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Insight into abscisic acid perception and signaling to increase plant tolerance to abiotic stress

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ABSTRACT

As changes occur in climate, abiotic stress to agricultural production is an inevitable threat to farmers' ability to meet an increasing demand to feed people. Plants have developed a stress tolerance mechanism to reduce the effects of such environmental conditions by engaging various stress-responsive genes. Accordingly, various signal transduction networks are used to fabricate stress tolerance. Engineering of the phytohormone abscisic acid (ABA) could be a choice method for scientists to mitigate abiotic stress because of its widespread role in response to salt, drought, heat, and cold stresses including triggering stomatal regulation and leaf senescence. In addition, it plays a crucial role in seed maturation, seed dormancy, stomatal opening/closure and increases resistance against pathogens through callose depositions and regulates physiological strategies in stress signaling pathways through synchronizing of hormonal crosstalk. The transcriptional regulation can be achieved through ABA-dependent and ABA-independent signaling cascades. ABA15 and RD29A genes are regulated in ABA-dependent and independent manners to mitigate stress tolerance. ABA regulatory components (RCARs) including pyrabactin resistance PYR/PYL genes, SnRK2 type protein kinases, transcription factors (WRKY, NAC, AREB1, bZIP, RGL2, and ABRE), reactive oxygen species, jasmonic acid and cytokinin hormones regulate ABA gene action in response to abiotic stresses.

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1. Introduction

Abiotic stresses activate several biochemical, physiological, and molecular mechanisms that have an impact on cellular pathways. There is an urgent need to devise dynamic and novel approaches to combat emerging environmental challenges, hence, engineering of phytohormones might be the best option to enhance productivity. Various hormones have been reported that play a vital role in stress response. Abscisic acid (ABA) is an important plant hormone that plays a central regulatory function in abiotic stress tolerance. Severe environmental stresses activate the pathways to produce ABA, and its level increases through the ABA biosynthesis pathway. In response to stresses, the ABA level is enhanced, and it immediately initiated signaling transduction by binding to its receptor, hence ABA is termed a stress hormone (Mehrotra et al. 2014). Initially, it was assumed that ABA only had a major role in the progression of abscission related to fruit maturity (Ohkuma et al. 1963). Later, it was revealed that ABA also plays a vital role in abscising to promote a stress response and senescence that leads to abscission (Finkelstein 2013). Abiotic stresses, i.e. salt, low temperature, and drought, limit the availability of water which

induces osmotic stress. Closing of stomata, modification in gene expression, as well as adaptive physical responses coincided with the enhanced level of ABA (Kim et al. 2013). ABA also plays a significant role in several developmental functions of plants like modulation of root architecture, seed dormancy, seed development, germination, and vegetative growth (Harris 2015).

In 2009, two new findings were addressed, namely core signaling complexes and soluble ABA receptor proteins (Ma et al. 2009), which provide the opportunity to exploit new ideas in ABA signaling. A gateway to new horizons was unlocked for the development of crops using ABA-engineered agrochemicals (Park et al. 2015). In physiological processes of plants, the role of ABA is still mysterious as it has a protective role in the plant's life cycle but at the same time, it is also involved in abscission. In addition, ABA is involved in promoting stress response and senescence. The discovery of pathways in the ABA signaling cascade provided information on how signals are received and transmitted to set up a molecular event. ABA plays a dual role in stress tolerance and plant growth regulation. So, it is important to dissect the ABA regulatory mechanisms that will allow

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engineering of stress-tolerant crop plants, which is a prime objective for a plant biotechnologist. The present review will focus on recent developments and insights in ABA biosynthesis, its functions, and a cellular cascade of molecular relevance against abiotic stress tolerance response in crop plants.

2. Biosynthesis of ABA

2.1. ABA biosynthesis pathway

ABA is synthesized mainly in plant chloroplast and plastid-containing cells, but it is also synthesized in animals including humans and fungi (Li et al. 2011). It is a sesquiterpene ($C_{15}H_{24}$) synthesized from isopentenyl pyrophosphate (IPP) in the 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway. Neoxanthin is formed from IPP with intermediate products of zeaxanthin and violaxanthin via an intermediate (antheraxanthin) in plastids. All-trans-neoxanthin, all-trans-violaxanthin and 9-cis-neoxanthin can all act as precursors for xanthoxin in ABA synthesis. After that, xanthoxin is oxidized to ABA in the cytosol through ABA aldehyde. The regulatory component of ABA is synchronized by the nucleo-cytoplasmic receptor PYL/RYL. Autophosphorylation of SNF1 allied protein kinases are regulated by a ternary complex (PP2C, ABA, and PYR) (Bouvier et al. 1996; Marin et al. 1996; Danquah et al. 2014). In response, the guard cell is depolarized which stimulates the SLAC1 and restrains the K^+ channel (Daszkowska-Golec and Szarejko 2013). This leads to the closure of stomata due to a decrease in turgidity in response to water loss (Figure 1).

ABA can move actively as well as passively across various transporters, but when it is protonated, it can easily diffuse passively because in this state, it is a weak acid (Ng et al. 2014). The first report of ABA transporters was revealed in *Arabidopsis* through ATP binding cassettes (ABC) (Kang et al. 2015). ABC has specific importers and exporters, e.g. a full-size transporter, AtABCG25, is responsible for the movement of ABA from vascular tissue while a half-size transporter, AtBCG40, imports ABA in plant cells (Kuro-mori et al. 2010).

The SnKR2 protein family was reported in *A. thaliana* as 'open stomatal' (OST1), i.e. involved in ABA-mediated stomatal closure. Studies revealed that this family plays a vital role in plant response to abiotic stress, and this family is divided into 3 subgroups viz. groups I, II, and III. It is evident that subgroup I does not respond to ABA, while subgroup II does not or weakly responds to ABA, whereas subgroup III regulates the ABA-dependent pathway for gene expression (Kulik et al. 2011). Phosphorylation of AREBs (ABA-responsive element binding factor)/ ABFs (ABA-responsive binding factor) is also carried out by ABA activated SnRK2 kinase. AREBs/ABFs are involved in both *in vivo* and *in vitro* conditions. Another transcription factor, ABAI5, is phosphorylated, and SnRK2 kinases are activated *in vitro* by ABA (Wang, Chang et al. 2014).

