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REVIEW ARTICLE

Significance of ABA Biosynthesis in Plant Adaptation to Drought Stress

Shah Zareen[1] · **Akhtar Ali**[1,2] · **Dae-Jin Yun**[1]

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Abstract

Environmental stresses have major impacts on the morphological, physiological, and biochemical processes of plants. Among these stresses, drought is the major one which greatly restricts crop productivity globally. When challenged by drought, plants promote the expression of ABA biosynthesis genes which results in ABA accumulation. Increase in ABA level promotes stomatal closure to increase plant's adaptative response to drought stress. To handle and restrain the negative impact of drought stress, it is important to understand how plants respond to drought and the involvement of ABA in plant adaptation to drought stress at a molecular level. Under drought stress, ABA biosynthesis is the most significant event to protect plants from the dehydration stress. ABA biosynthesis is a complicated process that is mainly regulated by ABA biosynthetic enzymes. This review highlights the recent advancements in ABA biosynthesis and its involvement in plant adaptation to drought stress to improve their growth and development under water-deficient conditions.

Keywords ABA biosynthesis · Abiotic stresses · Drought stress · E3-lagases

Introduction

Being sessile by nature, plants face several challenges that alter their growth and development (Zhu 2016). These challenges are known as stresses and trigger several changes such as gene expression, growth retardation, and cellular metabolism, which can reduce overall yields. Very few plant species show tolerance to a given stress in a time-dependent manner after being exposed to it (Oh et al. 2014; Verma et al. 2013). Environmental stresses are categorized into two classes: biotic and abiotic. Biotic stress occurs when plants are exposed to biological factors that affect their growth and development, such as pathogen and insect attacks. In contrast, abiotic stresses are imposed on plants by chemical or physical factors in the environment, such as drought, salinity, and temperature (Verma et al. 2013; Chen et al. 2021). Such stresses represent the main causes of crop failures worldwide, reducing crop productivity and the average yields of economically important crops by amounts that may be life-threatening (Bray et al. 2000; Huang et al. 2008). Severe stress can lead to the death of a plant by restricting flowering and seed formation and promoting senescence (Verma et al. 2013). Thus, environmental stresses have been one of the most fascinating areas of research for plant scientists over the past 20 years.

Understanding how plants deal with these stresses and how they sense, transduce, and react to environmental stimuli has been given significant attention in the last two decades (Swain et al. 2023). Signal transduction provides strong support for different stress responses in plants on multiple levels (Markham and Greenham 2021). For instance, salinity and drought stresses induce osmotic stress, which promotes the accumulation of secondary metabolites to control ion toxicity, plasma membrane disruption, reactive oxygen species (ROS) accumulation, and cell wall disorder (Praveen et al. 2023). Plants respond to abiotic stresses most commonly through signal transduction, which in turn reacts to DNA methylation (Yu et al. 2024). Following that, RNA transcription occurs, which further leads to protein translation (Alberts et al. 2022). Next, it produces fresh and new proteins that promote an adaptative response to abiotic stress (Fig. 1).

Shah Zareen and Akhtar Ali equally contributed to this work.

✉ Dae-Jin Yun
djyun@konkuk.ac.kr

[1] Department of Biomedical Science & Engineering, Konkuk University, Seoul 05029, South Korea

[2] Institute of Glocal Disease Control, Konkuk University, Seoul 05029, South Korea

A typical signal transduction pathway begins with signal perception, followed by the generation of secondary messengers such as calcium, inositol phosphates, and ROS. Finally, it modulates the intracellular calcium level in the cytosol, which is sensed by calcium-binding proteins called Ca^{2+} sensors. These sensors tend to be free of any enzymatic activity and exhibit structural modifications that are $Ca2^{+}$-dependent (Ryder et al. 2023). These sensors interact with their potential partners to initiate a phosphorylation cascade and regulate transcription factors or stress-responsive transcription mediators, which regulate the expression of target genes (Guan et al. 2013; Chen et al. 2021; Wu et al. 2022). The end products of these stress-responsive genes promote plant adaptation to the initiating stress (Mahajan and Tuteja 2005) (Fig. 1). This highlights the fact that the adaptation of a plant to stress is a completely mechanistic package that includes several metabolic processes, signaling cascades, and gene expression (Dong et al. 2015; Chen et al. 2021).

Plant Response to Drought Stress

Drought stress is a major environmental stimulus and has a significant impact on global crop security (Chieb and Gachomo 2023). Water constitutes 80–95% of the body of a plant as fresh biomass, which plays important roles in several physiological processes (Abbasi and Abbasi 2010; Brodersen et al. 2019). Consequently, scientists firmly believe that drought is the single biggest threat to future worldwide agricultural production, especially for crops cultivated in vulnerable areas (O'Connell 2017; Diatta et al. 2020). Irregularity in the rainfall distribution, evapotranspiration, and water-holding ability of the rhizosphere are the major factors that contribute to the unpredictable nature of drought. There are also times when plants are unable to obtain water from the soil despite a sufficient amount of moisture in the root zone, a phenomenon called physiological drought (Daryanto et al. 2017).

There are several factors that significantly affect the response of a plant to drought stress, including the growth stage, species, drought severity, and timing (Gray and Brady 2016). Therefore, the ability to withstand the effects of stress and adapt their growth capabilities varies among plant species (Osakabe et al. 2014; Bielach et al. 2017). At the molecular level, the responses of plants to drought stress are improved by several mechanisms, including those involved in signal transduction (Kaur and Asthir 2017; Zandalinas et al. 2020). To tolerate a water-deficit condition, plants promote ion transportation and modulate the activity of transcription factors, as well as ABA biosynthesis and stomatal movement (Prakash et al. 2019). Under drought stress, the transpiration rate from

