these downstream responses. First, we should figure out the role of basal ABA. Plant

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growth is severely impaired both in ABA biosynthesis and signaling mutants even under well-watered conditions, indicating the growth promotion role of basal ABA signaling (Zhao et al. 2018). Next, how ABA regulates carbon allocation should be further studied. Carbon allocation is accompanied with leaf senescence, bud and seed dormancy, and is closely related to the harvest index of crops (Savage et al. 2016). Third, how ABA functions in stem cell maintenance and differentiation should be resolved (Han et al. 2010; Zhang et al. 2010; Wu et al. 2018). As sessile organisms, plants cannot “flight” as animals during stresses, and have to “fight” against stresses. Stem cells might be the “secret weapon” for plants to deal with stresses for re-development of tissues and organs. Finally, how we could breed productive and resistant varieties with cutting-edge technology broking the tradeoffs between growth and defense. Together, it is urgent to decipher the role of ABA in diverse physiological processes of plants and provide theoretical basis addressing critical problems regarding production, quality and resistance.

**ACKNOWLEDGMENTS**

This work was supported by the Shanghai Center for Plant Stress Biology from the Chinese Academy of Sciences, the Chinese Academy of Sciences Strategic Pilot Science and Technology Special (B) funding (XDB27040107), the National Natural Science Foundation China (31970293), and the Shanghai Pujiang Program (18PJ1410900).

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## Figure legends

### Figure 1. ABA biosynthesis, catabolism, and (de)conjugation in plants

Plants synthesize ABA using the carotenoid pathway initiated from β-carotene (C40). Processes that convert C40 to xanthoxin (C15) all take place in plastids, and in the cytoplasm, ABA2 and AAO3 convert xanthoxin into ABA. Among these processes, conversion of 9'-*cis*-neoxanthin and 9'-*cis*-violaxanthin to xanthoxin by NCEDs is a rate-limiting step in ABA biosynthesis. ABA catabolism is controlled by both ABA conjugation and catalytic hydroxylation. ABA can be glucosylated into ABA-GE by UGT71C5, whereas AtBG1 and AtBG2 can transform ABA-GE to active ABA. ABA can be catalyzed to phaseic acid (PA) by CYP707As, which in turn is catalyzed to dihydrophaseic acid (DPA) by PA reductase (PAR).

