Phytohormone Signaling in Response to Drought

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Abstract Under natural conditions, plants are often exposed to both biotic (pathogens, wounding, insects) and abiotic stresses (drought, salinity, heat, high or low temperature, UV light, heavy metals, ozone) simultaneously. Among the various abiotic stresses, drought along with salinity and alkalinity confers osmotic stress and causes major yield losses, with water scarcity (drought) contributing to maximum losses. On perceiving stress, plants respond by activating signal transduction cascades that interact with other pathways (phytohormones) for an optimal response for survival. Hormones also control the response to environmental factors, but do so by influencing each other at a biosynthesis or signaling level rather than by discrete pathways. This coordination leads to a network of signal transduction that integrates various inputs leading to a comprehensive output resulting in a physiological adaptation to stress. The points of hormones interacting with one another are where crosstalk occurs, which helps in switching the response from one pathway to another. Published literature provide comprehensive information on the response of plants to drought and the role of hormones in regulating the response to drought from experiments directly imposing drought stress (dehydration stress-withholding water) or osmotic stress (turgor loss due to extracellular solutes) and experiments with mutants and others involving the functions of hormones and other signals. Changes in gene expression induced by drought overlap with gene expression regulated by hormones. This chapter presents the signal transduction pathways of hormones under drought stress and how they cross talk with each other in regulating the drought stress response in plants.

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1 Introduction

A number of environmental stresses (abiotic—drought, salinity, high and low temperature—and biotic) affect plant growth and productivity. Under stress, both hormonal and redox processes are imbalanced. Plants alter their gene and protein expression in response to signal cascades that are transduced when plants perceive stress (Munns and Tester 2008; Mittler et al. 2011; Munné-Bosch et al. 2013), which leads to a change in metabolic and physiological responses that help plants survive under stressful situations. Phytohormones, that under optimal growth conditions play a critical role in plant growth and development, also play a central role in integrating signal transduction occurring under stressful conditions. Phytohormones help in linking and reprogramming the stress-adaptive signaling cascades (Ma et al. 2006; Golldack et al. 2014).

The growth regulators abscisic acid (ABA) and ethylene (ET) play a vital role in signaling drought stress and conferring drought tolerance. Jasmonic acid (JA) and salicylic acid (SA), known for their role in biotic stress signaling and tolerance, also play a role in abiotic stress signaling and tolerance. In addition, the growth regulators cytokinins (CKs), auxin (AUX), gibberellic acid (GA), brassinosteroids (BRs), and strigolactones (SLs) play a role in abiotic stress tolerance (Zhao and Schaller 2004; Cheng et al. 2013; Wu et al. 2007; Cela et al. 2011; Jayakannan et al. 2015; Magome et al. 2008; Wu et al. 2014a, b; He et al. 2005; Divi et al. 2010). Most of the time, these phytohormones are involved in crosstalk with other phytohormones and other signaling cascades.

Among the abiotic stress, drought stress negatively affects crop growth and productivity (Anjum et al. 2017). Plants exposed to drought stress adapt a drought-escape, avoidance or tolerance mechanism to overcome the stress (Hussain et al. 2018). Under drought escape, plants maintain a short life cycle or adapt developmental plasticity. Under drought avoidance, plants increase their water uptake and decrease water loss such that they avoid physiological drought. However, under drought tolerance, cells tolerate drought by regulating mechanisms such as osmoprotection, antioxidative capacity, and tolerance. Plants maintain a balance among the different mechanisms.

Drought tolerance is a complex trait that operates at morphological, physiological and molecular levels (Tanveer et al. 2018). Traits such as earliness; stomata shape, size and structure; leaf number, orientation, and rolling; the presence of a cuticle; wax on leaf and stem; growth habit; and rooting pattern contribute to morphological characters associated with drought resistance and tolerance. Traits such as photosynthetic rate, transpiration rate, osmotic adjustment, and stomatal closure contribute to physiological characters. Regulation of these traits at the molecular level by regulating gene expression and protein synthesis contribute to molecular characteristics.