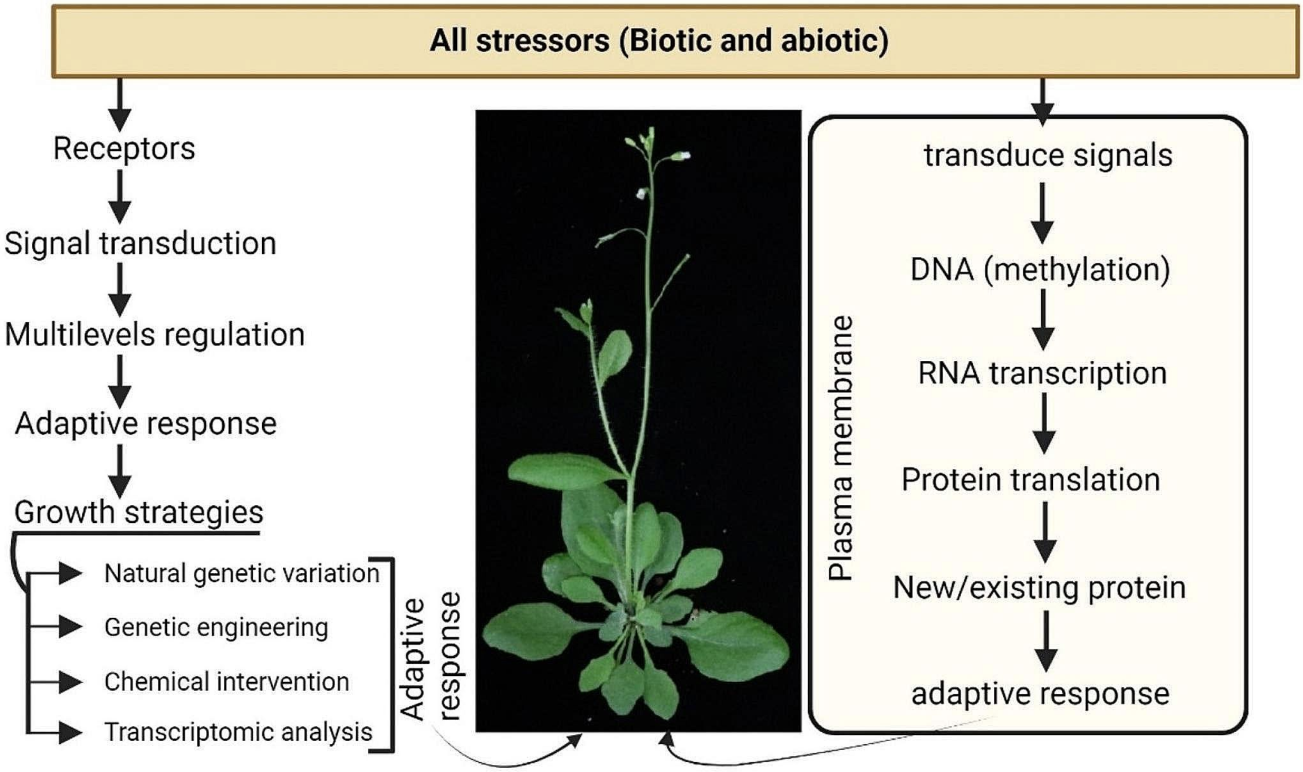


Fig. 1 Plant adaptive responses to abiotic stresses. A representative diagram highlighting the responses of plants to abiotic stress at the molecular level starting from signal transduction

the leaves reduces the water-uptake efficiency of the roots (Goche et al. 2020). The adaptation of a plant to drought mainly involves closing its stomatal aperture to reduce water loss and expanding its roots to absorb more water from the soil (Martínez-Vilalta and Garcia-Forner 2017).

Drought stress affects plants in various physiological, biochemical, morphological, and ecological ways (Ortiz et al. 2015). The physiological aspects include the promotion of stomatal closure, a reduced photosynthesis efficiency, enhanced oxidative stress, changes in the cell-wall integrity, a reduced transpiration rate, an increase in its internal body temperature, a reduced CO_2 level, and proline accumulation (Hu et al. 2022). The biochemical aspects include decreases in the Rubisco and photochemical efficiencies, the promotion of ROS production, changes in the cell-wall integrity, decreases in its growth ability and water transpiration, an increase in its body temperature, reduced CO_2, the cessation of assimilation, and the accumulation of proline contents. The morphological aspects include drought escape (DE), dwarfness, reduced leaf size, the promotion of leaf rolling, changes in the stomata position and leaf color, reduced leaf longevity, permanent leaf wilting, and changes in the leaf angle (Riboni et al. 2013, 2016; Corso et al. 2020; Fig. 2). To mitigate the effects of drought, plants depend on the previous occurrence of drought, drought intensity, and existence of other stresses (Thomason and Battaglia 2020).

Drought Stress and Accumulation of ABA

Phytohormones play crucial roles in plant growth and development and stress responses (Sah et al. 2016; Ali et al. 2024). Drought stress is a well-known cause of the accumulation of several phytohormones that promote adaptive responses in plants (Ismail et al. 2018). These accumulated phytohormones enhance several physiological and developmental processes, such as the osmotic balance, negative phototropism in roots, and stomatal closing (Lim et al. 2015). Among the phytohormones, ABA plays a central role in drought stress responses (De Ollas et al. 2013). The drought-induced accumulation of ABA improves the resilience of a plant to drought stress (Ng et al. 2014). In addition to drought tolerance, ABA is important for the growth and development of plants under non-stress conditions (Lee et al. 2006). ABA also promotes and maintains seed dormancy (Rodríguez-Gacio et al. 2009). Furthermore, ABA alters the root structure and architecture, which changes the growth pattern in plants (Puértolas et al. 2015). ABA also induces leaf senescence, as evidenced by the late-senescence phenotypes of several ABA-deficient mutants (Yang et al. 2003; Passioura 2006). Under non-stress conditions, ABA and elevated CO_2 levels enhance partial or complete stomatal closure (Kim et al. 2010). When elevated by drought, ABA promotes stomatal closure, which reduces the water loss from leaves (Hasan et al. 2021). The ABA accumulated as a result of drought regulates the expression of several genes, particularly drought-responsive genes, which play key roles in the drought tolerance of a plant (Fujita et al. 2011). Several transcriptomic studies have shown that 50% of ABA-regulated genes are governed by drought stress. Among these, 245 genes have already been identified in Arabidopsis (Seki et al. 2002). Like Arabidopsis, 43 out of 73 stress-responsive genes in rice have been reported to be regulated by ABA and drought stress (Rabbani et al. 2003). Together, these reports suggest that drought-induced ABA accumulation plays an important role in the response of plants to

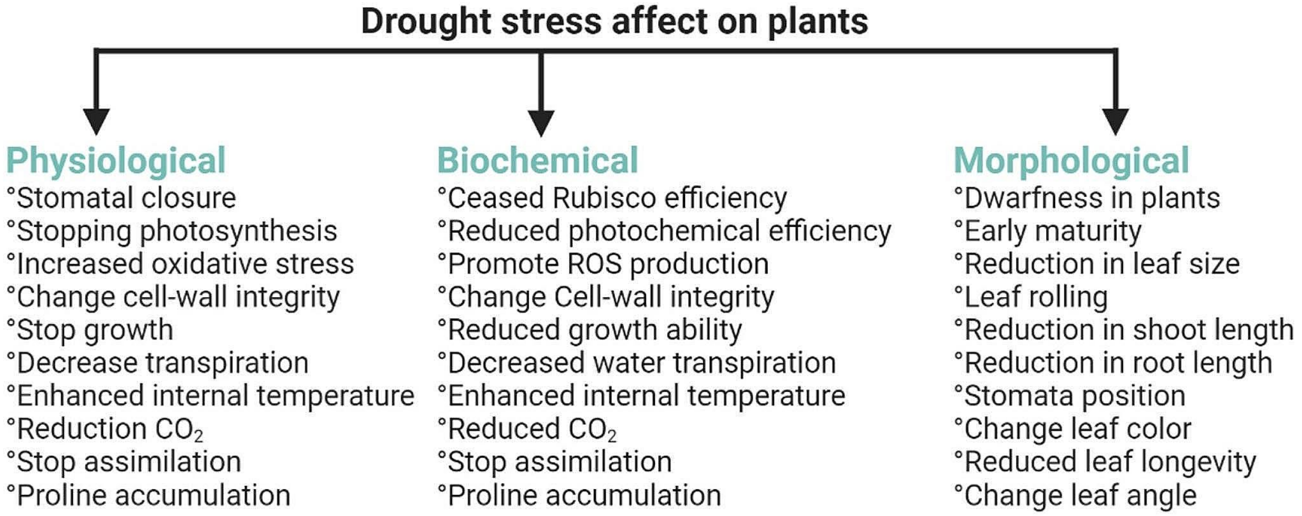


Fig. 2 Representative chart for drought stress effect on plants. This representative chart illustrates the drought stress impacts on plants, including physiological, biochemical, and morphological events

drought stress, specifically by promoting stomatal closure to prevent water loss from leaves.

Role of ABA Biosynthesis Enzymes in Drought Stress

Drought-induced ABA synthesis is a critical process that supports the adaptive responses of plants during drought stress. Previous studies have shown that the phytohormones accumulated as a result of drought promote adaptation responses via several signal transduction mechanisms (Bharath et al. 2021). A drought stress-activated ABA biosynthesis pathway was proposed by Xiong and Zhu (2003). This process involves redox signals, Ca^{+2} signaling, phosphoprotein cascades, and transcription factors that activate the expression of ABA biosynthetic genes (Xiong and Zhu 2003). ABA biosynthesis is a ubiquitous C_{15} isoprenoid process during drought stress, which is well characterized through forward genetic screening and several other enzymatic steps that have been identified in different plant species (Marin et al. 1996; Tan et al. 1997; Burbidge et al. 1999; Agrawal et al. 2001; Xiong and Zhu 2003; Dong et al. 2015; Liu et al. 2020).