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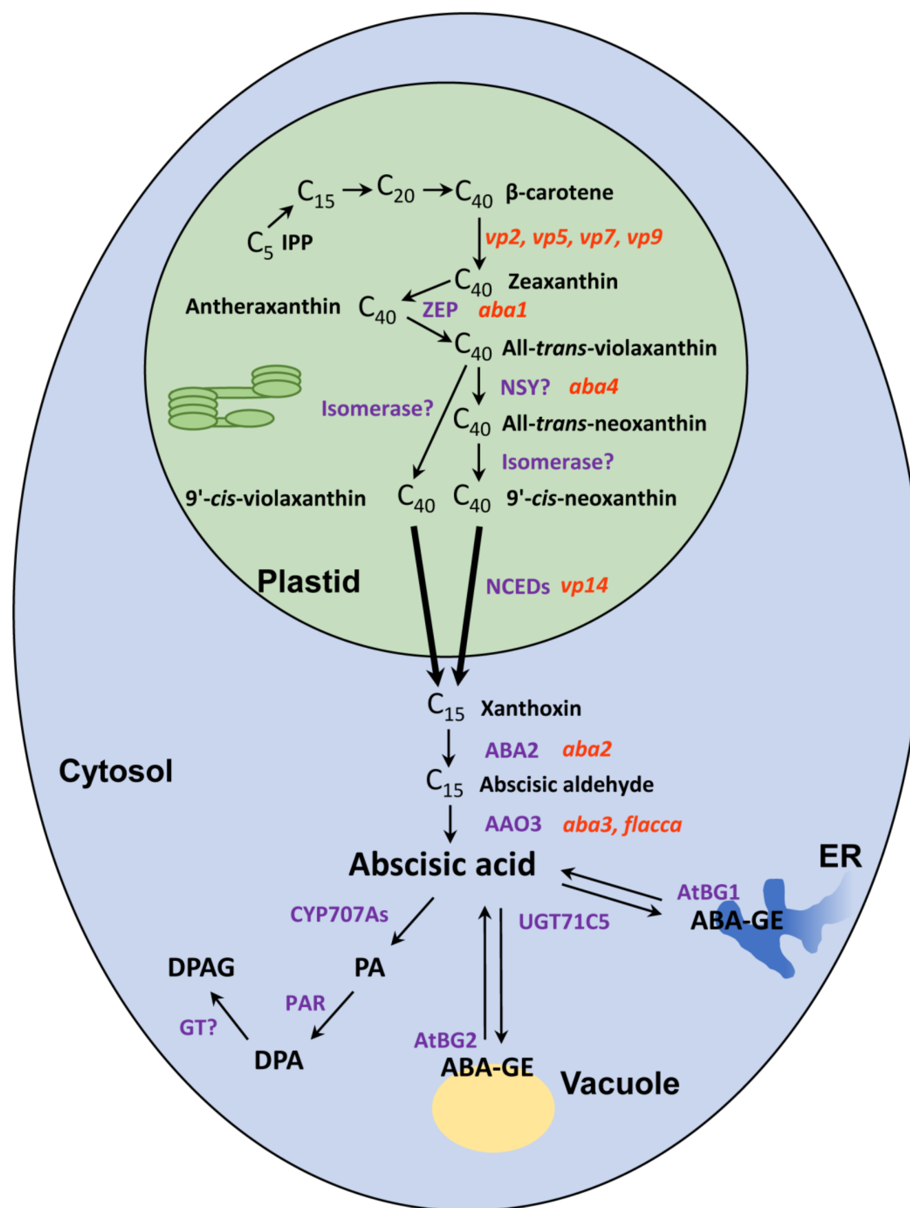


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**Figure 2. Regulations of core ABA signaling components**

In the absence of ABA, clade A PP2Cs interact with and inhibit SnRK2s. In the presence of ABA, PYLs form complexes with the PP2Cs, allows the activation of SnRK2s and downstream responses. The core ABA signaling components are tightly regulated by multiple regulators. PYLs are phosphorylated by multiple protein kinases including TOR, AEL, CEPR2, and CARK1. TOR phosphorylates and inactivates PYLs, while AEL and CEPR2 phosphorylate PYLs and promote their degradation. CARK1 phosphorylates PYLs and may enhances its activity, whereas NO inactivates PYLs by tyrosine nitration. The degradation of PYLs is regulated both by DDA1 and RSL1 via the ubiquitin-proteasome system, and by the ESCRT-I components VPS23A and ALIX through the endosomal-vacuole pathways. Activities of PP2Cs can be enhanced by EAR1 and the receptor-like kinase PR5K2, whereas their activity can be reduced by RDK1. PP2Cs are degraded by the 26S proteasome pathway through the PUB12/13 U-box, RGLG1/5 RING-type and CUL3-RING-based E3 ligases by interacting with BPMs. SnRK2s can be activated by several other kinases including RAF10 and BIN2. Besides clade A PP2Cs, the clade E PP2C EGR2 also inhibits SnRK2s. Although PYLs are essential for ABA mediated activation of SnRK2s, they also are involved in antagonistic regulation of SnRK2 activation during osmotic stress.