2.2. Plant organs of ABA biosynthesis

It is important to determine the endogenous sites for the synthesis of ABA, its method of transport to various organelles, and its response to various physiological and biochemical phenomenon. Studies revealed that initially ABA was found in roots followed by the lower stem then the upper

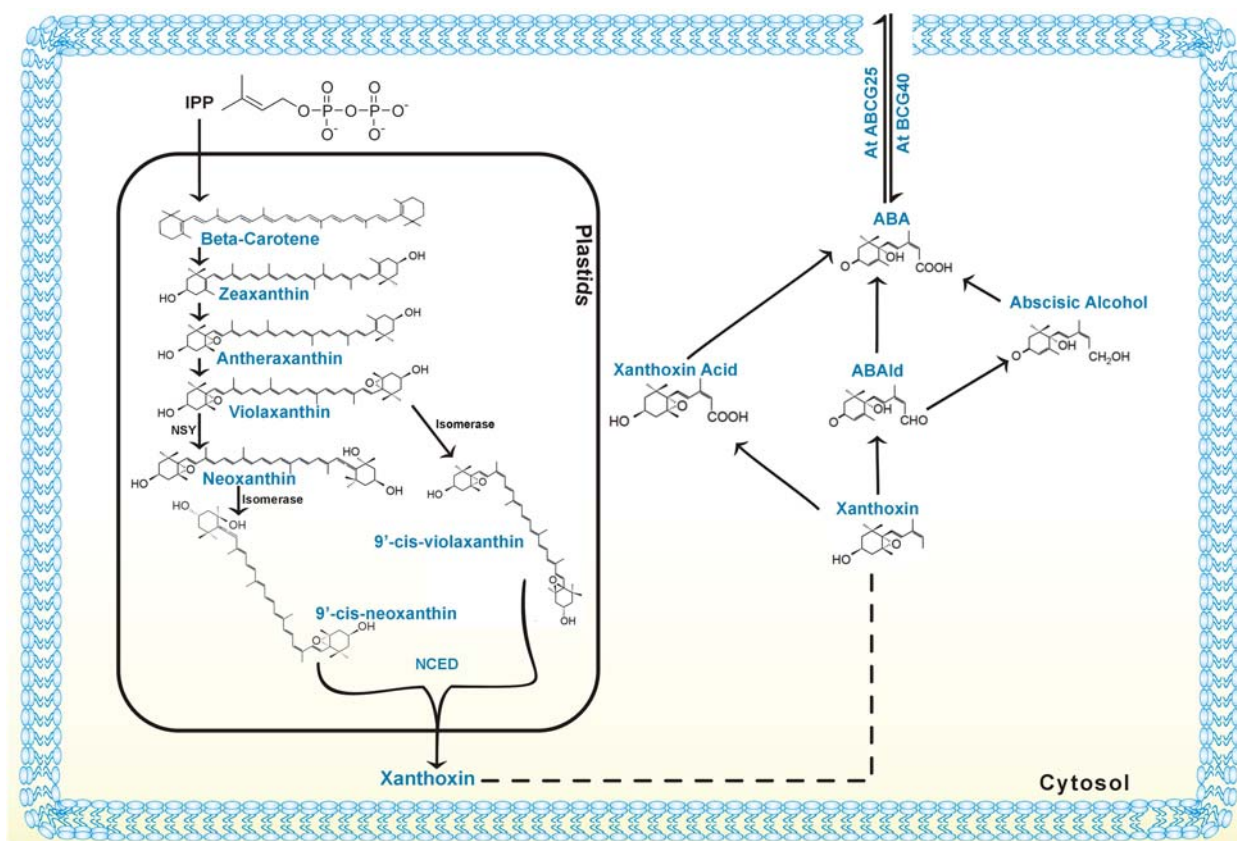


Figure 1. Formation of 9-cis-epoxycarotenoid dioxygenase and its cleavage in plastid and reactions in the cytosol for the formation of ABA.

stem during the seedling stage, and ABA was later found in leaves during the fruiting stage of peanuts (Hu, Hong et al. 2013). It is also known that ABA is biosynthesized in *Arabidopsis* in vegetative tissues then endogenously translocated to seeds. In response to drought, ABA is synthesized in leaf vascular tissues and transported to guard cells to protect stomata (Seo and Koshiba 2011). Small amounts of ABA have also been found in leaves then transported to phloem and shoot tips in *Ricinus communis* L. (Zeevaert 1977). In general, leaves are the main sites of ABA synthesis rather than any other tissues (Zhang et al. 2018).

3. ABA signaling pathway and mechanism transduction

3.1. Receptors of ABA signaling

The receptors of ABA signaling are FCA, ABAR (CHLH or GUN5), GCR2, GTG1/GTG2, PYR1/PYL/RCAR.

3.1.1. FCA: flowering time control protein

Researchers have used light studies to reveal that the flowering time control protein (FCA) is an ABA receptor that plays a vital role in the metabolism of RNA to control flowering time in *Arabidopsis* (Razem et al. 2006). FCA levels decrease as germination proceeds in barley, and FCA plays a role in gene regulation due to its localization in the nucleus (Kumar et al. 2011). By the formation of various protein complexes, ABA may play important roles in root development as well as flowering time in oranges (Ai et al. 2016). Moreover, FCA, an ABA binding protein (ABAR), and the G protein-coupled receptor 2 (GCR2) along with other receptors of ABA regulate stomatal responses (Gong et al. 2018). In a contradictory study, it has been reported that FCA cannot bind ABA (Risk et al. 2008). The disagreement between these findings raises more questions in our understanding of the role of FCA mediated by ABA. The future challenge is to answer these questions.

3.1.2. ABAR (ChlH or GUN5): Mg-chelatase H subunit ABAR/ChlH

An ABA binding protein (ABAR) was found to be involved in stomatal signaling, and magnesium (Mg) chelatase (ChlH) is a key component in both plastid to nucleus signaling and chlorophyll biosynthesis. It was observed that ABAR/ChlH is a ubiquitous protein found in plant tissues that can discern the ABA signals (Shen et al. 2006). ABA is perceived by the H subunit of Mg-ChlH and ABAR/ChlH, and these receptors are involved in stomatal response, root growth, germination, and seed dormancy (Gong et al. 2018). Similarly, the H subunit of Mg-ChlH positively regulates guard cell signaling in response to ABA. An ABA-regulated relationship was also identified between SnRK2.6/OST1 and ABAR/ChlH in guard cell signaling (Du, Zhang et al. 2012; Liang et al. 2015). The putative ABA receptor (ABAR)/ Mg-chelatase H subunit attached to ABA and hampered the WRKY transcription repressor group to mitigate ABA-responsive genes of inhibition (Wang and Zhang 2014). ABAR/ChlH chloroplast Mg-chelatase H subunit has also been localized in *Arabidopsis* and bind with ABA to play a role in ABA signaling (Wu et al. 2009; Shang et al. 2010). Still, the molecular mechanism of ABAR remains

largely unknown, and genome information may pave the way to understand the signaling pathway.

3.1.3. GCR2, GTG1/GTG2: the G protein-coupled receptor

It has been reported that G protein-coupled receptor (GPCR) type G proteins (GTGs) are highly conserved membrane proteins in plants and are classified as ABA receptors in *Arabidopsis* (Jaffé et al. 2012). Upon their discovery as ABA receptors, GTGs were proposed as a new class of GPCRs. The speculated GTG protein arrangements are like GPCR. However, GTP binding GTPase activity is present in GTG proteins but is absent in classical GPCRs. GPCR type G protein 1 (GTG1) and GPCR type G protein 2 (GTG2) showed that GTPase activity started the ABA cascade (Pandey et al. 2009). GTGs interrelate with the α subunit of the heterotrimeric G protein, GAP1, while GTPase activity is hampered by bounded forms of GTP. The binding of GTP with ABA is relatively weaker as compared to the binding of GDP and GTGs with ABA. ABA hypersensitivity was exhibited in seedling growth, seed germination, and stomatal closure of the *gtg1/gtg2* double mutant. The response of ABA was not completely removed in the *gtg1/gtg2* double mutant, suggesting the existence of active ABA signaling sites. ABA binding was observed very low stoichiometrically due to difficulty in separation of a transmembrane protein. This observation indicates that a better quality protein is a prerequisite for binding activity (Risk et al. 2008; Christmann and Grill 2009; Pandey et al. 2009). Based on the above findings, it is proposed that an improved methodology is needed to identify the ABA binding sites.