The ABA biosynthesis process begins in plastids with the precursor carotenoid *zeaxanthin*. This is first repeatedly epoxidized into violaxanthin by zeaxanthin epoxidase (ZEP), which is also known as ABA deficient1 (ABA1) (Koornneef et al. 1982; Bouvier et al. 1996). Violaxanthin is then converted into neoxanthin by ABA4 (North et al. 2007). An unidentified isomerase then isomerizes both violaxanthin and neoxanthin at the C9–C10 (C9′–C10′) double bond, resulting in the production of 9-cis-violaxanthin and 9′-cis-neoxanthin (Dong et al. 2015). The *9-CIS*-epoxycarotenoid dioxygenases (NCEDs) enzymes cleave these *9(′)-cis-epoxycarotenoids* at the C11–C12 (C11′–C12′) double bond, producing a C25 apocarotenoid and the ABA precursor xanthoxin (C15) (Schwartz et al. 1997; Qin and Zeevaart 1999; Tan et al. 2003; Dong et al. 2015). This cleavage reaction is known as the rate-limiting step in the ABA biosynthesis pathway. Then, ABA2/3 and ABSCISIC aldehyde oxidase 3 (AAO3) enzymes convert xanthoxin into ABA after being translocated from plastids to the cytoplasm (Seo et al. 2000; González-Guzmán et al. 2002; Dong et al. 2015; Fig. 3). ABA2 is a cytosolic short-chain reductase that converts xanthoxin into abscisic aldehyde (González-Guzmán et al. 2002), and AAO3 is an aldehyde oxidase that mediates the oxidation of abscisic aldehyde into ABA (Seo et al. 2000; Dong et al. 2015), while ABA3 is a molybdenum cofactor sulfurase that provides enzymatic activity to AAO3 (Xiong et al. 2001).

Generally, drought stress enhances the expression of genes coding for ABA biosynthetic enzymes to accumulate endogenous ABA such as *ZEAXANTHIN EPOXIDASE* (*ZEP/LOS6* [*LOW EXPRESSION OF OSMOTIC STRESS-RESPONSIVE* 6]/*ABA1*), the *ALDEHYDE OXIDASE* (*AAO3*), a *9-CIS-EPOXYCAROTENOID DIOXYGENASE* (*NCED3*), and *MOLYBDENUM COFACTOR SULFURASE* genes (*MCSU*; also known as *LOS5/ABA3*) (Dar et al. 2017). However, some transcription factor families such as *bZIP*, *MYB*, *MYC*, *NAC*, *ERF*, and *DREB*/*CBF* also controlled their expression (Verma et al. 2016). In the ABA biosynthesis pathway, *ZEP* was the first identified gene, whose expression has been studied in all parts of the diverse plant species (Audran et al. 1998; Xiong et al. 2002). It was thought that *ZEP* does not limit ABA biosynthesis in photosynthetic tissues. Because the amount of 9-cis-epoxycarotenoid (precursor that occurs downstream of the ZEP-catalyzed reaction) is several times higher in photosynthetic tissues on a molar basis than ABA produced during stress. The transcript level of ZEP gene in the leaves of tobacco and tomato remains unchanged in drought, however, unexpectedly, it increases during the daytime (Audran et al. 1998; Thompson et al. 2000), which reflects circadian rhythm regulation. Unlike tobacco and tomato, the Arabidopsis *ZEP* gene shows basal transcript levels in non-stress condition, however, its expression level clearly increases in drought stress both in shoots and roots (Xiong et al. 2002). The transcriptomic studies with other ABA biosynthesis enzymes (such as ABAs, SDR, MCSU, AAO3, etc.) are less controversial. However, the cleavage step, particularly rate-limiting enzymes got huge attention in the last two decades. Drought stress rapidly increased the expression levels of NCEDs genes in tobacco (Tan et al. 1997), tomato (Burbidge et al. 1999), bean (*Phaseolus vulgaris*; (Qin and Zeevaart 1999), Arabidopsis (Iuchi et al. 2001), cowpea (*Vigna unguiculata*; (Iuchi et al. 2000), and avocado (*Persea americana*; (Chernys and Zeevaart 2000). The oversight of ABA biosynthesis is crucial for regulating ABA levels, adjusting plant stress responses, and developmental programs. Stress-inducible ABA biosynthesis genes may therefore be controlled by DRE/CRT class of stress-responsive genes (Xiong et al. 2002), because they contain both the DRE- and ABRE-like cis-elements in their promoters (Xiong et al. 2001; Bray, 2000). To better understand, research requires at molecular level of transcription factors with the *cis*-elements that activate the ABA biosynthesis genes. Indeed, several loci were found in over six different screening techniques, however, did not find a direct regulator of ABA biosynthesis. The correlative studies on sugar, ethylene, and ABA biosynthesis in growth and physiological processes (Ghassemian et al. 2000; Hansen and Grossmann 2000; González-Guzmán et al. 2002), indicates