Functional genomic approaches (gene expression analysis) have aided in understanding the molecular mechanism of stress tolerance. A number of genes are regulated under stress conditions and can be grouped broadly in two categories based on function. One group involves the regulation of genes encoding proteins involved in cellular homeostasis and stress protection such as osmoprotectants, water channels, antioxidative enzymes, metabolic enzymes, and lipid-transfer proteins. The other group involves genes that code for kinases, transcription factors (TFs) and proteins or products that mediate stress signal transduction and result in the expression of stress-responsive genes. Among them are also genes that are associated with signaling pathway(s) of various phytohormones. Auxins, GA, CKs, ABA, ET, SA, JA, BR, and SLs are the major hormones produced by plants. Although all play a role in the stress response, the hormones ABA, SA, JA, and ET play a major role in the plant response to biotic and abiotic stresses (Bari and Jones 2009; Nakashima and Yamaguchi-Shinozaki 2013). On sensing stress (abiotic or biotic stress), several signaling pathways are initiated in plant cells. Some lead to the induction and alteration of intercellular levels of Ca^{2+}, reactive oxygen species (ROS), and inositol phosphate and activation of the kinase cascade.

2 Abscisic Acid (ABA)

Abscisic acid plays major role in the plant response to osmotic stress induced by cold, high salinity and drought. It is an endogenous messenger of the plant's water status. Plant hormone, ABA is typically synthesized in response to stress due to enhanced expression of its biosynthetic genes (Swamy and Smith 1999; Zhu 2002). Treating plants with ABA mimics exposure to stress. Abscisic acid plays a critical role in response to various stress signals. It triggers reprogramming of the transcriptome and stomatal closure to control transpirational water loss (Christmann et al. 2007; Cutler et al. 2010; Raghavendra et al. 2010).

Signaling under stress involves various proteins leading to regulation of stress-responsive gene expression. Under stress, signaling pathways occurring under stress (osmotic or drought stress) can be broadly classified as ABA-dependent- or independent. TFs that bind to ABA-responsive element (ABRE) *cis*-elements play a major role in ABA-dependent gene expression and those that bind to the dehydration-responsive element/C-repeat (DRE/CRT) *cis* element are involved in ABA-independent gene expression in response to drought stress (Fujita et al. 2011; Qin et al. 2011).

Abscisic acid signaling has been extensively studied, and various components have been identified. The proteins PYRABACTIN RESISTANCE/PYR1-LIKE/REGULATORY COMPONENTS OF ABA RECEPTORS (PYR/PYL/RCARs) function as soluble ABA receptors, as demonstrated by chemical genetic and biochemical approaches. Besides their identification in *Arabidopsis*, they have been identified in rice (*Oryza sativa*), maize (*Zea mays*), sorghum (*Sorghum bicolor*), soybean (*Glycine max*), grapevine (*Vitis vinifera*), citrus (*Citrus sinensis*), and tomato (*Solanum lycopersicum*) (Klingler et al. 2010; Sun et al. 2011; Boneh et al. 2012; Kim et al. 2011; Romero et al. 2012). GPCR-type G protein 1 (GTG1)/GTG2 are membrane proteins with homology to G-protein coupled receptors (GPCRs). ChlH (or GENOMES UNCOUPLED 5 [GUN5]) and GTG1/GTG2 may be ABA receptors. However, neither ChlH/GUN5 nor GTG1/GTG2 can bind the biologically active ABA isomer (Shen et al. 2006; Pandey et al. 2009).