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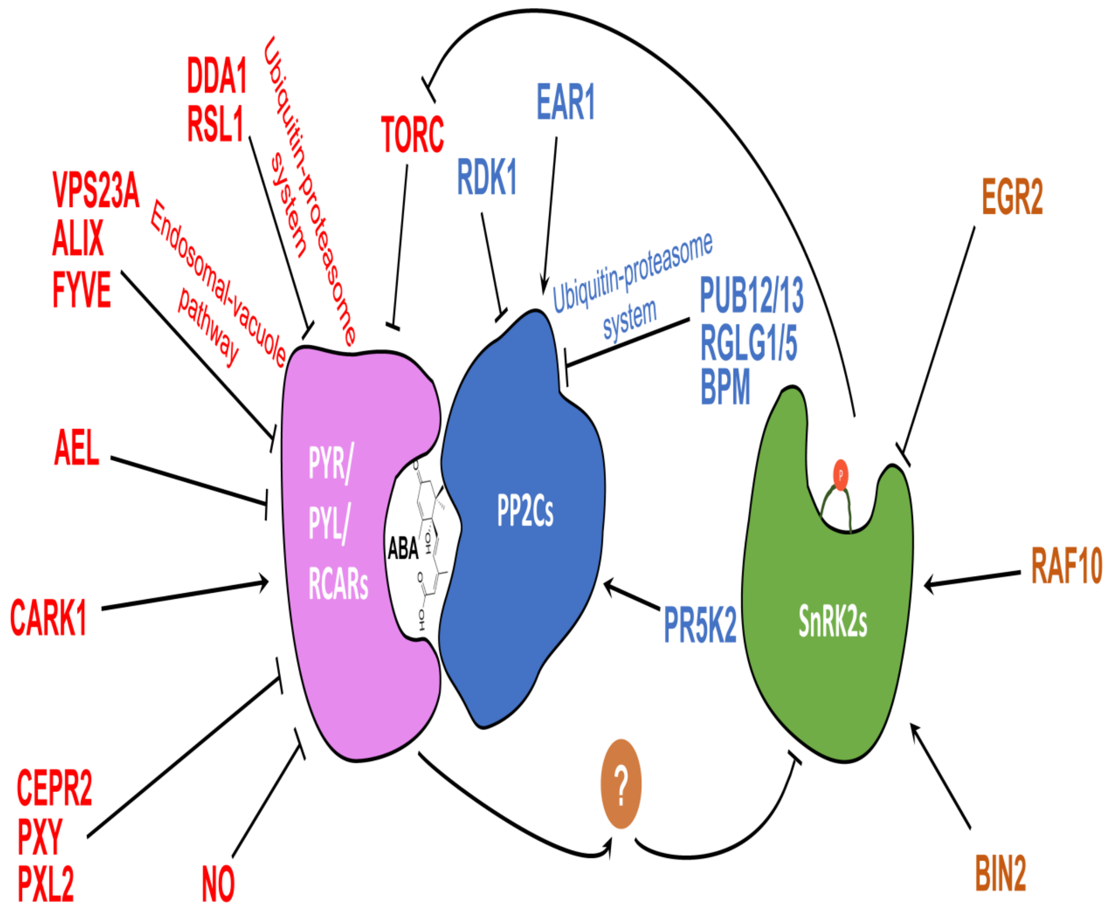


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**Figure 3. Modulation of ABA-induced stomatal closure**

ABA induces stomatal closure by both $Ca^{2+}$-dependent and $Ca^{2+}$-independent pathways. ABA-induced $Ca^{2+}$ signal involves the induction of ROS and $IP_3$, and may be decoded by CPK3/4/6/10/11/21/23 through activation of SLAC1 and SLAH3 to promote efflux of $Cl^-$, which is also regulated by GHR1. CPK21 activates the $K^+$ outward rectifying channel GOAK, while CPK13 inactivates KAT1 and KAT2, two $K^+$ influx channels. CIPK23, CPK8-CAT3 and CPK11-Di19-PR1/2/5 modules also regulate stomatal closure. The ABA activated SnRK2.6/OST1 is a key regulator of $Ca^{2+}$-independent stomatal closure. OST1 activates SLAC1, KUP6 and QUAC1 to promote efflux of $Cl^-$, $K^+$, and malate$^{2-}$, and inhibits KAT1 to reduce influx of $K^+$. OST1 can also phosphorylates and inhibits AKS1 to reduce expression of *KAT1*. Together, ABA induces stomatal closure by regulating guard cell ion fluxes.