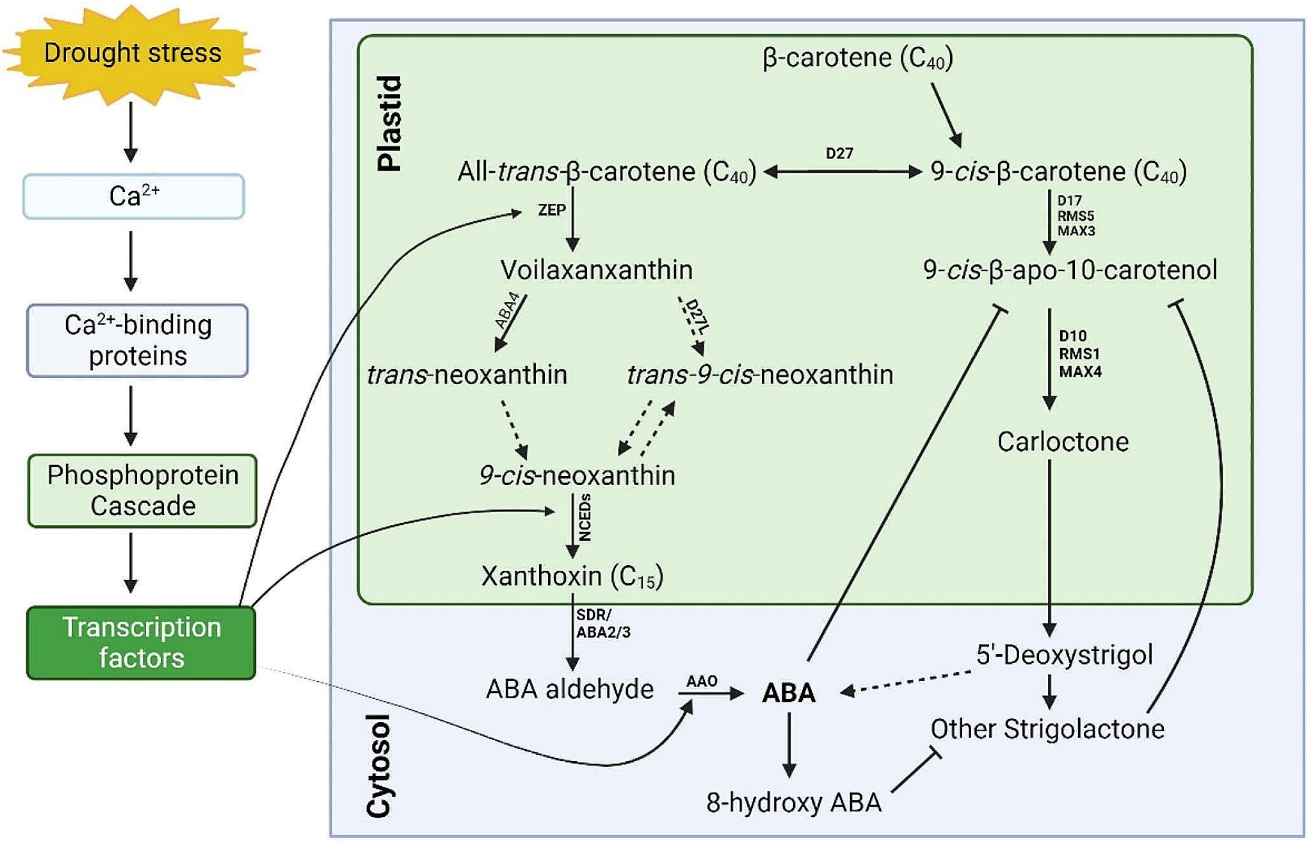


Fig. 3 Schematic representation of ABA biosynthesis pathway. Illustration of ABA biosynthesis pathway with different events. The first step occurs in the plastid, and the last step occurs in the cytosol. In the plastid, *ZEP* and *NCED* genes play essential roles in the synthesis into cytosol, whereas *SDR* and *AAO* are very important to the synthesis of ABA in the cytosol

the possibility of some signaling components in other hormone response pathways. Like *era3* (enhanced response to ABA 3) and *ein2* (ethylene insensitive 2) could be two examples of this coregulation. The *ZEP* transcript level was higher in *ein2*, suggesting that enhanced ABA biosynthesis is likely the reason why *era3/ein2* plants had a basal ABA level twice that of the wild type (Ghassemian et al. 2000). The clear effect of *ein2* mutation on ABA biosynthesis may result from the intricate interaction between several hormonal pathways.

Alternative tests such as gas exchange (sensitivity to CO2) and guard cell regulation (Mustilli et al. 2002), may identify new loci that control ABA biosynthesis or signaling. Molecular genetic techniques, like the one employed in the screen for stress signal transduction mutants (Ishitani et al. 1997), may be more effective in identifying signal transduction components since gene expression is more responsive to stress regulation than some of the apparent phenotypes. This method involves transcriptionally fusing the promoters of stress-inducible ABA biosynthesis genes such as AtNCED3, AtMCSU, and AtAAO3 to a reporter gene. This allows for the isolation of mutants exhibiting changed reporter gene expressions in response to abiotic stresses. These tests could reveal new ABA biosynthesis regulating mechanisms (Xiong and Zhu 2003). With the full genome of Arabidopsis available and a wealth of expression data, reverse genetics techniques ought to make it easier to find novel regulatory elements in the signaling pathway that leads to the synthesis of ABA. Molecular biology, biochemistry, genetics, and genomics will all need to be combined to fully comprehend how ABA production is regulated.

Epigenetic Regulation of ABA Biosynthesis Genes in Drought Stress

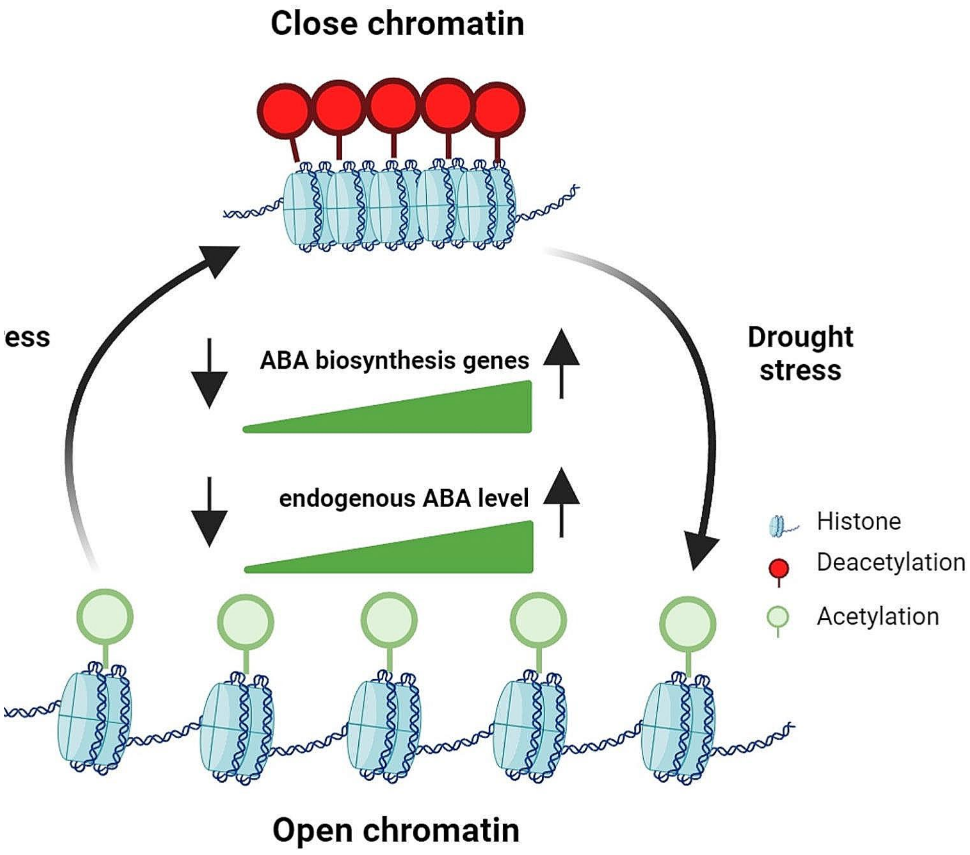
The genetic manipulation of ABA biosynthesis is a very established process, however, in the recent past, several reports stated that epigenetic modification is also an integral part of the endogenous ABA regulation during drought stress (Chinnusamy et al. 2008; Baek et al. 2020; Khan et al. 2020; Gu et al. 2021). Several plant species have been reported to regulate drought stress epigenetically including histone acetylation and deacetylation (Li et al. 2021; Praveen et al.

2023), as well as the chromatin remodelers that regulate ABA biosynthesis genes via transcription activation and deactivation (Khan et al. 2020). The dynamic activity of histone acetyltransferases (HATs) and histone deacetylases (HDAs) in response to drought stress has been widely studied in drought resilience across different plant species (Baek et al. 2020; Khan et al. 2020; Zhang et al. 2020; Hou et al. 2021; Li et al. 2022). In Arabidopsis, the acetylation mark at lysine 9 (H3K9ac) acts as a major regulator of chromatin modification at the promoters of several drought-responsive genes to control their transcript abundance (Zheng et al. 2016). Dehydration increases the endogenous ABA level by promoting histone acetylation of ABA anabolism genes and reducing histone methylation of the ABA biosynthesis genes (Gu et al. 2021), indicating a correlation between epigenetic modification and ABA accumulation (Fig. 4). The HATs and HDAs dynamic activity also controls the ABA biosynthesis pathway, which is also the primary signaling pathway for drought stress in plants (Kumar et al. 2021; Li et al. 2021). In contrast to ABA biosynthesis, the ABA catabolic pathway also working in drought stress, as we previously reported that HDA9-PWR making a complex with ABI4 to regulate histone status of *CYP707A1/2* (ABA catabolic enzyme) in drought tolerance (Baek et al. 2020; Khan et al. 2020), suggesting the importance of epigenetic regulations of ABA catabolic genes under drought stress.