Forward genetic screening using mutants resistant to the ABA agonist pyrabactin and a search for biochemical interacting partners of ABA insensitive 1 (ABI1) and ABI2 led to the identification of PYR1 and RCAR1 among the 14 genes that code for PYR/PYL/RCARs (Ma et al. 2009; Nishimura et al. 2009). On activation, the receptor interacts with partners such as type 2C protein phosphatase (PP2C) and sucrose nonfermenting 1-related protein kinase 2 (SnRK2) complex (Umezawa et al. 2009, 2010). In the absence of ABA, PP2C binds to SnRK2 and mediates its dephosphorylation. Binding of ABA to its receptor (PYR/PYL/RCARs) fits well into the active site of PP2C enzyme, thereby inhibiting the phosphatase activity of PP2C. This situation results in phosphorylated SnRK2s, which can activate relevant TFs, and in turn leads to activation of an ABA-induced transcriptional cascade (Kline et al. 2010). Therefore, an increase in endogenous ABA due to environmental and/or developmental cues leads to sequestration of PP2C and ABA-induced release or activation of SnRK2.6. Autophosphorylation of SnRK2s then phosphorylates downstream proteins such as ABA-responsive element binding proteins/ABA-responsive element binding factor/basic-leucine zipper (AREB/ABF/bZIP) proteins and anion channels (Cutler et al. 2010; Klingler et al. 2010; Umezawa et al. 2010; Seiler et al. 2014). SnRK2s can be further regulated by a positive regulator, ARK (B3-MAPKKKs), and a negative regulator, casein kinase 2 (CK2) (Saruhashi et al. 2015; Meggio and Pinna 2003; Vilela et al. 2015).

The *Arabidopsis* genome encodes 112 phosphatases, of which 76 code for PP2Cs and at least 6 are involved in ABA signaling with well-characterized ABI1/2 and homolog of ABI1 (HAB1). The mutants *abi1* and *abi2* display ABA hypersensitivity, insensitive phenotypes and reduced seedling growth, seed dormancy, drought tolerance, and stomatal regulation. Other members of PP2Cs include ABA-hypersensitive germination 1 (AHG1), AHG3/AtPP2CA from *Arabidopsis*, and OsPP108 from rice (Leung et al. 1994, 1997; Meyer et al. 1994; Saez et al. 2004; Singh et al. 2015).

The protein kinase SnRK2 family is a group of plant-specific serine/threonine kinases that participate in cellular responses to drought and dehydration (Hrabak et al. 2003; Saruhashi et al. 2015). Depending on the affinity toward ABA, the SnRK2 family is divided into three subgroups. Subgroup I does not respond to ABA, subgroup II includes weak respondents, and subgroup III includes active respondents of ABA that are key players of ABA-dependent gene expression (Hrabak et al. 2003; Boudsocq et al. 2007). *Arabidopsis* has 10 SnRK2 members (SnRK2.1-2.10); ABA activates five SnRK2s (SnRK-2.2, -2.3, -2.6, -2.7, -2.8). Mutation in three SnRKs (*snrk2.2/2.3/2.6*) blocks all main ABA responses (Fujii and Zhu 2009; Fujita et al. 2009; Waadt et al. 2015). In addition, all SnRK2s are involved in ABA and stress signaling except SnRK2.9, which is activated by osmotic stress (Boudsocq et al. 2007; Furihata et al. 2006; Yoshida et al. 2006). ABA-activated protein kinase (AAPK), the ortholog of Arabidopsis open stomata 1 (OST1)/SnRK2.6, was the first protein kinase identified (from *Vicia faba*).

SnRK2 kinases phosphorylate the TFs ABFs/AREBs and ABI5, both in vitro and in vivo, involved in ABA responsive gene expression (Kobayashi et al. 2005; Furihata et al. 2006; Sirichandra et al. 2010; Nakashima et al. 2009). In addition, SnRK2 (OST1/SNRK2.6) phosphorylates plasma membrane proteins anion channel slow anion channel-associated 1 (SLAC1), potassium channel protein KAT1 and NADPH oxidase AtrbohF involved in regulating stomatal aperture (Geiger et al. 2009; Sato et al. 2009; Sirichandra et al. 2009). Phosphoproteomic and mutation study approach has identified ascorbate peroxidase, Ca^{2+}/H^{+} antiporter regulator protein, G-protein beta subunit-like protein, glyoxysomal malate dehydrogenase, manganese superoxide dismutase, triose phosphate isomerase and others as potential SnRK2 targets (He and Li 2008; Umezawa et al. 2013).