3.1.4. PYR/PYL/RCAR family structure

Physiological, biochemical, and genetic studies support the PYR/PYL/RCAR family as ABA receptors. Crystal structures of PYL9/RCAR1 and PYR1/RCAR11 have been deciphered recently in the apo form (ABA-free), while ABA/PYR/PP2C is in the ABA-bound form. Research further identified that PYR/PYL/RCARs are responsible for ABA signal transduction and perception for a biochemical response of protein phosphatase 2C (PP2C) and PYR. Mutation, biochemical and structural studies showed that PYR/PYL/RCARs are homodimers with one subunit binding ABA to isolate the dimer. The flanked gate and latch loop structure of PYR/PYL/RCARs in the ABA binding cavity fold over and close after binding an ABA molecule (Melcher et al. 2009; Miyazono et al. 2009; Santiago et al. 2009; Yin et al. 2009). Two independent reports found that the ABA receptors RCAR and PYR/PYL belong to the START (star-related lipid transfer) protein family. RCAR was identified with a yeast two hybrids assay, while PYR1 was identified through pyrabactin receptor1 (Ma et al. 2009; Park et al. 2009). Hence, conformational changes occurred and lead to a new reaction surface of PP2C located at an enzymatic active site. Conversely, the phosphatase activity of PP2C was hampered by obstructing their substrates. The binding of pyrabactin with PYR1 can trigger functional changes that are responsible for the deactivation of PP2C. On the contrary, upon attachment of unfavorable PYR/PYL/RCARs like PYL2, the interaction between PP2C and PYR/PYL/RCAR could happen due to incomplete conformational changes (Hao et al. 2010; Peterson et al. 2010). Regulatory components of stomatal regulation are targeted by SnRK2 and KAT (Pilot

et al. 2001; Vahisalu et al. 2008). Phosphorylation of SnRK2s activates KAT and SLAC1, depolarizes the plasma membrane and activates the outward movement of the K^+ channel. Guard cells lose their turgidity which leads to stomatal closure from leakage of K^+ and anions. This process is involved in seed dormancy, seed germination, leaf water loss, and expression of marker genes (Mori et al. 2000; Liu et al. 2007; Lee et al. 2009). When PP2C releases SnRK2, it regulates the phosphorylation of downstream factors like bZIP, AREB/ABF (Umezawa et al. 2010) (Figure 2).

3.2. ABA signaling response with transcription factors at gene expression level against abiotic stresses

Transcription factors work with their analogous cis-regulatory elements to integrate hormonal, environmental, and developmental signals in plants (Jaradat et al. 2013). Under ABA treatment or high salt dehydration, AREB1/ABF2, ABF3, and AREB/ABF4 transcription factors could be activated in vegetative cells to induce drought tolerance. ABA-responsive promoter genes, RD29A and RD29B, play a critical function in drought tolerance (Hu, Chen et al. 2013). LT178/COR78/RD29A genes are overexpressed in ABA-dependent as well as independent pathways during drought, cold and salinity stress, while ABRE and DRE are involved in ABA-dependent and independent pathways, respectively. In various abiotic stresses, ABA plays a role in signal transduction with multiple transcription factors. NAC transcription factors were overexpressed in transgenic rice due to ABA-mediated signaling (Cheng, Wang et al. 2016) with enhanced ABA biosynthesis genes and endogenous levels of ABA (Redillas et al. 2012; Liang et al. 2014). Expression of SNAC1, OsNAC3, OsNAC4, OsNAC5, and OsNAC6 is enhanced during low temperature, salinity, and drought. OsNAC5 and OsNAC6 are stimulated by ABA while the

rest are stimulated by jasmonic acid (JA), whereas SNAC1 showed transient induction. Studies have found three types of ABA-responsive elements (G/TC; ACGTG; ABREs). Osmotic stress tolerance in *Arabidopsis* is due to overexpression of RD26 or ANAC072. ANAC072 is a component of the ABA signaling module that carries SnRK2, PP2C, RCAR, and PYR/PYL while RD26 is also involved in cold tolerance (Fujii et al. 2011). ABA-mediated SDIR1 selectively stimulates ABA15 rather than ABF3 or ABF4 in plant salt stress response (Zhang et al. 2015). Drought and heat tolerance is developed through exploitation of heat stress response (HSR) gene expression by heat shock factor HSF6b which is activated by ABA-mediated AREB1 (Huang et al. 2016a).

In the rice N22oe transgenic cultivar, increased stomatal movement with enhanced root diameter was observed during drought due to the overexpression of ONAC002, ONAC009, or ONAC122 (Jeong et al. 2013). It was also revealed that exogenous application of ABA enhanced the expression of ONAC022 which leads to the regulation of drought and salt stress (Hong et al. 2016). In transgenic varieties, OsNCED, an ABA biosynthesis gene, exhibited overexpression as compared to the wild type. ABA also enhanced the expression of NAC3, NAC4, and NACTFs from *Caragana intermedia* leading to salt tolerance in transgenic *Arabidopsis* (Han et al. 2015). ABA plays a key role with heat shock protein 70 during heat stress in plants despite stomatal closure (Li et al. 2014). ABA also is involved in reactive oxygen species (ROS)-mediated heat stress tolerance. Similarly, overexpression of RhNAC3 in *Arabidopsis* and *Rosa indica* stimulated the seed germinating and stomatal closure in response to drought and ABA treatment (Xue-Xuan et al. 2010). Enhanced expression of WRKY transcription factors namely AtWRKY18, AtWRKY40, AtWRKY60, and AtWRKY63 were observed in response to ABA which led to the interaction of the gene family with their C-

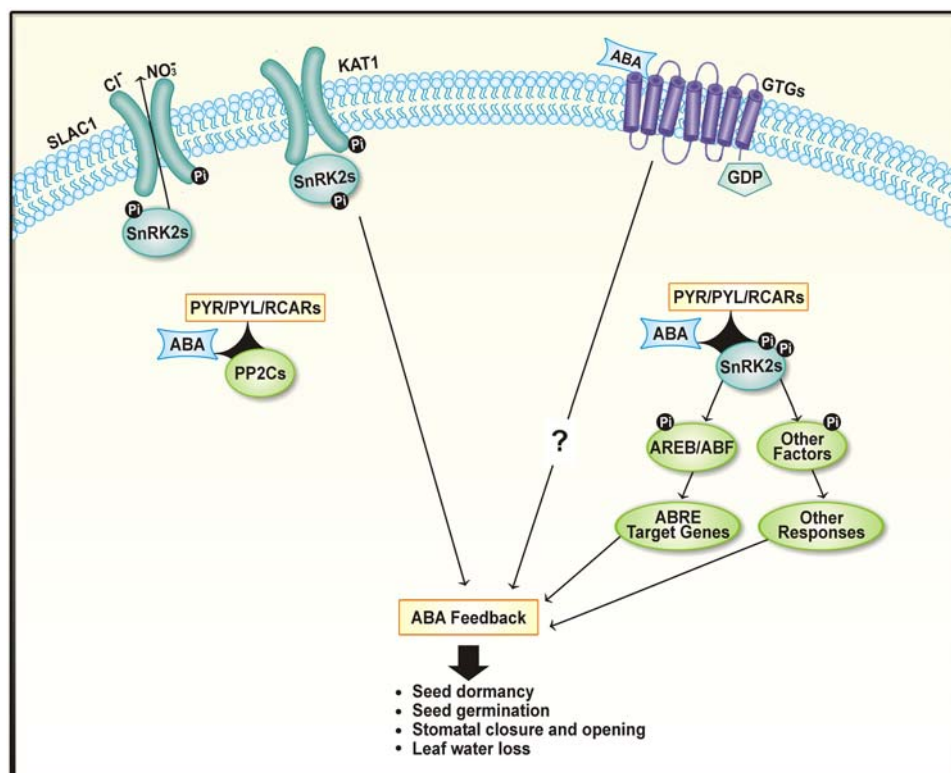


Figure 2. A model of PYR/PYL/RCAR involved PP2C and SnRK2 in the major ABA signaling pathways.