Role of E3-ligases in ABA Biosynthesis

Previous studies have shown that a significant number of E3-ubiquitin ligases in plant genomes have been identified as regulators of phytohormone biosynthesis (Liu and Stone 2011). The Arabidopsis XERICO is an E3-ubiquitin ligase with a small RING-H2 domain, which regulates the endogenous ABA level and expression of the NCED3 gene in the drought-stress response (Ko et al. 2006). The senescence-associated E3 ubiquitin ligase 1 (SAUL1), which is also known as PLANT U-BOX 44 (PUB44), controls ABA production by enhancing the activity of the AAO3 enzyme to prevent premature senescence (Raab et al. 2009). Previously, we have shown that HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 (HOS15), a WD40 domain protein, is a multifunctional protein that regulates several physiological processes and stress responses in plants (Ali and Yun 2020). We have also shown that HOS15 is involved in freezing stress, drought stress, floral transition, plant immunity, leaf senescence, and miRNA biogenesis (Park et al. 2018, 2019; Ali et al. 2019; Shen et al. 2020;

Fig. 4 Schematic representation chromatin remodeling in drought stress. Illustration of chromatin status in normal and drought condition. In normal conditions, the condensed status of chromatin does not promote the ABA level due to inactivation of ABA biosynthesis genes. Under drought stress, the active and open status of chromatin promotes the endogenous ABA level through the activation of ABA biosynthesis genes



Zareen et al. 2022; Lim et al. 2023; Park et al. 2023). In addition, we have shown that HOS15 negatively regulates ABA signaling and drought stress by affecting OPEN STOMATA 1 (OST1) stability, which is a core component of the ABA signaling cascade (Ali et al. 2019). However, it is unclear how HOS15 interferes with ABA biosynthesis and whether HOS15-mediated drought stress responses involve ABA biosynthesis. Nonetheless, some indications suggest that HOS15 may be involved in the ABA biosynthesis pathway because HOS15 regulates the expression levels of ABA biosynthetic genes such as *NCED2/3/5/6/9*, and *hos15-2* plants show higher ABA contents under dehydration stress (Ali et al. 2019). Further molecular studies are required to better understand how HOS15 regulates the ABA biosynthesis pathway.

Concluding Remarks

According to prior studies, the mechanism by which plants respond to drought stress is highly complicated, involving multiple single and complex components that help to control stress responses. The genetic disruption of several genes has been identified to contribute to the morphological phenotypes of plants as well as their stress responses. This review summarized the importance of ABA biosynthesis, which is crucial to the physiological, biochemical, and morphological functions of plants and improves their adaptability to water-deficient conditions. Drought stress primarily activates the ABA biosynthesis enzymes involved in ABA production to improve stomatal closure, which reduces the severe effects of drought stress on plants. Several ABA biosynthesis components have been reported, including AAO3, NCEDs, and ABA1/2/3/4. These have different molecular mechanisms that contribute significantly to the adaptative responses of plants to drought stress. The importance of the ABA biosynthesis pathway under drought stress is still an open debate among scientists and researchers, necessitating further investigation to acquire in-depth knowledge.

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Declarations

Conflict of Interest The authors declare no conflict of interest.

References

Abbasi T, Abbasi SA (2010) Biomass energy and the environmental impacts associated with its production and utilization. Renew Sustain Energy Rev 14(3):919–937. https://doi.org/10.1016/j.rser.2009.11.006

Agrawal GK, Yamazaki M, Kobayashi M, Hirochika R, Miyao A, Hirochika H (2001) Screening of the Rice Viviparous mutants generated by endogenous retrotransposon *Tos17* insertion. Tagging of a Zeaxanthin Epoxidase Gene and a Novel *OsTATC* Gene. Plant Physiol 125(3):1248–1257. https://doi.org/10.1104/pp.125.3.1248

Alberts B, Johnson A, Lewis J, et al. (2022) Molecular biology of the cell. 4th edition. New York: Garland Science. https://www.ncbi.nlm.nih.gov/books/NBK21054/

Ali A, Kim JK, Jan M, Khan HA, Khan IU, Shen M, Park J, Lim CJ, Hussain S, Baek D et al (2019) Rheostatic Control of ABA signaling through HOS15-Mediated OST1 degradation. Mol Plant 12(11):1447–1462. https://doi.org/10.1016/j.molp.2019.08.005

Ali A, Yun D-J (2020) Arabidopsis HOS15 is a multifunctional protein that negatively regulate ABA-signaling and drought stress. Plant Biotechnol Rep 14(2):163–167. https://doi.org/10.1007/s11816-020-00600-1

Ali A, Zareen S, Park J, Ali Khan H, Lim CJ, Bader ZE, Hussain S, Chung WS, Gechev T, Pardo JM et al (2024) ABI2 promotes flowering by inhibiting OST1/ABI5-dependent FLC activation in Arabidopsis. J Exp Bot erae029. https://doi.org/10.1093/jxb/erae029

Audran C, Borel C, Frey A, Sotta B, Meyer C, Simonneau T, Marion-Poll A (1998) Expression studies of the Zeaxanthin Epoxidase Gene in *Nicotiana plumbaginifolia*. Plant Physiol 118(3):1021–1028. https://doi.org/10.1104/pp.118.3.1021

Baek D, Shin G, Kim MC, Shen M, Lee SY, Yun D-J (2020) Histone deacetylase HDA9 with ABI4 contributes to abscisic acid homeostasis in drought stress response. Front Plant Sci 11:143

Bharath P, Gahir S and Raghavendra AS. Abscisic Acid-Induced Stomatal Closure: an important component of Plant Defense against Abiotic and biotic stress. Front Plant Sci. 2021:12:615114. https://doi.org/10.3389/fpls.2021.615114

Bielach A, Hrtyan M (2017) Plants under stress: involvement of Auxin and Cytokinin. IJMS 18(7):1427. https://doi.org/10.3390/ijms18071427

Bouvier F, d'Harlingue A, Hugueney P, Marin E, Marion-Poll A, Camara B (1996) Xanthophyll Biosynthesis. J Biol Chem 271(46):28861–28867. https://doi.org/10.1074/jbc.271.46.28861

Bray EA, Bailey-Serres J, Weretilnyk E (2000) In: Gruissem W, Jones R (eds) Responses to abiotic stress. Biochemistry & molecular biology of plants. American Society of Plant Physiologists, pp 1158–1203

Brodersen CR, Roddy AB, Wason JW, McElrone AJ (2019) Functional status of Xylem through Time. Annu Rev Plant Biol 70(1):407–433. https://doi.org/10.1146/annurev-arplant-050718-100455

Burbidge A, Grieve TM, Jackson A, Thompson A, McCarty DR, Taylor IB (1999) Characterization of the ABA-deficient tomato mutant *notabilis* and its relationship with maize *Vp14*. Plant J 17(4):427–431. https://doi.org/10.1046/j.1365-313X.1999.00386.x

Chen X, Ding Y, Yang Y, Song C, Wang B, Yang S, et al. (2021) Protein kinases in plant responses to drought, salt, and cold stress. J Integr Plant Biol 63:53–78

Chernys JT, Zeevaart JAD (2000) Characterization of the 9-Cis-epoxycarotenoid dioxygenase Gene Family and the regulation of Abscisic Acid Biosynthesis in Avocado. Plant Physiol 124(1):343–354. https://doi.org/10.1104/pp.124.1.343

Chieb M, Gachomo EW (2023) The role of plant growth promoting rhizobacteria in plant drought stress responses. BMC Plant Biol 23(1):407. https://doi.org/10.1186/s12870-023-04403-8

Chinnusamy V, Gong Z, Zhu J (2008) Abscisic acid-mediated epigenetic processes in Plant Development and stress responses. JIPB 50(10):1187–1195. https://doi.org/10.1111/j.1744-7909.2008.00727.x