TFs that play a significant role in ABA-regulated gene expression include ABFs/AREBs, ABI5, myeloblastosis (MYB), myelocytomatosis (MYC), NAM: no apical meristem (NAC), *Arabidopsis* transcription activation factor (ATAF), cup-shaped cotyledon (CUC), and ethylene response factor (ERF). ABFs/AREBs are regulated by SnRK2-mediated phosphorylation (Fujita et al. 2011; Nakashima et al. 2012; Rushton et al. 2012). ABFs/AREBs and ABI5 encode proteins belonging to the bZIP family regulate ABA and stress responses by binding to ABRE in promoters of target genes (Choi et al. 2000; Uno et al. 2000; Lopez-Molina et al. 2001). AREB1/ABF2, AREB2/ABF4, ABF3 and ABRE binding protein 9 (ABP9) are involved in signaling drought stress (Riechmann et al. 2000; Yoshida et al. 2010). MYC and MYB, belonging to the basic helix loop helix (bHLH) subfamily, also regulate ABA signaling by regulating stress-inducible genes. AtMYB60, AtMYB44, AtMYB15, and AtMYC2 mediate drought stress signaling (Abe et al. 1997, 2003, Jaradat et al. 2013). In addition, NAC (AtNAC) and ERF (AtERF7)-type TFs are involved in regulating ABA signal transduction under drought stress (Song et al. 2005; Zhang and Gan 2012).

3 Ethylene (ET)

This simple two-carbon molecule plays a major role in regulating biotic and abiotic stress signaling (Morgan and Drew 1997; van Loon et al. 2006). Biosynthesis of ET is simple, consisting of three steps. Methionine is used as precursor and is converted to S-adenosyl methionine (SAM), which is converted to ET by the action of ACC synthase (ACS) and ACC oxidase (ACO). ACS is regulated by drought stress, thereby regulating ET levels under drought stress.

Endoplasmic reticulum membrane-localized proteins perceive ET, are negative regulators of ET signaling, and play a role as ET receptors. Arabidopsis has five ET receptors: ET response 1 (ETR1) and ET response sensor 1 (ERS1), belonging to subfamily I, and ETR2, ERS2, and ET insensitive 4 (EIN4), belonging to subfamily II (Chen et al. 2005; Lacey and Binder 2014). Similarly, rice has five receptors: OsERS1 and OsERS2, belonging to subfamily I, and OsETR2, OsETR3, and OsETR4, belonging to subfamily II (Watanabe et al. 2004; Yau et al. 2004). Constitutive triple response 1 (CTR1), also a membrane protein and central transducer, is a negative regulator of ET signaling and acts downstream of the receptor, which is a Raf-like Ser/Thr protein kinase. Downstream of this is ETI2, also localized to the endoplasmic reticulum membrane that activates EIN3 and EIN3-like 1 (EIL1), which function as TFs inducing the expression of ERF1 and inducing or repressing that of many ET response genes (Kendrick and Chang 2008; Stepanova and Alonso 2009).

Therefore, in the absence of ET, CTR1 kinase activity is induced, which phosphorylates EIN2 and prevents its localization to the nucleus (Kieber et al. 1993; Bisson and Groth 2010; Ju et al. 2012). In addition, two F-box proteins—ETI2-targeting protein 1 (ETP1) and ETP2—reduce levels of EIN2 protein (Qiao et al. 2009). EIN2 is localized to the nucleus on its dephosphorylation and cleavage of its C-terminus, in the presence of ET, and it regulates activation of EIN3/EIL1 leading to the ET response (Ju et al. 2012). Similar to EIN2, two F-box proteins—ETI3 binding F-box protein 1 (EBF1) and EBF2—that are downregulated by ET, reduce EIN3/EIL1 protein levels in the absence of ET. Among the ET signal transduction pathway, ERFs are key players of abiotic-stress tolerance induced by drought stress. ERFs are also induced by various other abiotic stresses. ERFs belong to the APETALA2/ERF TF family. The expression of ERFs increases under drought stress, and many ERFs bind to DREs and regulate tolerance to abiotic stress.