Terminal domains of the chloroplastic ABA (Rushton et al. 2012). RD29A and ABF2, primary genes for the regulation of drought and salt, were stimulated by AtWRKY63. Furthermore, RhNAC3 was reported in ABA signaling regulation in *Rosa indica* and *Arabidopsis* (Jiang et al. 2014).

A major transcription factor, bZIP, mediates the regulatory environmental stress signaling pathway in crop plants. Overexpression of ABA stimulated by bZIP is involved in combating abiotic stresses. For example, activation of OsABF1 regulated signaling of ABA stress response in the shoot and root of rice plants (Hossain et al. 2010). Similar function was observed for OsbZIP23 and OsbZIP71 (Liu et al. 2014). Genes that have promoters for bZIP, including ABI and AtAREB/ABF, can regulate drought and salinity tolerance in *Arabidopsis*, barley, and rice respectively (Roychoudhury and Paul 2012). Abiotic stress tolerance was induced by OSAREB2, ZmABI5, TaABL, PtrABF, and MsZIP in rice, maize, wheat, *Poncirus trifoliata*, and *Medicago sativa*, respectively (Xu et al. 2014). Furthermore, AtbZIP63 regulated the ABA glucose-induced stress pathway (Matiolli et al. 2011). Studies revealed that during low temperature, high salt, drought, and ABA, GmbZIP1 expression enhanced the stomatal closure and led to abiotic stress tolerance in soya bean (Gao et al. 2011). Overexpression of BnbZIP3 was found in China grass in response to multiple abiotic stresses, i.e. excess cadmium, dehydration, and salinity, as well as ABA signaling and ABA treatments (Huang et al. 2016b).

The MYB transcription family regulates growth, developmental processes, environmental stresses, the cell cycle, and the hormonal signaling pathway in plants (Dubos et al. 2010). MYB transcriptional factors are also modulated by ABA-mediated stress responses and dependent pathways. In *Arabidopsis thaliana*, AtMYB2, AtMYB15 and AtMYB44 are involved in ABA-regulated response against drought. Similarly, MdSIMYB1 and TaMYB56-B/MYB transcription factors regulate salinity stress in apple and wheat, respectively (Zhang et al. 2012; Wang, Cao et al. 2014). When AtMYB15, AtMYB44, AtMYB60 were involved in salt and drought stress tolerance, closure of stomata was observed (Jaradat et al. 2013). The FtMYB9 gene encodes R2R3MYB in buckwheat and was reported to induce ABA under salt and drought treatments in transgenic *Arabidopsis* (Gao et al. 2017). The gene PacMYBA encoding anthocyanin biosynthesis from sweet cherry gives resistance to plant pathogens by encoding ABA (Shen et al. 2017). Another R2R3MYB gene family member, PtrSS from *Populus trichocarpa*, showed salt stress tolerance in *Arabidopsis thaliana* by ABA mediating (Fang et al. 2017).

About 160 basic helix-loop-helix (bHLH) genes have been identified that are involved in environmental stress management, light signaling, and developmental processes via hormonal regulation of signal transduction. It was also revealed that bHLH-mediated ABA treatment plays a vital role in cold, salt, and osmotic signaling in crop plants (Tian et al. 2015). Another member of the bHLH family, AtMYC2, regulates drought tolerance by ABA (Abe et al. 2003). A number of bHLH members are reported in ABA-mediated stress tolerance in plants, including AtbHLH32, AtbHLH92 m AtAIG, AtbHLH17/AtAIB, AtASK3/AtbHLH, ATASK2/AtbHLH128 and AASK/AtbHLH122 (Babitha et al. 2013; Li et al. 2014). Similarly, another family member AtbHLH68 was found in regulation of drought

tolerance by ABA-mediated signaling network in *A. thaliana* (Le Hir et al. 2017). In tobacco, ABA-regulated TabHLH1 was involved in the tolerance of osmotic stress. It was observed that SnRK2 (NtSAPK2;1) kinase encoding genes and ABA receptors (NtPYL12) up-regulated the expression of TabLH1 and reduced leaf water loss (Yang et al. 2016). Overexpression of a RNA binding protein in *Arabidopsis* enhanced drought and salt tolerance that led to the closure of stomata by regulation of ABA, ultimately an increased accumulation of osmoprotectant (Ambrosone et al. 2015). Consequently, the transcription factors mentioned in this section elucidate the modulation of ABA-dependent transcription network cascades in plants under abiotic conditions. Hence, transcription factors identifying non-ABRE regulatory elements, i.e. MYC/MYB and NAC, may be responsible for mediating these ABA-responsive genes. But it is still unknown whether the ABA activated SnRK2s played a role in regulation of these transcription factors.

4. ABA metabolism in plants

ABA is a vital hormone that communicates abiotic stress tolerance in crops (Schroeder et al. 2001). During stress conditions, it escalates the tolerance of plants against drought and extreme salinity circumstances (Ng et al. 2014). ABA is also active during non-stress conditions to promote growth and development (Figure 3).

4.1. Seed dormancy and germination

Seed germination and dormancy are the main components of the plant life cycle. Two types of hormones, ABA and gibberellic acid (GA), control the germination and dormancy of seed and maintain a balance between them. GA and ABA metabolic balance as regulated by MYB96 control dormancy as well as germination (Lee et al. 2015). ABA prevents the embryo from germinating and shows a fundamental role in the stimulation and maintenance of seed dormancy. ABA is a major endogenous factor that positively mediates the maintenance and induction of seed dormancy (Tuan et al. 2018). Research also revealed that TaCYP707A1 and



Figure 3. Roles of ABA in plant growth and development from germination to maturity.

TaCYP707A2 genes are involved in ABA-mediated seed dormancy in roots of wheat genotypes (Chitnis et al. 2016). It was also observed that seed dormancy and germination in barley after imbibition were mediated by the balance between ROS and ABA (Ishibashi et al. 2017).

ABA metabolism is regulated during water stress tolerance. Occasionally, ABA appears active in the shoot through movement in the xylem and phloem (Rodríguez-Gacio et al. 2009; Miransari and Smith 2014). Interestingly, ABA was also suggested to play a predominant role in the transition from seed maturation to germination (Yan and Chen 2017). Significant progress has been made in recent years in the elucidation of molecular mechanisms for the regulation of ABA. The extent of seed dormancy and germination vary depending on a range of environmental conditions. The mechanism of seed dormancy and germination is still open to debate.