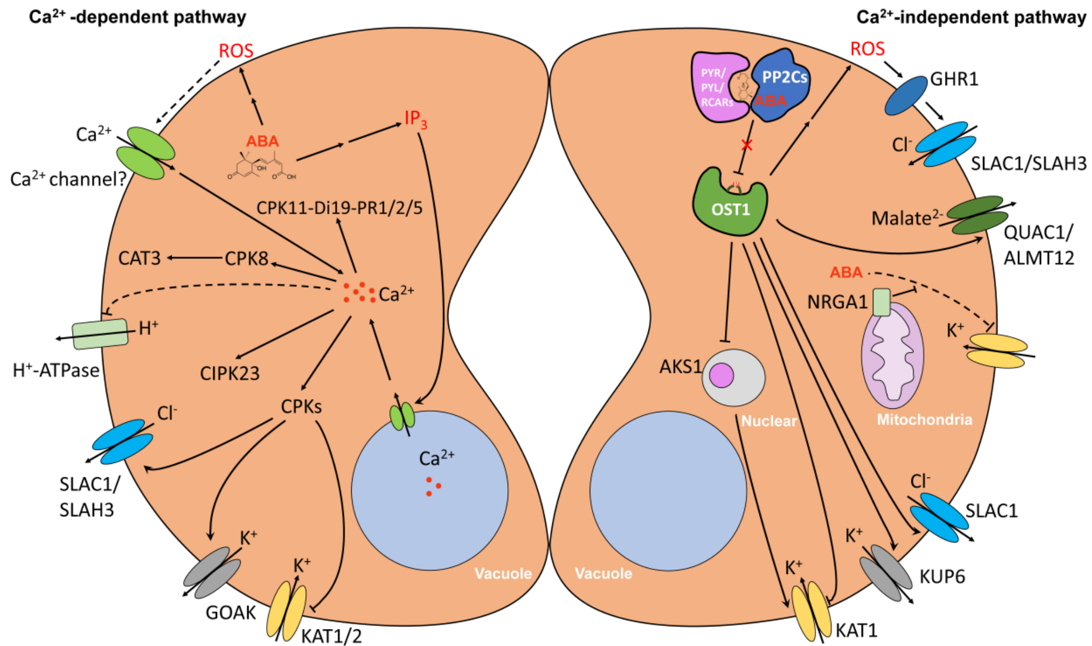


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**Figure 4. Regulations in seed development through ABA**

Time ordered developmental processes consist of embryogenesis, storage product accumulation, desiccation tolerance, dormancy, germination and post-germination growth arrest, which are deeply relied on transcriptional regulations. Embryogenesis is controlled by FUS3-LEC1-LEC2 network independent of ABI3. Both LAFL network and ABA signaling involve in storage product accumulation. Among the storage products, LEAs, together with HSPs, are pivotal for desiccation tolerance. The antagonism between ABA and GA largely contributes to the dormancy and germination. After germinating, stress induces post-germination growth arrest.