ERF induces the expression of P5CS, germin-like protein 9, osmotin 34, similar to RCD one 5 (SRO5), responsive to dessication 29B (RD29B), early response to dehydration (ERD7) and RD20, leading to drought tolerance (Cheng et al. 2013). In addition, OsDERF1 directly binds promoters of the ERF repressors *OsERF3* and *OsAP2-39* that suppress ET synthesis and regulate drought tolerance (Wan et al. 2011; Zhang et al. 2013). Although most ERFs are transcriptional activators, two (ERF8 and ERF9) are transcriptional repressors. ERF8 is an inhibitor of cell division and leaf growth and thereby regulates the drought stress response (Thao et al. 2015; Dubois et al. 2013, 2018).

4 Jasmonic Acid (JA)

The JAs collectively include JA and its conjugates methyl jasmonate (MeJA) and jasmonyl-isoleucine (JA-Ile) (Ghasemi et al. 2014). They are lipid-derived oxylipins, synthesized from linolenic acid via the octadecanoid pathway as a result of oxidation by lipoxygenases (Feussner and Wasternack 2002).

Jasmonic acids are well known for their role in developmental processes, secondary metabolite synthesis and the plant defense response against pathogens and wounding (McConn et al. 1997; Reymond and Farmer 1998; Wasternack and Hause 2002; Lorenzo and Solano 2005; Schommer et al. 2008). Despite reports of the role of JA in the abiotic stress response, its role in drought stress is little known (Maksymiec et al. 2005; Brossa et al. 2011; Dong et al. 2013; Qiu et al. 2014; Zhao et al. 2013; Clarke et al. 2009). Jasmonic acid basically imparts drought tolerance by modulating stomatal closure and minimizing transpiration water loss. In addition, MeJA increases root hydraulic conductivity and helps plants uptake more water under drought stress (Tanaka et al. 2005; Munemasa et al. 2007; Daszkowska-Golec and Szarejko 2013; Sánchez-Romera et al. 2014). In addition, JAs play an important role in signaling the drought-induced antioxidant response by enhancing the expression and activity of the antioxidant enzymes superoxide dismutase, peroxidase, and catalase (Nafie et al. 2011; Anjum et al. 2011). However, JA biosynthesis, crosstalk and signal transduction is more or less similar between biotic and abiotic stress, with unique aspects being identified for abiotic stress response.

An F-box protein coronatine insensitive 1 (COI1), jasmonate ZIM domain (JAZ) proteins, multi-component E3 ubiquitin ligase-Skp/Cullin/F-box complex (SCF-COI1) and 26S proteasome are key players in JA signaling (Thines et al. 2007; Deshaies 1999; Turner et al. 2002). JA-Ile functions as a ligand and promotes the assembly of COI1 and JAZ proteins (Thines et al. 2007). JAZ proteins are repressors or negative regulators of JA signaling that are targeted for degradation by the $\mathrm{SCF}^{\mathrm{COI1}}$-dependent 26S proteasome pathway. In addition, JAZ proteins interact with co-repressor Topless (TPL) and TPL-related proteins (TPRs) via an adaptor protein, novel interactor of JAZ (NINJA), in JA signaling (Pauwels et al. 2010). Hence, JA-mediated destruction of JAZ transcription repressors leads to the activation of downstream genes (Staswick 2008; Thines et al. 2007; Pauwels and Goossens 2011). JAZ proteins target and regulate TFs belonging to bHLH factors (AtMYC2, OsBHLH1, RERJ1, MYC3, MYC4, Glabra3-GL3, enhancer of glabra 3 1 [EGL1] and transparent testa [TT8]). A few are regulated under drought stress (RERJ1, OsbHLH148), and their overexpression results in enhanced drought tolerance (Kiribuchi et al. 2005; Seo et al. 2011). JAZ proteins interact with the Apetala 2 group of TFs—target of eat 1 (TOE1) and TOE2—and repress transcription (Zhai et al. 2015). An intermediate of JA biosynthesis, 12-OPDA, also plays a role in JA signaling and has a major role in drought response (Savchenko et al. 2014).