4.2. Modulation of root architecture

The architecture of roots is controlled by three factors, i.e. lateral root length, root length, and angle with parent root. During the life of plant, its root structure perseveres through the changing interface among roots and their environment (Harris 2015). One of the major functions of ABA is to adjust root architecture as the plant grows and to provide for dormancy. Abiotic stress is caused during conditions of limited and uneven water availability. Under these circumstances, the level of ABA changes with changes in amount of water. Such changes in the root environment alter local and systemic ABA response (Puértolas et al. 2015).

ABA also regulates ion and water flow in roots. It increases the water influx in roots by decreasing transpiration rates (Glinka and Reinhold 1971). ABA is necessary for growth because a minimum amount of ABA during low water conditions increases root growth as compared to its complete absence. Similarly, accumulation of ABA in roots under stress conditions maintains primary root elongation, and ABA also disrupts the production of ethylene with that occurs with enhanced root elongation (Spollen et al. 2000). Ethylene plays a significant role in lateral root expansion; therefore, ABA must maintain a balance between too much and too little ethylene production. It is assumed that over time ABA signaling through root-specific activation shifts the stability of root growth away from resource consumption (Duan et al. 2013). Root elongation in maize was observed together with ABA accumulation, and it enhanced the plant's ability to grow under abiotic stress conditions. Furthermore, ABA was involved in the maintenance of the root meristem (Liang et al. 1997) as well as stem cells by promoting the quiescent center (QC) and suppressing stem cell differentiation (Zhang et al. 2010). Interestingly, GA and ABA antagonistically regulate root architecture and root growth (Vishal and Kumar 2018; Lin et al. 2020). Adjustment of ABA and GA balance facilitates the role of ethylene to mediate seedling growth and post-germination starch degradation in storage conditions (Sun et al. 2020). Treatment with ABA and graphene oxide facilitates root growth by regulating indole acetic acid (IAA) and ABA (Xie et al. 2019). Under salt stress conditions, ABA regulates auxin distribution for lateral root development. Hence, it helps the plant to survive in saline conditions (Lu et al. 2019). ABA induces a delay in cell elongation by inhibiting

cytokinin signaling, consequently root architecture is altered, and root growth is retarded (Wang et al. 2019). Root senescence was controlled by the regulation of jasmonate and ABA (Wojciechowska et al. 2020). ABA, salicylic acid and methyl jasmonate increased the sulphoraphane and glucosinolate accumulation in taproots (Chen et al. 2019). Both carotenoid derived hormones ABA and strigolactones were triggered by zaxinone metabolite and involved in abiotic stress tolerance (Ablazov et al. 2020). Research also revealed that abiotic stress activated ABA which downregulated the LBD14 protein to control the growth of lateral root branching (Jeon and Kim 2018). All the mentioned effects of ABA on roots are involved to modulate root architecture to cope with the environmental challenges.

4.3. Effect on leaf senescence

Leaf senescence plays an important role in plant development. Climatic conditions and endogenous compounds are regulated through leaf senescence (Lim et al. 2007). Under these processes, ABA elucidates a significant effect on leaf senescence (Xue-Xuan et al. 2010). Similarly, in rice and maize, foliar spraying of ABA has been shown to uphold leaf senescence (He and Jin 1999). The findings of various researchers showed that green cultivar translocation has been blocked from root to shoots due to low-level ABA effects on leaf senescence. Moreover, it was observed that ABA also stimulated yellowing of leaves which is also creating leaf senescence (Yang et al. 2003; Fang et al. 2008).

Similarly, ABA can help in senescence and elicit the appearance of more than a few specific senescence-related genes (Xue-Xuan et al. 2010; Finkelstein 2013). The molecular mechanism of ABA-mediated leaf senescence uncovered the key role of PYL9 in promoting resistance to leaf senescence to extreme abiotic stress conditions (Zhao et al. 2016). The research revealed that mutants of Arabidopsis displayed altered senescence when exposed to limited ABA biosynthesis (Passioura 2006). It was also observed that receptor kinase (RPK1)-mediated ABA-induced senescence in older leaves (Lee et al. 2011). In rice and Arabidopsis, leaf senescence was controlled by various NAP transcription factors (NAC like, activated by *apetala3/distillate*) (Liang et al. 2014). Moreover, *SAG113* inhibited stomatal closure and upregulated ABA-induced leaf senescence ultimately enhancing water loss in senescing leaves (Zhang and Gan 2012). Overexpression of *OsNAP* (an NAC-like gene) in rice can increase leaf senescence and vice versa (Liang et al. 2014). Additionally, expression *OsNAP* can be increased or reduced by ABA. The expression of *OsNAP* controls ABA-mediated leaf senescence through a feedback mechanism (Liang et al. 2014). Recently, a subfamily of stress-responsive NAC transcription factors (SNAC-A) was found to be involved in ABA-induced leaf senescence in Arabidopsis. Likewise, a NAP-like transcription factor (GhNAP) was recently identified in cotton (Fan et al. 2015; Takasaki et al. 2015). Efforts to visualize ABA-mediated leaf senescence by NAC type transcription factor and PYL9 provide new insights into the molecular mechanism of leaf senescence.

4.4. Effect on stomatal regulation

Stomata are responsible for plant gas exchange processes and can be present on lower and upper surfaces of the

plant leaves. Increased levels of CO₂ and ABA are responsible for incomplete closing of stomata. Light is one of the main factors affecting the stomatal opening (Kim et al. 2010). When stomata are closed, photosynthetic production is reduced due to low gaseous exchange processes in leaves (Mittler and Blumwald 2015). ABA is responsible for stomatal opening and controls ABA-activated protein kinase (AAPK) in *Vicia faba* (Li and Assmann 1996). Moreover, by using plasma membrane anion channels, ABA-induced stomatal closure is regulated by AAPK (Li 2000). Enhanced cytosolic Ca²⁺ levels regulate the release of the anion from guard cells (Schroeder et al. 2001). It is reported that only S-type anion channels control the ABA-regulated stomatal closure (Joshi-Saha et al. 2011). Two independent research groups have shown that SLAC1 (Slow anion channel associated 1) influences membrane depolarization which is mandatory for the stomatal closing process (Negi et al. 2008). In *Arabidopsis*, ABA is induced by closing of stomata (Mustilli et al. 2002). A unique function of aquaporins was also reported to be responsible for ABA-triggered stomatal closure. Aquaporins are involved to escalate the permeability of guard cells through OST1 dependent phosphorylation of PIP2;1 (Grondin et al. 2015). Further, increased levels of OST1 kinase can bind directly to help in phosphorylation of the SLAC1 anion channel that releases the anion from guard cells and allows stomata to close (Geiger et al. 2010). SnRK2.6/OST1 target the K⁺ channel of KAT1 and its phosphorylation at the C-terminal region. Therefore, it was determined that regulation of ion channels is controlled by phosphorylation (Sato et al. 2009). ABA-mediated CPK8 controls stomatal regulation by controlling catalase3 (CAT3) activity as well as phosphorylates CAT3 (Zou et al. 2015). ABA hampers the activity of guard cell plasma membrane H⁺-ATPase for depolarization (Hayashi et al. 2011). ABA can mediate the assembly of reactive oxygen species (ROS) that are present in guard cells for closing of stomata. In *Arabidopsis*, AtrbohD and AtrbohF (NADPH oxidases) in guard cells are responsible for ABA-regulated ROS production (Kwak 2003). ABA is responsible for ROS production in guard cells (Pei et al. 2000). Opening of Ca²⁺ channels is assisted by ABA for stomata to close. Moreover, enhanced cytosolic Ca²⁺ in guard cells enhanced the production of inositol 1,4,5-triphosphate and ROS (Pei et al. 2000). So, in guard cells, increased levels of ROS accumulation result in a positive feedback loop to activate stomatal closing (Mittler and Blumwald 2015). ABA levels in guard cells can be increased by *de novo* synthesis. The quick response of closing of stomata induced by the environment is usually dependent on guard cells (Merilo et al. 2015). Stomatal aperture regulation is mainly controlled by ABA, and it helps the plants to survive and grow under abiotic stress conditions. Moreover, channel protein ABA also controls the second messengers, i.e. Ca²⁺, nitric oxide, protein kinases and ROS, that could target the ion channel.