Corso D, Delzon S, Lamarque LJ, Cochard H, Torres-Ruiz JM, King A, Brodribb T (2020) Neither xylem collapse, cavitation, or changing leaf conductance drive stomatal closure in wheat. Plant Cell Environ 43(4):854–865. https://doi.org/10.1111/pce.13722

Dar NA, Amin I, Wani W, Wani SA, Shikari AB, Wani SH, Masoodi KZ Abscisic acid: a key regulator of abiotic stress tolerance in plants. Plant Gene. 2017:11:106–111. https://doi.org/10.1016/j.plgene.2017.07.003

Daryanto S, Wang L, Jacinthe P-A Global synthesis of drought effects on cereal, legume, tuber and root crops production: a review. Agric Water Manage. 2017:179:18–33. https://doi.org/10.1016/j.agwat.2016.04.022

De Ollas C, Hernando B, Arbona V, Gómez-Cadenas A (2013) Jasmonic acid transient accumulation is needed for abscisic acid increase in citrus roots under drought stress conditions. Physiol Plant 147(3):296–306. https://doi.org/10.1111/j.1399-3054.2012.01659.x

Diatta AA, Thomason WE, Abaye O, Thompson TL, Battaglia ML, Vaughan LJ, et al. (2020) Assessment of nitrogen fixation by mungbean genotypes in different soil textures using 15N natural abundance method. J Soil Sci Plant Nutr 20:2230–2240. https://doi.org/10.1007/s42729-020-00290-2

Dong T, Park Y, Hwang I (2015) Abscisic acid: biosynthesis, inactivation, homoeostasis and signalling. Essays Biochem 58:29–48. https://doi.org/10.1042/bse0580029

Fujita Y, Fujita M, Shinozaki K, Yamaguchi-Shinozaki K (2011) ABA-mediated transcriptional regulation in response to osmotic stress in plants. J Plant Res 124(4):509–525. https://doi.org/10.1007/s10265-011-0412-3

Ghassemian M, Nambara E, Cutler S, Kawaide H, Kamiya Y, McCourt P (2000) Regulation of Abscisic Acid Signaling by the Ethylene Response Pathway in Arabidopsis. Plant Cell 12(7):1117–1126. https://doi.org/10.1105/tpc.12.7.1117

Goche T, Shargie NG, Cummins I, Brown AP, Chivasa S, Ngara R (2020) Comparative physiological and root proteome analyses of two sorghum varieties responding to water limitation. Sci Rep 10(1):11835. https://doi.org/10.1038/s41598-020-68735-3

González-Guzmán M, Apostolova N, Bellés JM, Barrero JM, Piqueras P, Ponce MR, Micol JL, Serrano R, Rodríguez PL (2002) The short-chain alcohol dehydrogenase ABA2 catalyzes the Conversion of Xanthoxin to Abscisic Aldehyde[W]. Plant Cell 14(8):1833–1846. https://doi.org/10.1105/tpc.002477

Gray SB, Brady SM (2016) Plant developmental responses to climate change. Dev Biol 419(1):64–77. https://doi.org/10.1016/j.ydbio.2016.07.023

Guan Q, et al. (2013) A nuclear calcium-sensing pathway is critical for gene regulation and salt stress tolerance in arabidopsis. PLoS Genet 9(8):e1003755. https://doi.org/10.1371/journal.pgen.1003755

Gu D, Yang J, Wu S, Liao Y, Zeng L, Yang Z (2021) Epigenetic regulation of the Phytohormone Abscisic Acid Accumulation under Dehydration stress during Postharvest Processing of Tea (*Camellia sinensis*). J Agric Food Chem 69(3):1039–1048. https://doi.org/10.1021/acs.jafc.0c07220

Hansen H, Grossmann K (2000) Auxin-Induced Ethylene triggers Abscisic Acid Biosynthesis and Growth Inhibition. Plant Physiol 124(3):1437–1448. https://doi.org/10.1104/pp.124.3.1437

Hasan MM, Gong L, Nie Z-F, Li F-P, Ahammed GJ, Fang X-W (2021) ABA-induced stomatal movements in vascular plants during dehydration and rehydration. Environ Exp Bot 186104436. https://doi.org/10.1016/j.envexpbot.2021.104436

Hou J, Ren R, Xiao H, Chen Z, Yu J, Zhang H, Shi Q, Hou H, He S, Li L (2021) Characteristic and evolution of HAT and HDAC genes in Gramineae genomes and their expression analysis under diverse stress in Oryza sativa. Planta 253(3):72. https://doi.org/10.1007/s00425-021-03589-1

Huang XL, Yang WZ, Loeb NG, Ramaswamy V (2008) Spectrally resolved fluxes derived from collocated AIRS and CERES measurements and their application in model evaluation: Clear sky over the tropical oceans. J Geophys Res 113:D09110. https://doi.org/10.1029/2007JD009219

Hu H, He B, Ma L, Chen X, Han P, Luo Y, Liu Y, Fei X, Wei A (2022) Physiological and transcriptome analyses reveal the photosynthetic response to drought stress in drought-sensitive (Fengjiao) and drought-tolerant (Hanjiao) Zanthoxylum bungeanum cultivars. Front Plant Sci 13968714. https://doi.org/10.3389/fpls.2022.968714

Ishitani M, Xiong L, Stevenson B, Zhu J-K (1997) Genetic Analysis of Osmotic and Cold Stress Signal Transduction in Arabidopsis: interactions and convergence of Abscisic Acid-Dependent and Abscisic Acid-Independent pathways. Plant Cell 9(11):1935. https://doi.org/10.2307/3870555

Ismail, Hamayun M, Hussain A, Iqbal A, Khan SA, Lee I-J (2018) Endophytic fungus *aspergillus japonicus* mediates host plant growth under normal and heat stress conditions. Biomed Res Int 2018:1–11. https://doi.org/10.1155/2018/7696831

Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, Kato T, Tabata S, Kakubari Y, Yamaguchi-Shinozaki K, Shinozaki K (2001) Regulation of drought tolerance by gene manipulation of 9- *cis* -epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in *Arabidopsis*. Plant J 27(4):325–333. https://doi.org/10.1046/j.1365-313x.2001.01096.x

Iuchi S, Kobayashi M, Yamaguchi-Shinozaki K, Shinozaki K (2000) A stress-inducible gene for 9-cis-epoxycarotenoid dioxygenase involved in Abscisic Acid Biosynthesis under Water stress in Drought-Tolerant Cowpea. Plant Physiol 123(2):553–562. https://doi.org/10.1104/pp.123.2.553

Kaur G, Asthir B (2017) Molecular responses to drought stress in plants. Biol Plant 61(2):201–209. https://doi.org/10.1007/s10535-016-0700-9

Khan IU, Ali A, Khan HA, Baek D, Park J, Lim CJ, Zareen S, Jan M, Lee SY, Pardo JM et al (2020) PWR/HDA9/ABI4 Complex Epigenetically regulates ABA Dependent Drought stress tolerance in Arabidopsis. Front Plant Sci 11623. https://doi.org/10.3389/fpls.2020.00623

Kim T-H, Böhmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard Cell Signal Transduction Network: advances in understanding Abscisic Acid, CO $_2$, and ca $^{2+}$ signaling. Annu Rev Plant Biol 61(1):561–591. https://doi.org/10.1146/annurev-arplant-042809-112226

Ko J, Yang SH, Han K (2006) Upregulation of an Arabidopsis RING-H2 gene, *XERICO*, confers drought tolerance through increased abscisic acid biosynthesis. Plant J 47(3):343–355. https://doi.org/10.1111/j.1365-313X.2006.02782.x