5 Salicylic Acid (SA)

Similar to JA, the phytohormone SA plays an important role in response to biotic stresses, pathogenesis, plant growth and development, although antagonizing gene induction by JA. In addition, it participates in signaling abiotic stress responses (drought, salinity, high and low temperature, ozone, UV light and heavy metals) (Rivas-San Vicente and Plasencia 2011; Hara et al. 2012). However, its utility depends on its concentration: low concentration enhancing antioxidant capacity and high concentration inducing oxidative stress and leading to cell death (Hara et al. 2012).

The synthesis of endogenous SA levels is increased in plants exposed to drought stress, and plants susceptible to drought show reduced SA level. SA probably protects plants under stress by regulating the induction of SA-inducible PR genes (Munné-Bosch and Penuelas 2003; Sawada et al. 2006; Miura et al. 2013).

In plants, SA is synthesized in plastids via two distinct pathways: the isochorismate (IC) pathway, the major pathway, and the phenylalanine ammonia-lyase (PAL) pathway. Both pathways begin with chorismic acid, an end product of the shikimate pathway (Wildermuth et al. 2001; Catinot et al. 2008). IC synthase (ICS), responsible for converting chorismic acid to IC, is regulated by biotic stress and also drought stress (Nawrath and Métraux 1999; Hunter et al. 2013). Mutants (*adr1, myb96-1d, siz1, acd6*, and *cpr5*) that accumulated endogenous SA showed both SA-dependent disease resistance and drought tolerance (Seo and Park 2010; Miura et al. 2013).

Well-known systemic acquired resistance is induced by SA and leads to an immune response against pathogens via transcriptional reprogramming (Durrant and Dong 2004). Under drought stress, plants are protected against oxidative stress induced by drought stress by the induction of stress proteins such as glutathione S-transferases, ascorbate peroxidase (APX), and 2-cysteine peroxiredoxin by enhanced SA levels (Kang et al. 2012). Exogenous application of SA and high endogenous SA level promote stomatal closure during water deficit to conserve water, which leads to reduced photosynthesis likely because of ROS induced by SA (Senaratna et al. 2000; Korkmaz et al. 2007).

Jasmonic acid binds to effector proteins such as catalase, APX, methyl SA esterase, and carbonic anhydrase (Sanchez-Casas and Klessig 1994; Du and Klessig 1997; Slaymaker et al. 2002; Forouhar et al. 2005). However, mutant studies predicted that non-expressor of PR genes 1 (NPR1) was an SA receptor candidate (Delaney et al. 1995; Cao et al. 1997). NPR1 functions as a positive regulator of the SA-mediated defense response. In addition, NPR3 and NPR4, paralogs of NPR1, are SA receptors (Fu et al. 2012). They have a direct role in defense gene expression and affect disease resistance (Fu et al. 2012; Wu et al. 2012). They interact with cullin 3 (CUL3) ubiquitin E3 ligase and recruit NPR1 for proteasome-mediated degradation dependent on SA. Studies of mutants of the mitochondrial succinate dehydrogenase (SDH) pathway, disrupted in stress response 1 (*dsr1*) and SDH assembly factor 2 (*sdhaf2*), demonstrated that SA directly contributes to stress signaling by increasing mitochondrial H_2O_2 production.

6 Brassinosteroids (BRs)

Brassinosteroids are a plant-specific steroid group of plant hormones known for their role in growth, development, reproduction, and stress response (Sharma et al. 2015; Vardhini and Anjum 2015; Tang et al. 2016; Wei and Li 2016; Xia et al. 2009, 2014). Brassinolide (BL) is synthesized from campesterol via a series of reductions, hydroxylations, epimerizations, and oxidations, whereas the mevalonic acid-dependent triterpenoid pathway is used for synthesis of other major BRs (Fujioka et al. 1998; Fujioka and Yokota 2003; Chung and Choe 2013). BRs actively participate in drought stress response and tolerance, as demonstrated by enhanced drought of plants overexpressing the BR biosynthetic gene encoding cytochrome p450 (Tiwari et al. 2017). Brassinosteroids also help reduce the photoinhibition that commonly occurs under abiotic stress conditions (Ahammed et al. 2015)