4.5. Abiotic stress tolerance

After the recognition of ABA as a stress-responsive hormone, a series of experiments were conducted to determine the molecular and biochemical signaling mechanisms providing abiotic stress tolerance. Genetic engineering of ABA

phytohormones in crops could provide alternative strategies to manage abiotic stress (Sah et al. 2016). Mutants deficient in ABA signaling and metabolism were more susceptible to salt and heat stress than wild types (Suzuki et al. 2016). ABA-regulated JrWRKY53 and JrWRKY6 provided significant plant tolerance against heat, osmotic stress, and salinity (Yang et al. 2017). HSFA6b is an essential gene for heat tolerance which is manipulated as an ABA-mediated downstream regulator (Huang et al. 2016a). MAPK signaling and crosstalk with the ABA cascade provide evidence that it is involved in building tolerance against drought, salt, and cold (Huang et al. 2012). The OsPYL10 gene causes overexpression of the ABA receptor and has been identified as a potential source to enhance cold and drought tolerance in rice (Verma et al. 2019). ABA receptors RCAR12 and RCAR13 can improve cold and heat tolerance (Zhang et al. 2019). The ABA-dependent signaling cascade involving CsbZIP18 negatively regulates freezing tolerance (Yao et al. 2020). Furthermore, PtPYRL1 and PtPYRL5 genes are needed to enhance resistance to osmotic, drought, and cold by ABA-mediated signaling in poplar (Yu et al. 2017). Application of ABA and GA3 influence the synthesis of primary and secondary metabolites, and it improves abiotic stress tolerance in crop plants (Xie et al. 2019). The cytokinin and ABA signaling pathways have multiple molecular components that jointly regulate drought stress response, thus reflecting the coordination between these hormones (Huang et al. 2018). It was speculated that more complex mechanisms were needed to adjust ABA and brassinosteroids under drought stress conditions (Wang et al. 2019). Salicylic acid and ABA were involved in pathways regulating salt stress tolerance (Saleh et al. 2020). We know that carotenoids are a source of both ABA and strigolactones, hence, interactions between these two important hormones at a regulatory level or biosynthetic level can be anticipated. Research results revealed that both strigolactone and ABA pathways are connected and have a crucial role in drought tolerance (Haider et al. 2018). Osmotic stress is potentially one of the most devastating stresses. Cross talk between ABA and auxin was identified during changing environmental conditions, especially osmotic stress (Asghar et al. 2019). It was also observed that exogenous IAA improved drought tolerance by regulating JA, ABA and auxin (Zhang et al. 2020). A similar type of interaction was observed between brassinosteroid, gibberellins, IAA and ABA in response to drought conditions (Li et al. 2019). ABA and ethylene interacted with each other, and this interaction served as the underlying mechanism of drought stress tolerance (Müller 2021). In summary, during stress conditions, ABA plays a role as a facilitator of tolerance. These stresses (drought, salt, and osmotic) reduce water levels, but salt and osmotic stress also increase the complexity of stress tolerance because osmotic potential is increased and ionic content is increased in the soil. The intricacy of the ABA-regulated signaling cascade for abiotic stress tolerance needs to be uncovered in more detail.

5. Crosstalk between ABA and other hormones

The response of plants to abiotic stresses through a well-organized mechanism depends upon the ability of a plant to adjust in changing environmental conditions. Crosstalk is the point where various hormones in one signal

transduction cascade affect another. ABA, JA, and salicylic acid are considered vital phytohormones in stress signaling. When a plant is exposed to water stress, it accumulates ABA which interacts with nitric acid, and JA acid, in turn, activates genes and ultimately closes the stomata. JA is always activated in response to ABA for stomatal closure by triggering a Ca^{2+} influx that eventually mediates the CDPK signaling cascade. Furthermore, to identify the putative link between ABA and JA in stress tolerance, studies revealed that *PYL6* (*RCAR9*) and an ABA receptor with the corresponding transcription factor *MYC2* influenced the expression of *JAZ6* and *JAZ8* (Aleman et al. 2016).

Another hormone, cytokinin (CK), is involved in leaf expansion, cell growth, and delayed senescence. However, a negative correlation has been observed between ABA and CK, which ultimately leads to stomatal closure and reduced water loss (Qin et al. 2011). Similarly, the same relationship has been identified between *Arabidopsis* histidine phosphotransferase proteins and CK receptor kinase that negatively regulates ABA levels, although stress tolerance was also observed in CK deficient mutants (Tran et al. 2007; Nishiyama et al. 2013). Conversely, ethylene has displayed an inverse relationship between leaf and root growth and gas exchange in response to drought by hampering ABA (Sharp 2004; Wilkinson et al. 2012). *ABI5* was induced in response to increasing ABA levels which regulates *LEA* genes that act as an osmoprotectant for the seed in stress conditions (Finkelstein and Lynch 2000; Lopez-Molina and Chua 2000). ABA and GA also exhibited an antagonistic relationship, and their balance-mediated seed dormancy and germination. *DELLA* proteins play a vital role in the interaction of ABA and GA signaling during abiotic stresses. *RGL2* (a member of the *DELLA* protein family) has been found to induce the *RINGH2* factor encoding *XERICO* that mediates ABA signaling, ABA accumulation, and *ABI5* activity to disturb GA levels (Ko et al. 2006). Therefore, *RGL2* was identified as the key player in breaking seed dormancy by inactivating through 26S proteasome pathway and enhance GA level (Jiang and Fu 2007; Achard and Genschik

2009). MFT was also found in ABA and GA signaling because MFT was regulated by *RGL2* for phosphatidylethanolamine binding protein which was negatively correlated with *ABI5* but positively correlated with *ABI3* (Xi et al. 2010). Overwhelmingly, ABA plays a vital role in phytohormone-mediated crop plant growth and development during environmental stresses by interacting with other related plant hormones. However, the biochemical and molecular mechanisms that lead to the signal transduction pathway (Figure 4) as well as ABA-mediated genes involved in abiotic stresses (Table 1) require further detailed study.