Koornneef M, Jorna ML, Brinkhorst-van Der Swan DLC, Karssen CM (1982) The isolation of abscisic acid (ABA) deficient mutants by selection of induced revertants in non-germinating gibberellin sensitive lines of Arabidopsis thaliana (L.) heynh. Theoret Appl Genet 61(4):385–393. https://doi.org/10.1007/BF00272861

Kumar V, Thakur JK, Prasad M (2021) Histone acetylation dynamics regulating plant development and stress responses. Cell Mol Life Sci 78(10):4467–4486. https://doi.org/10.1007/s00018-021-03794-x

Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, et al. (2006) Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. Cell 126:1109–1120

Li H, Liu H, Pei X, Chen H, Li X, Wang J, Wang C (2022) Comparative genome-wide analysis and expression profiling of histone acetyltransferases and histone deacetylases involved in the response to Drought in Wheat. J Plant Growth Regul 41(3):1065–1078. https://doi.org/10.1007/s00344-021-10364-9

Lim C, Baek W, Jung J, Kim J-H, Lee S (2015) Function of ABA in Stomatal Defense against Biotic and Drought stresses. IJMS 16(12):15251–15270. https://doi.org/10.3390/ijms160715251

Lim CJ, Park KS, Ali A, Park J, Ryou SM, Shen M, Khan HA, Bader ZE, Zareen S, Bae MJ, Choi JH, Xu Z-Y, Pardo JM, Yun D-J (2023) Negative regulation of floral transition in Arabidopsis by HOS15-PWR-HDA9 complex. Front Plant Sci 13:1105988

Li S, He X, Gao Y, Zhou C, Chiang VL, Li W (2021) Histone acetylation changes in Plant Response to Drought stress. Genes 12(9):1409. https://doi.org/10.3390/genes12091409

Liu H, Stone SL (2011) E3 ubiquitin ligases and abscisic acid signaling. Plant Signal Behav 6(3):344–348. https://doi.org/10.4161/psb.6.3.13914

Liu X, Hu Q, Yan J, Sun K, Liang Y, Jia M, Meng X, Fang S, Wang Y, Jing Y et al (2020) ζ-Carotene isomerase suppresses Tillering in Rice through the coordinated biosynthesis of Strigolactone and Abscisic Acid. Mol Plant 13(12):1784–1801. https://doi.org/10.1016/j.molp.2020.10.001

Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: an overview. Arch Biochem Biophys 444(2):139–158. https://doi.org/10.1016/j.abb.2005.10.018

Marin E, Nussaume L, Quesada A, Gonneau M, Sotta B, Hugueney P, Frey A, Marion-Poll A (1996) Molecular identification of zeaxanthin epoxidase of Nicotiana plumbaginifolia, a gene involved in abscisic acid biosynthesis and corresponding to the ABA locus of Arabidopsis thaliana. EMBO J 15(10):2331–2342. https://doi.org/10.1002/j.1460-2075.1996.tb00589.x

Markham KK, Greenham K (2021) Abiotic stress through time. New Phytol 231(1):40–46. https://doi.org/10.1111/nph.17367

Martínez-Vilalta J, Garcia-Forner N (2017) Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. Plant Cell Environ 40(6):962–976. https://doi.org/10.1111/pce.12846

Mustilli A-C, Merlot S, Vavasseur A, Fenzi F, Giraudat J (2002) Arabidopsis OST1 protein kinase mediates the regulation of Stomatal aperture by Abscisic Acid and acts Upstream of reactive oxygen species production. Plant Cell 14(12):3089–3099. https://doi.org/10.1105/tpc.007906

Ng LM, Melcher K, Teh BT, Xu HE (2014) Abscisic acid perception and signaling: structural mechanisms and applications. Acta Pharmacol Sin 35(5):567–584. https://doi.org/10.1038/aps.2014.5

North HM, Almeida AD, Boutin J, Frey A, To A, Botran L, Sotta B, Marion-Poll A (2007) The Arabidopsis ABA-deficient mutant *aba4* demonstrates that the major route for stress-induced ABA accumulation is via neoxanthin isomers. Plant J 50(5):810–824. https://doi.org/10.1111/j.1365-313X.2007.03094.x

O'Connell E (2017) Towards Adaptation of Water Resource Systems to climatic and Socio-Economic Change. Water Resour Manage 31(10):2965–2984. https://doi.org/10.1007/s11269-017-1734-2

Oh DH, Hong H, Lee SY, Yun DJ, Bohnert HJ, Dassanayake M (2014). Genome structures and transcriptomes signify niche adaptation for the multiple-ion-tolerant extremophyte Schrenkiella parvula. Plant Physiol 164:2123–2138. https://doi.org/10.1104/pp.113.233551

Ortiz N, Armada E, Duque E, Roldán A, Azcón R (2015) Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. J Plant Physiol 174:87–96. https://doi.org/10.1016/j.jplph.2014.08.019

Osakabe Y, Osakabe K, Shinozaki K, Tran L-SP Response of plants to water stress. Front Plant Sci. 2014:5. https://doi.org/10.3389/fpls.2014.00086

Park HJ, Baek D, Cha J-Y, Liao X, Kang S-H, McClung CR, Lee SY, Yun D-J, Kim W-Y (2019) HOS15 interacts with the histone deacetylase HDA9 and the Evening Complex to Epigenetically regulate the Floral Activator *GIGANTEA*. Plant Cell 31(1):37–51. https://doi.org/10.1105/tpc.18.00721

Park J, Giudicatti AJ, Bader ZE, Han MK, Møller C, Arce AL, Xu Z-Y, Yang SW, Manavella PA, Yun D-J (2023) The HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE15–HISTONE DEACETYLASE9 complex associates with HYPONASTIC LEAVES 1 to modulate microRNA expression in response to abscisic acid signaling. Plant Cell 35(8):2910–2928. https://doi.org/10.1093/plcell/koad132

Park J, Lim CJ, Shen M, Park HJ, Cha J-Y, Iniesto E, Rubio V, Mengiste T, Zhu J-K, Bressan RA et al (2018) Epigenetic switch from repressive to permissive chromatin in response to cold stress. Proc Natl Acad Sci USA 23115. https://doi.org/10.1073/pnas.1721241115

Passioura J (2006) The drought environment: physical, biological and agricultural perspectives. J Exp Bot 58(2):113–117. https://doi.org/10.1093/jxb/erl212

Prakash V, Singh VP, Tripathi DK, Sharma S, Corpas FJ Crosstalk between nitric oxide (NO) and abscisic acid (ABA) signalling molecules in higher plants. Environ Exp Bot. 2019:161:41–49. https://doi.org/10.1016/j.envexpbot.2018.10.033

Praveen A, Dubey S, Singh S, Sharma VK (2023) Abiotic stress tolerance in plants: a fascinating action of defense mechanisms. 3 Biotech 13(3):102. https://doi.org/10.1007/s13205-023-03519-w

Puértolas J, Conesa MR, Ballester C, Dodd IC (2015) Local root abscisic acid (ABA) accumulation depends on the spatial distribution of soil moisture in potato: implications for ABA signalling under heterogeneous soil drying. J Exp Bot 66(8):2325–2334. https://doi.org/10.1093/jxb/eru501

Qin X, Zeevaart JAD (1999) The 9- *cis* -epoxycarotenoid cleavage reaction is the key regulatory step of abscisic acid biosynthesis in water-stressed bean. Proc Natl Acad Sci USA 96(26):15354–15361. https://doi.org/10.1073/pnas.96.26.15354

Raab S, Drechsel G, Zarepour M, Hartung W, Koshiba T, Bittner F, Hoth S (2009) Identification of a novel E3 ubiquitin ligase that is required for suppression of premature senescence in Arabidopsis. Plant J 59(1):39–51. https://doi.org/10.1111/j.1365-313X.2009.03846.x