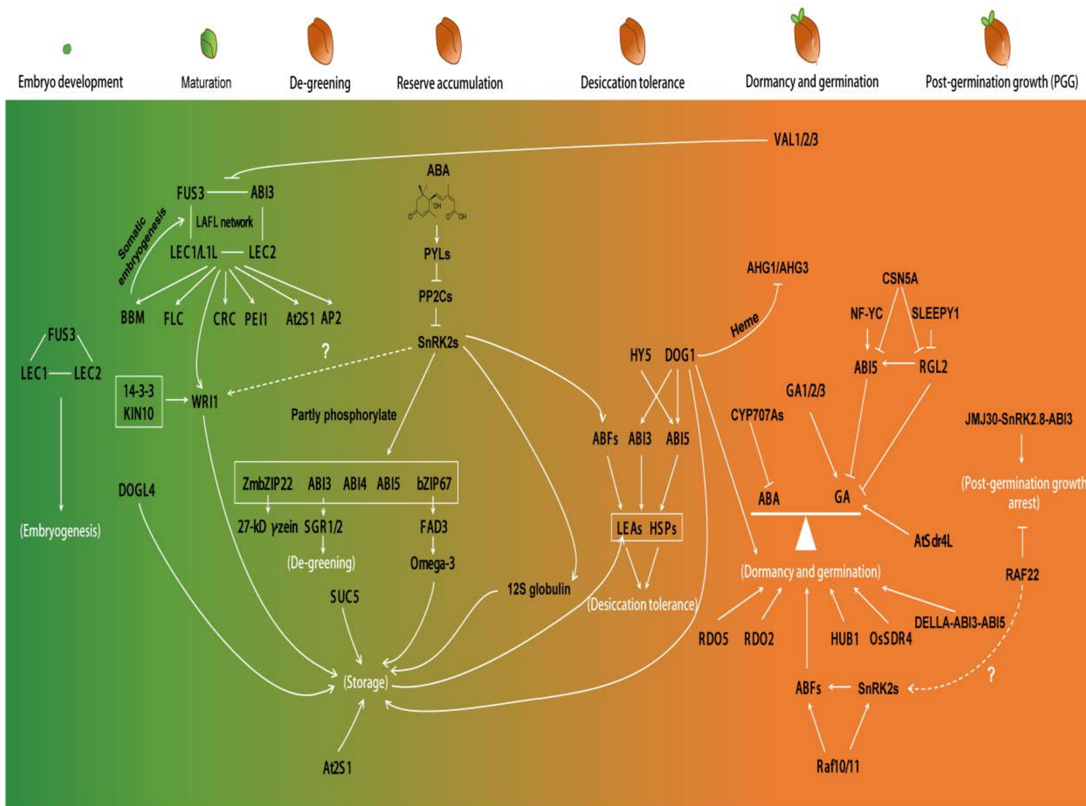


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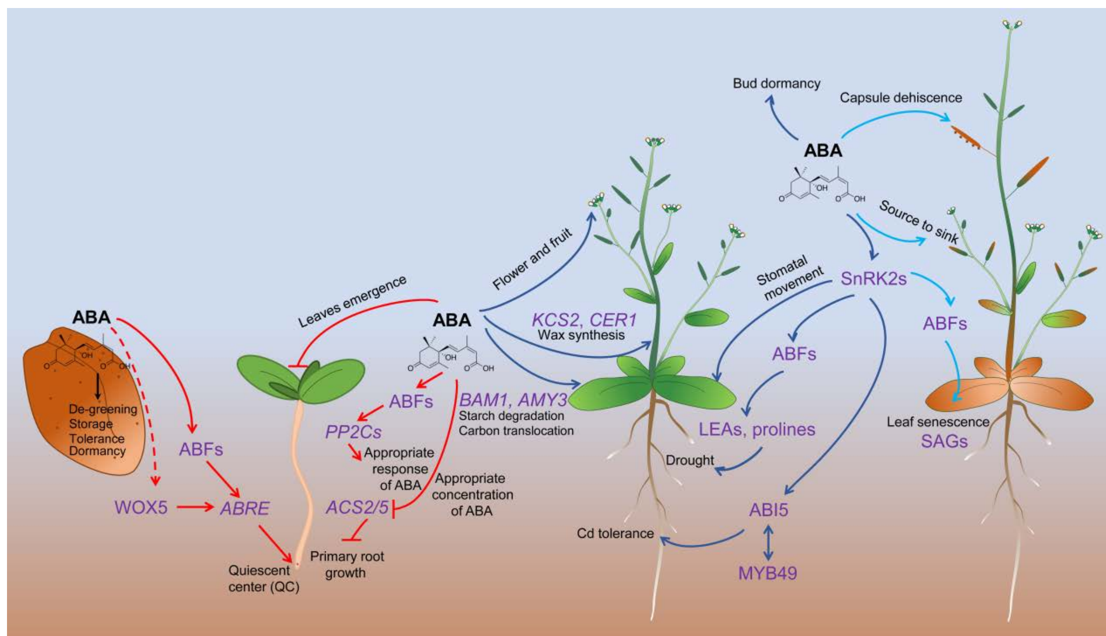
Figure 5. ABA functions in different stages during plant growth