6. Alternative forms for ABA-mediated signaling pathways

In response to ABA, gene expression is regulated by post-transcriptional RNA binding proteins including translocation of mRNA, RNA localization, RNA splicing, and RNA stabilization (Glisovic et al. 2008). Recent studies revealed that *SRP1* (stress associated RNA binding protein) mediating *C2C2* (zinc finger protein) has been involved in post transcription of ABA signaling through hampering the expression of *ABI2* (Xu et al. 2017). In *Arabidopsis*, hyponastic leaves (*HYL1*) was responsible for regulating double-stranded RNA binding protein and was supersensitive to drought, and ABA was conversely hypersensitive to both when silenced (Lu and Fedoroff 2000; Xiong et al. 2001). Mutation in *ABH1*, *LOS4* (RNA helicase gene), and mRNA cap-binding protein resulted in cold-tolerant phenotype and ABA hypersensitivity (Hugouvieux et al. 2001; Gong et al. 2005). Moreover, two DEAD-box RNA helicases have been identified in *Arabidopsis* that were restrained upon the presence of ABA, and they confer abiotic stress tolerance (Kant et al. 2007). Moreover, a ribonucleoprotein *AKIP1* from *Vicia faba* and DEAD-box RNA *ZmDRH1* represented a relocation in subnuclear structure and interacted with *MA16* (Glycine rich RNA binding protein), respectively (Li et al. 2002; Gendra et al. 2004).

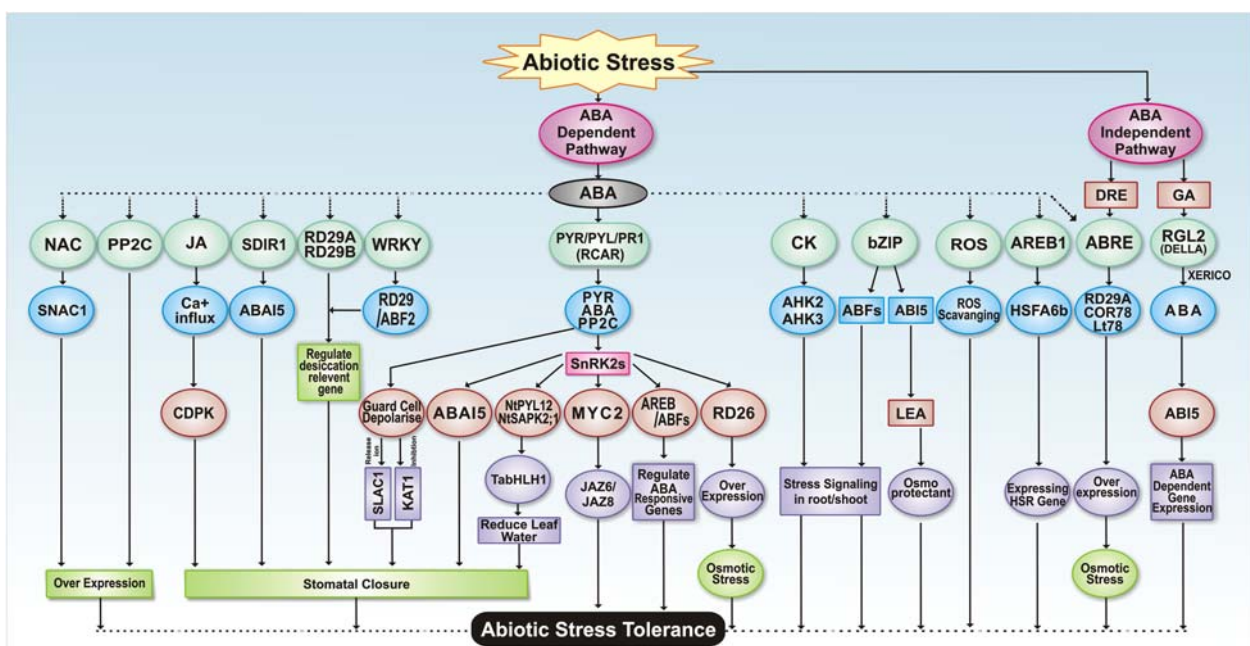


Figure 4. ABA-dependent and independent pathway leads to abiotic stress tolerance and hormonal cross talk.

Table 1. Genes related to ABA-mediated abiotic stress tolerance.

Stress type	Gene	Crop	Reference	
Cold	RCAR5/PYL11	<i>Arabidopsis thaliana</i>	Lim and Lee (2020)	
	TaDREB3	<i>Hordeum vulgare</i>	Li et al. (2017)	
	AM1	<i>Cynodon dactylon</i>	Cheng, Jin et al. (2016)	
	WCOR14	<i>Triticum aestivum</i>	Tsvetanov et al. (2000)	
	OsWRKY45	<i>Oryza sativa</i>	Tao et al. (2011)	
	CbCOR15b	<i>Nicotiana tabacum</i>	Wu et al. (2012)	
	PtCBF	<i>Poncirus trifoliata</i>	He et al. (2012)	
	VaCBF1	<i>Vitis amurensis</i>	Dong et al. (2013)	
	VaCBF4	<i>Vitis amurensis</i>	Li et al. (2013)	
	COR25	<i>Brassica napus</i>	Chen et al. (2011)	
	CsICE1, CsICE2	<i>Camellia sinensis</i>	Wang et al. (2012)	
	SICZFP1	<i>Oryza sativa</i>	Zhang et al. (2011)	
	OsGH3-2	<i>Oryza sativa</i>	Du, Wu et al. (2012)	
	Cold and Salinity Drought	TaMYB56-B	<i>Triticum aestivum</i>	Zhang, Zhao et al. (2012)
		ABI5	<i>Arabidopsis thaliana</i>	Brocard et al. (2002)
		ARR1	<i>Arabidopsis thaliana</i>	Nguyen et al. (2016)
		AtLOS5	<i>Gossypium hirsutum</i>	Yue et al. (2012)
ZmCPK4		<i>Zea mays</i>	Jiang et al. (2013)	
CPK8		<i>Arabidopsis thaliana</i>	Zou et al. (2015)	
CaMLQ2		<i>Capsicum annuum</i>	Lim and Lee (2014)	
OsCPK9		<i>Oryza sativa</i>	Wei et al. (2014)	
GaMYB85		<i>Gossypium arboreum</i>	Butt et al. (2017)	
GhNAC2		<i>Gossypium herbaceum</i>	Gunapati et al. (2016)	
GhNAC18		<i>Gossypium hirsutum</i>	Evans et al. (2016)	
TaNAC29		<i>Triticum aestivum</i>	Huang et al. (2015)	
PP2C		<i>Populus deltoides</i>	Arshad and Mattsson (2014)	
WRKY30		<i>Vitis vinifera</i>	Zhu et al. (2018)	
GmWRKY54		<i>Glycine max</i>	Wei et al. (2019)	
HvSNAC1		<i>Hordeum vulgare</i>	Al Abdallat et al. (2014)	
OsPYL/RCAR5		<i>Oryza sativa</i>	Kim et al. (2012)	
PYL5		<i>Oryza sativa</i>	Kim et al. (2014)	
ZmRFP1		<i>Zea mays</i>	Xia et al. (2012)	
LEA4		<i>Zea mays</i>	Zamora-Briseño and de Jiménez (2016)	
OsASR5		<i>Oryza sativa</i>	Li et al. (2017)	
Drought and Salinity		GhABF2	<i>Gossypium hirsutum</i>	Liang et al. (2016)
		ABP9	<i>Gossypium hirsutum</i>	Wang et al. (2017)
		GhERF38	<i>Gossypium hirsutum</i>	Ma et al. (2017)
		CBF	<i>Gossypium hirsutum</i>	Ma et al. (2016)
		OoNAC72	<i>Oxytropis ochrocephala</i>	Guan et al. (2019)
		TaODORANT1	<i>Nicotiana tabacum</i>	Wei et al. (2017)
	RAV1	<i>Gossypium hirsutum</i>	Li et al. (2015)	
	GbRLK	<i>Gossypium barbadense</i>	Zhao et al. (2013)	
	GhWRKY68	<i>Nicotiana tabacum</i>	Jia et al. (2015)	
	ZmPP2C	<i>Zea mays</i>	Liu et al. (2009)	
	GhWRKY17	<i>Nicotiana benthamiana</i>	Yan et al. (2014)	
	Drought, Salinity and Cold	MYB3R	<i>Triticum aestivum</i>	Cai et al. (2011)
		MbDREB1	<i>Malus communis</i>	Yang et al. (2011)
	Heat	HSFA6b	<i>Arabidopsis thaliana</i>	Huang et al. (2016a)
APX1 and MBF1c		<i>Arabidopsis thaliana</i>	Zandalinas et al. (2016)	
TaHSFC2a		<i>Triticum aestivum</i>	Hu et al. (2018)	
AsHSP17		<i>Agrostis stolonifera</i>	Sun et al. (2016)	
HSFA2c		<i>Festuca arundinacea</i>	Wang et al. (2017)	
TaWRKY33		<i>Triticum aestivum</i>	He et al. (2016)	
Salinity		FHY3 and FAR1	<i>Arabidopsis thaliana</i>	Tang et al. (2013)
	OsHsfB2b	<i>Oryza sativa</i>	Xiang et al. (2013)	
	CsCOR1	<i>Nicotiana tabacum</i>	Li et al. (2010)	
	OsP5CS1 and OsP5CR	<i>Oryza sativa</i>	Sripinyowanich et al. (2013)	
	GsAPK	<i>Glycine soja</i>	Yang et al. (2012)	
	OsCam1-1	<i>Oryza sativa</i>	Saeng-ngam et al. (2012)	
	GhMPK17	<i>Gossypium hirsutum</i>	Zhang et al. (2014)	
	Oshox22	<i>Oryza sativa</i>	Zhang, Haider et al. (2012)	
	OsZIP71	<i>Oryza sativa</i>	Liu et al. (2014)	
	AtHSP17.8	<i>Lactuca sativa</i>	Kim et al. (2013)	