Rabbani MA, Maruyama K, Abe H, Khan MA, Katsura K, Ito Y, Yoshiwara K, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) Monitoring expression profiles of Rice genes under Cold, Drought, and high-salinity stresses and Abscisic Acid Application using cDNA microarray and RNA gel-blot analyses. Plant Physiol 133(4):1755–1767. https://doi.org/10.1104/pp.103.025742

Riboni M, Galbiati M, Tonelli C, Conti L (2013) GIGANTEA enables drought escape response via abscisic acid-dependent activation of the florigens and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1. Plant Physiol 162:1706–1719

Riboni M, Robustelli Test A, Galbiati M, Tonelli C, Conti L (2016) ABA-dependent control of GIGANTEA signalling enables drought escape via up-regulation of FLOWERING LOCUS T in Arabidopsis thaliana. J Exp Botany 67: 309–6322

Rodríguez-Gacio MDC, Matilla-Vázquez MA, Matilla AJ (2009) Seed dormancy and ABA signaling: the breakthrough goes on. Plant Signal Behav 4(11):1035–1048. https://doi.org/10.4161/psb.4.11.9902

Ryder S, Pedigo J, Ojennus DD (2023) Elucidating the role of a calcium-binding Loop in an *x* -Prolyl aminodipeptidase from

Lb. Helveticus. ACS Omega 8(38):35410–35416. https://doi.org/10.1021/acsomega.3c05639

Sah SK, Reddy KR, Li J (2016) Abscisic acid and abiotic stress tolerance in crop plants. Front Plant Sci 7. https://doi.org/10.3389/fpls.2016.00571

Schwartz SH, Tan BC, Gage DA, Zeevaart JAD, McCarty DR (1997) Specific oxidative cleavage of carotenoids by VP14 of Maize. Science 276(5320):1872–1874. https://doi.org/10.1126/science.276.5320.1872

Seki M, Ishida J, Narusaka M, Fujita M, Nanjo T, Umezawa T, Kamiya A, Nakajima M, Enju A, Sakurai T et al (2002) Monitoring the expression pattern of around 7,000 Arabidopsis genes under ABA treatments using a full-length cDNA microarray. Funct Integr Genom 2(6):282–291. https://doi.org/10.1007/s10142-002-0070-6

Seo M, Peeters AJM, Koiwai H, Oritani T, Marion-Poll A, Zeevaart JAD, Koornneef M, Kamiya Y, Koshiba T (2000) The *Arabidopsis* aldehyde oxidase 3 (*AAO3*) gene product catalyzes the final step in abscisic acid biosynthesis in leaves. Proc Natl Acad Sci USA 97(23):12908–12913. https://doi.org/10.1073/pnas.220426197

Shen M, Lim CJ, Park J, Kim JE, Baek D, Nam J, Lee SY, Pardo JM, Kim W-Y, Mackey D et al (2020) HOS15 is a transcriptional corepressor of NPR1-mediated gene activation of plant immunity. Proc Natl Acad Sci USA 117(48):30805–30815. https://doi.org/10.1073/pnas.2016049117

Swain R, Sahoo S, Behera M, Rout GR Instigating prevalent abiotic stress resilience in crop by exogenous application of phytohormones and nutrient. Front Plant Sci. 2023:14:1104874. https://doi.org/10.3389/fpls.2023.1104874

Tan B-C, Joseph LM, Deng W-T, Liu L, Li Q-B, Cline K, McCarty DR Molecular characterization of the *Arabidopsis* 9 *-cis* epoxycarotenoid dioxygenase gene family: AtNCED *gene family in* Arabidopsis. Plant J. 2003:35(1):44–56. https://doi.org/10.1046/j.1365-313X.2003.01786.x

Tan BC, Schwartz SH, Zeevaart JAD, McCarty DR (1997) Genetic control of abscisic acid biosynthesis in maize. Proc Natl Acad Sci USA 94(22):12235–12240. https://doi.org/10.1073/pnas.94.22.12235

Thomason W, Battaglia M (2020) Early defoliation effects on corn plant stands and grain yield. Agron J 112(6):5024–5032. https://doi.org/10.1002/agj2.20402

Thompson AJ, Jackson AC, Symonds RC, Mulholland BJ, Dadswell AR, Blake PS, Burbidge A, Taylor IB (2000) Ectopic expression of a tomato 9- *cis* -epoxycarotenoid dioxygenase gene causes over-production of abscisic acid. Plant J 23(3):363–374. https://doi.org/10.1046/j.1365-313x.2000.00789.x

Verma S, Nizam S, Verma PK Biotic and Abiotic Stress Signaling in Plants. In. Stress signaling in plants: Genomics and Proteomics Perspective, Volume 1, Sarwat M, Ahmad A, Abdin M (eds) (Springer New York: New York, NY), pp. 25–49. https://doi.org/10.1007/978-1-4614-6372-6_2

Verma V, Ravindran P, Kumar PP (2016) Plant hormone-mediated regulation of stress responses. BMC Plant Biol 16(1):86. https://doi.org/10.1186/s12870-016-0771-y

Wu X, et al. (2022) Linker histone variant HIS1-3 and WRKY1 oppositely regulate salt stress tolerance in arabidopsis. Plant Physiol 189(3):1833–1847

Xiong L, Ishitani M, Lee H, Zhu J-K (2001) The Arabidopsis *LOS5/ABA3* locus encodes a Molybdenum Cofactor Sulfurase and modulates cold stress– and osmotic stress–responsive gene expression. Plant Cell 13(9):2063–2083. https://doi.org/10.1105/TPC.010101

Xiong L, Lee H, Ishitani M, Zhu J-K (2002) Regulation of osmotic stress-responsive gene expression by theLOS6/ABA1 locus inArabidopsis. J Biol Chem 277(10):8588–8596. https://doi.org/10.1074/jbc.M109275200

Xiong L, Zhu J-K (2003) Regulation of Abscisic Acid Biosynthesis. Plant Physiol 133(1):29–36. https://doi.org/10.1104/pp.103.025395

Yang JC, Zhang JH, Wang ZQ, Zhu QS, Liu LJ (2003) Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. Plant Cell Environ 26(10):1621–1631. https://doi.org/10.1046/j.1365-3040.2003.01081.x

Yu G, Chen D, Ye M, Wu X, Zhu Z, Shen Y, Mehareb EM, Esh A, Raza G, Wang K et al (2024) H3K27 demethylase SsJMJ4 negatively regulates drought-stress responses in sugarcane. J Exp Bot erae037. https://doi.org/10.1093/jxb/erae037

Zandalinas SI, Fritschi FB, Mittler R (2020) Signal transduction networks during stress combination. J Exp Bot 71(5):1734–1741. https://doi.org/10.1093/jxb/erz486

Zareen S, Ali A, Lim CJ, Khan HA, Park J, Xu Z-Y, Yun D-J (2022) The Transcriptional Corepressor HOS15 mediates Dark-Induced Leaf Senescence in Arabidopsis. Front Plant Sci 13828264. https://doi.org/10.3389/fpls.2022.828264

Zhang J-B, He S-P, Luo J-W, Wang X-P, Li D-D, Li X-B (2020) A histone deacetylase, GhHDT4D, is positively involved in cotton response to drought stress. Plant Mol Biol 104(1–2):67–79. https://doi.org/10.1007/s11103-020-01024-9

Zheng Y, Ding Y, Sun X, Xie S, Wang D, Liu X, Su L, Wei W, Pan L, Zhou D-X (2016) Histone deacetylase HDA9 negatively regulates salt and drought stress responsiveness in Arabidopsis. EXBOTJ 67(6):1703–1713. https://doi.org/10.1093/jxb/erv562

Zhu J-K (2016) Abiotic Stress Signaling and responses in plants. Cell 167(2):313–324. https://doi.org/10.1016/j.cell.2016.08.029