The BRs are recognized by the BRASSINOSTEROID INSENSITIVE 1 (BRI1) cell-surface leucine-rich repeat kinase group of receptor proteins. BRI further interacts with co-receptor BRI-associated receptor kinase 1 (BAK1) and initiates a series of phosphorylation and dephosphorylation events resulting in the regulation of gene expression (Belkhadir and Jaillais 2015; Nakamura et al. 2017). BR-mediated signaling is transduced by the bHLH group of TFs such as CESTA and TEOSINTE BRANCHED 1, CYCLOIDEA, PCF1 (TCP) (Poppenberger et al. 2011).

Similarly, the TF BRASSINAZOLE RESISTANT 1 (BZR1), induced by BRs, plays a role in maintaining cell cycle progression even under stress (Hacham et al. 2011). In contrast, BRASSINOSTEROIDS AT VASCULAR AND ORGANIZING CENTER (BRAVO), an R2R3 MYB transcription factor, inhibits stem cell proliferation. In the root quiescent center, interaction with BRI1-EMS SUPRESSOR 1 (BES1) represses the activity of BRAVO (Vilarrasa-Blasi et al. 2014). In addition, BRs remodel the cell wall under abiotic stress by inducing genes responsible for cell wall remodeling: pectin lyase-like proteins, expansins, and xyloglucan endotransglucosylase/hydrolases (Rao and Dixon 2017). In addition, BRI1 receptor induces the expression of pectin methylesterases under stress, thereby resisting the loss of cell wall and maintaining the integrity of the cell wall via interaction of BAK1 and RECEPTOR-LIKE PROTEIN (RPL44) (Wolf et al. 2014). These mechanisms help plants in stress adaptation and increase longevity.

7 Hormonal Crosstalk

7.1 ABA Crosstalk

In response to environmental stress (drought), ABA regulates growth and development via crosstalk with other plant hormones. Abscisic acid interacts antagonistically with most plant hormones. ABA and auxin work in opposing directions in regulating growth and development. Both of these hormones control cell division, seed dormancy and germination, primary root growth, seedling growth, etc. Crosstalk between auxin and ABA in regulating growth occurs via regulation of auxin or ABA response pathways. Auxin activates the ABA response and or ABA biosynthesis. Under osmotic stress, ABA increases basipetal transport of auxin via AUX1 (an auxin influx transporter) and PIN2 (an auxin efflux transporter) (Sun and Li 2014; Wang et al. 2011; Belin et al. 2009; Liu et al. 2013; Xu et al. 2013). Similarly, ABA and CK crosstalk with each other. ABA regulates CK by regulating CK oxidase that degrades CK. Under stress, CK via cytokinin receptor kinases (AHK2 and AHK3) negatively regulates ABA, ABA signaling and stress gene expression (Tran et al. 2007; Jeon et al. 2010). ABA also acts antagonistically with ET in regulating stomatal closure. ET inhibits ABA signaling and thereby delays stomatal closure.

Similarly, ABA inhibits ET biosynthesis by regulating ERF1 and long hypocotyl 5 (HY5), thereby repressing ACS5 (ethylene biosynthesis gene). The TF HY5 is a key player in the crosstalk between ABA and ET (Harrison 2012; Tanaka et al. 2005; Li et al. 2011). However, the crosstalk between ABA and JA is complex. Reduction of ABA level upregulates JA. Multiple components of ABA and JA–ET signaling pathways antagonistically interact in regulating stress-responsive gene expression, with MYC2 playing a central role or being a major hub in the crosstalk (Anderson et al. 2004; Chen et al. 2011; Fernández-Calvo et al. 2011; Sun and Li 2014).