ABA regulates multiple developmental stages of plants. ABA promotes root stem cell maintenance through ABFs together with WOX5, and maintains primary root growth by restricting the ethylene production through *ACS2/5*. ABA limits water loss through promoting wax synthesis and stomatal closure. ABA may promote bud dormancy by coordinating leaf senescence, starch degradation and source to sink carbon translocation through transcriptional reprogramming. ABA also protects plants from drought stress by promoting accumulation of LEAs and prolines. Together, ABA regulates plant growth, development, and stress responses.

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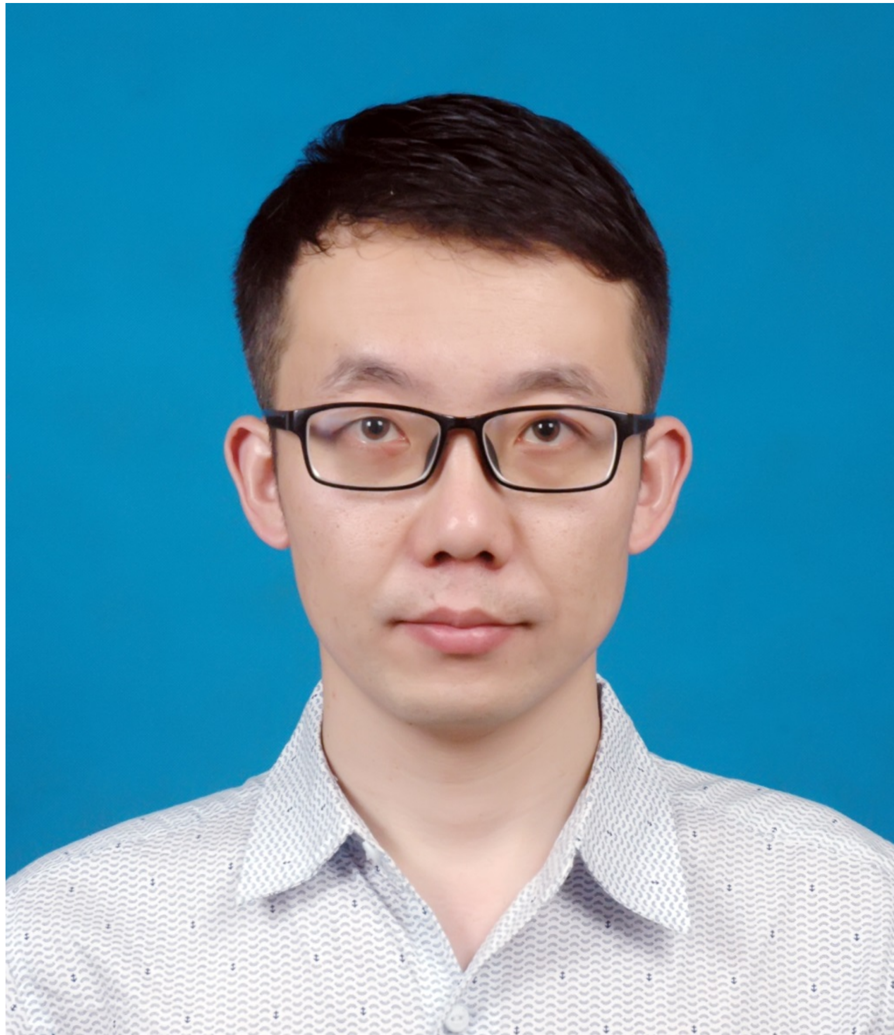

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