Proteins rich in serine/arginine presented a link between ABA response and alternative splicing. Similarly, in *Arabidopsis*, SR1 and SR33 in response to ABA experienced a change of alternative splicing and produced six SR genes that regulate ABA-related responses (Palusa et al. 2007; Cruz et al. 2014). Alternative splicing has also been dissected during drought stress in plants in ABA-dependent pathway mediating the expression of OST1 and MYB60 (Guerra et al. 2015). Downregulation of miR169a induced expression of NFYA5 controls stomatal movement, hence suggesting that miRNA also plays a role in

response to ABA-mediated abiotic stress (Li et al. 2008). ABA regulates as ubiquitination during abiotic stresses both negatively and positively. In negative regulation, DOR (drought tolerant repressor) mutant-mediated E3 ubiquitin ligase which enhanced ABA synthesis and facilitated drought tolerance (Zhang et al. 2008). A similar trend was noted for senescence-associated ubiquitin ligase 1 (SAUL1) which enhances the expression of AAO3 and triggers ABA degradation (Raab et al. 2009) whereas XERIC1 (E3 ubiquitin) also triggers the expression of NCED3 by positively regulating ABA (Ko et al. 2006). The response

of ABA in plants well regulated by E3 ubiquitin ligase DDA1 (DET1-DDB1 associated1) which is regulated by proteasomal degradation of PYLs (Irigoyen et al. 2014). ABA-responsive transcription factor also regulated by ubiquitination and it has been noticed that KEG (keep on going) interacts with both ABF1 and ABF3 (Chen et al. 2013). Sumoylation modification has been observed in response to ABA regulation which triggers the stress inducible genes and expression of ABA (Lois et al. 2003). Moreover, studies also revealed that MMS21 (methyl methane sulfonate sensitivity protein 21) has a negative relation with ABA synthesis because mutants of MMS21 represented enhanced ABA sensitivity and drought tolerance (Chen et al. 2013). Taken together, ABA-mediated abiotic stress response is tightly regulated and controlled post-transcriptionally as well as post-translationally.

7. Conclusion and future perspectives

The demand for food is increasing every day due to changes in climate and a rapidly growing population. There is an urgent need to increase food production to compete with this emerging situation. Therefore, it is important to understand the mechanisms of abiotic stress tolerance in plants because abiotic stresses can have devastating effects. Inducing seed dormancy, modification in root architecture, and stress-responsive gene expression are the routes for ABA to confer stress tolerance. ABA is a basic hormone, and it plays a role in the regulation of the plant's response to virus, disease, insect, salinity, low temperature, and drought. With the advancement of functional genomic techniques and molecular genetics, a deeper comprehension of the fundamental mechanisms of ABA in abiotic stress tolerance has been accomplished, but there is more to be revealed. Various physiological mechanisms regulated by ABA have been elucidated at the molecular level, i.e. accumulation of osmoprotectants, gene expression, and stomatal closure. Epigenetic modifications together with the ABA signal transduction pathway is a pre-requisite to produce superior transgenic plants that can withstand harsh climatic conditions without yield penalty. To further explore the plant dynamics, *cis* engineered genetic regulation could be practiced by designing tissue-specific promoters. At the translational level, ABA-mediated activation leads to the overexpression of genes related to stress tolerance. There is a need to dissect how ROS and Ca²⁺ signaling are transduced in ABA signaling. Future efforts should also be directed to investigating whether plants have additional ABA receptors other than FCA, ABAR (CHLH or GUN5), GCR2, GTG1/GTG2, PYR1/PYL/RCAR. Transcriptional actors namely bZIP, MYC/bHLH, MYB, and NAC have a robust role in mediating the expression of genes in stress tolerance. More work is required to uncover the mystery of each ABA gene product along with its interacting partners to explore the intricacy of the signal transduction pathway of abiotic stress. Despite the advancement in research, the ABA source in guard cells is still ambiguous. Furthermore, mechanisms/processes which upregulate the ABA synthesis genes through abiotic stress are still not fully understood. Moreover, elucidation is still needed for crosstalk of ABA with other phytohormone signaling cascade. Despite the multiple open questions, the recent advancement in Arabidopsis for ABA signaling design the route to appraise the fundamental abiotic stress response

in crop plants. Soon, it will be mandatory to screen the role of ABA genes, in response to multiple or combined stresses to acquire circumstantial insight into the functional role of ABA. It is also suggested that the best techniques are needed for determining the specific roles of individual miRNAs in response to ABA regulation.

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