7.2 ET Crosstalk

The ERF key regulatory proteins of ET signal transduction are also the hub of the crosstalk between ET and ABA, JA, SA, BR, and redox signaling. Under abiotic stress, both ABA and JA regulate ERFs. However, we have few reports on the crosstalk under drought stress. JA positively regulates the induction of ERFs [ERF6, JERF1, JERF3, Tsi1, OPBP1, and GmERF3 (Sewelam et al. 2013; Wu et al. 2007, 2008; Wang et al. 2004; Park et al. 2001; Zhang et al. 2009a, b)], but ABA negatively regulates the induction of few ERFs (ERF1/6) (Cheng et al. 2013; Sewelam et al. 2013). In contrast, ABA induces other ERFs (CsERF, GmERF3, LchERF, JERF3, TSRF1, TaERF1 and JERF1) (Ma et al. 2014; Zhang et al. 2009a, b; Wu et al. 2007, 2008, 2014a, b; Quan et al. 2010; Xu et al. 2007). Overexpression of TSRF1 results in enhanced drought tolerance (Quan et al. 2010; Cheng et al. 2013). The negative regulator AtERF7 inhibits ABA-induced gene expression, thereby decreasing drought stress tolerance (Song et al. 2005).

7.3 JA Crosstalk

The JA crosstalk with ABA at MYC2 is involved in drought stress signaling and activates genes such as RD22 and RD26, which are also upregulated under drought stress (Abe et al. 2003; Fujita et al. 2004, 2006; Harb et al. 2010). JA and GA also crosstalk, which is mediated by direct interaction between DELLA and JAZ proteins, thereby competing for the JAZ–MYC2 interaction that activates JA-responsive genes (Boter et al. 2004; Hou et al. 2010). Expression of the MYC2 target RGL3, which encodes DELLA, is induced by JA signaling (Wild et al. 2012). MYC2 is released when JA degrades JAZ. DELLA is also the hub of crosstalk between GA and ABA under abiotic stress. In addition, there is crosstalk between JA and ET: both activate Arabidopsis AtERF1, which imparts drought tolerance (Cheng et al. 2013).

7.4 SA Crosstalk

SA interacts with other phytohormones, and depending on the hormone, has a synergistic or antagonistic relation under optimal and stressful conditions. SA-induced ABA improves osmotic adaptation and growth under normal, salt and other abiotic stress (Szepesi et al. 2009; Szalai et al. 2011). Mitogen-activated protein kinases are key players of signaling components where antagonistic interaction between SA and JA occurs (Khan et al. 2012a, b). In addition, NPR1, the master regulator of SA-mediated defense, is a critical component of the epibassinolide-mediated increase in abiotic stress tolerance (heat and salt) (Divi et al. 2010).

7.5 BR Crosstalk

BR and ABA crosstalk via ABI3/viviparous1 (ABI3/VP1) and related to ABI3/VP1 (RAV1) and induce BRI expression (Saini et al. 2015). Maintenance of cell wall integrity is via interaction of BR with other hormones (Wolf et al. 2014). The long-distance effect of BR is via crosstalk with multiple hormones (Vriet et al. 2013; Gudesblat and Russinova 2011). BRs antagonistically cross-interact with ABA, ET, SA, auxin, GA and polyamines (Vardhini and Anjum 2015). Analysis of *det-2* and *bri-1* BR mutants demonstrated that BIN2 negatively regulates BR signaling in the presence of ABA signaling, which is via ABI1/2 (PP2Cs) that function downstream of BRI1 and upstream of BIN2 and regulate BR signaling (Zhang et al. 2009a, b). ABI1/2 dephosphorylate BIN2, and ABA inhibits BIN2 phosphorylation by BES1, thereby reducing BR signaling (Wang et al. 2018). BIN2 also interacts with ABI5 and phosphorylates it and mediates ABA signaling (Hu and Yu 2014). Both ABA and BR induce the expression of BRASSINOSTEROID-SIGNALING KINASE 5 (BSK5), a key player in ABA signaling. Similar crosstalk between ABA and BR occurs with a TF, BZR1 (Yang et al. 2016). BR and ET crosstalk via H_2O_2 and regulate stress tolerance (Zhu et al. 2016). BR signaling interacts with SA signaling via the TF WRKY70, which negatively regulates SA biosynthesis. NPR1, regulating SA signaling, interacts with BIN2 and BZR1 and regulates stress tolerance (Divi et al. 2010; Li et al. 2013).

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