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Review Article

Signaling Behaviour of Abscisic Acid on Physiological Activities in Plants Under Stress

Naimah, N. and Jahan, M. S.*

Department of Agriculture and Biotechnology, Faculty of Bioresources and Food Industry,
University Sultan Zainal Abidin, 22200 Besut, Terengganu, Malaysia

ABSTRACT

Plants manage water stress conditions through a variety of signalling networks, which maintain physiological balances of the plants. The phytohormone, abscisic acid (ABA), regulates growth and development of plants by acting on different physiological features of plants. Various stress factors including drought result in raising the endogenous ABA concentration in plant cells. Abscisic acid modifies gene function and its transformation in plants when plants are experiencing stress conditions. Molecular mechanisms show signalling functions of ABA in plants. Several researchers have demonstrated the different roles of ABA in plants such as regulation of stomatal aperture, production of secondary metabolites and signalling cross-link with other molecules. Researchers also show significant interest in and place importance on the signalling regulation of ABA on the growth and physiology of plants. Therefore, this review highlights the signalling pathway of ABA with or without other molecules to restrain growth and physiological parameters of plants under climate change conditions.

Keywords: Arabidopsis, glutathione, guard cells, plant growth, reactive oxygen species, signalling pathway, stomatal aperture, stress factors

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E-mail addresses:
noornaimahsyafiqah@gmail.com (Naimah, N.),
sarwarjahan@unisza.edu.my (Jahan, M. S.)
* Corresponding author

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INTRODUCTION

Abscisic acid (ABA) is recognised under stress conditions by plants, allowing it to amend physiological features of plants under stress to cope with multiple detrimental environmental indicators that challenge to abiotic and biotic consequences due to climate change. Currently, biochemical, molecular, genetic and genomic methodologies have shown the fundamental charter of the ABA signalling network in plants. Reports on ABA receptors, especially, have further clarified understanding of the functional mechanisms of ABA in plants (Zhang, 2014). Additionally and more importantly, a number of ABA-related genes has been engineered for improvement of stress resistance to provide chances for the progress of new varieties with superior stress resistance. ABA regulates physiological processes, primarily biosynthesis de novo ABA, by relevant enzymes rather than the relocation of remaining pools of ABA (Hartung et al., 2002). Genetic analysis has revealed that different physiological processes such as seed germination, osmotic stress and transpiration are linked to the ABA activity, emphasising the responsibility of ABA in signalling networking in plants (Seo & Koshiba, 2002).

In the last 30 years, several reports confirmed that ABA regulates the stomatal aperture of guard cells. Recent reports have stated that ABA functions with several factors to modulate the growth of plants (Jahan et al., 2008; Khokon et al., 2011; Okuma et al., 2011; Jahan et al., 2016). The status of water maintains ABA strength in the xylem stream. ABA-induced stomatal closure controls physiological functions such as photosynthesis (Davies et al., 1993), which may affect growth, physiology and development of stressed plants (Jahan et al., 2013; Khairi et al., 2015; Khairi et al., 2016). This review cites new understanding of the current roles of ABA to up-regulate plant physiological functions under climate change conditions for sustainable growth and production of plants.

Discovery and Catabolism of Abscisic Acid

Abscisic acid is a small molecule, which encompasses various functional groups. Addicott et al. (1963) isolated two liable compounds aimed at abscission fruit (cotton) i.e. abscisin I and abscisin II. Abscisic acid was formerly called ‘abscisin II’. It plays a significant role in abscission of fruit and bud dormancy and has inhibitory roles as well as promotes physiological functions in plants (Salisbury & Ross, 1992). Stability in biosynthesis and catabolism controls endogenous ABA levels in numerous plants. ABA is a compound that naturally synthesises in plants via a direct pathway, the mevalonic pathway, in chloroplast and via an indirect pathway, the methylerythritol phosphate (MEP) pathway, which appears to occur in cyanobacteria and eukaryotes (Schwartz & Zeevaart, 2010). Stress, for example drought and temperature, highlights the biosynthesis of ABA in plants. In the direct pathway, isomerisation of allofarnesene and oxidation synthesise ABA in fungi (Inomata et al., 2004). In the indirect pathway, carotenoids, chloroplast-produced pigments, which have 40 carbon molecules, appear in the ABA structure.

In the reaction centre, a molecule of violaxanthonin was seen in research to produce a molecule of xanthonin, which is unstable and therefore, transforms to ABA aldehyde (ABAld). Further oxidation methods used in research resulted in activation of ABA by two enzymes, abscisic aldehyde oxidase and molybdenum cofactor sulfurase. In wilt tomato mutants, flacca and sitiens, the transformation of ABAld to ABA was constructed in cell-free extracts due to oxidase enzyme (Taylor et al., 1988), which produces ABA (Leydecker et al., 1995). In several plant species, the hydroxylation phase in the ABA catabolic route in plants catalysed C-8′ of ABA and produced unstable 8′-hydroxy-ABA (Walton, 1983).

Transportation and Distribution of ABA

Water deficit synthesises ABA in cells sited across the vasculature; it is translocated to the guard cells and stimulates stomatal closure. In this relation, ABA exporter genes and importer genes are expressed; they determine the amount of mobile ABA present in the apoplastic space by balancing export and import of ABA content out of and into vascular tissue (Seo & Koshiba, 2002). ABA is capable of moving both up and down along the stem through the xylem and phloem tissues and parenchyma cells in plants, which do not show polarity with other growth regulators such as auxins (Salisbury & Ross, 1992). Abscisic acid is synthesised in leaves and roots and freely moves from plant to soil as well as from soil to plant. Roots grow well under soil solution, which contains plants hormones. If the ABA is not at equilibrium, ABA transport from root to soil is disrupted, which also disrupts the signalling relationship between the roots and the shoot (Sauter et al., 2001). Translocation of ABA from cell-to-cell is done through the plasmodesmata and transmembrane transport, after which it is synthesised in the cells. In addition, ABA presences in xylem sap is exported to the outside of the cells (Hartung et al., 2002). After that, ABA is moved to other cells to stimulate physiological reactions in plants.

A plant may uptake ABA from acidic soil, which increases external take-up of ABA concentration by the roots (Freundl et al., 2000). In contrast, roots lose ABA content under high soil pH condition (Degenhardt et al., 2000). This is due to the effects of the reduction of ABA content in the surrounding medium (Freundl et al., 2000). Several factors other than water stress such as salt content, phosphorus deficiency and ammonium increment stimulate ABA biosynthesis in the root but nitrate deficiency and alkaline reduces it (Wolf et al., 1990; Jaschke et al., 1997; Freundl et al., 2000). Therefore, water stress and salt accumulate a higher concentration of ABA in the roots of plants (Sauter et al., 2001). The increment of ABA in roots may increase the flow of ABA in the cells of roots through the symplastic and apoplastic pathway under stress conditions, then translocate to the guard cells to close the stoma (Sauter et al., 2001; Jahan et al., 2016). In contrast, increasing water flow rapidly decreases ABA concentration through bypass flow of ABA to the endodermis, leading to ABA homeostasis in the xylem (Tardieu et al., 1992; Freundl et al., 1998).

The pH of cells affects the delivery of ABA. ABA biosynthesis occurs in the cytosol when the pH level is at 7.2. Therefore, most of the ABA is ionised in the cytosol and exists as ABA−, followed by ABA efflux. Then, the ABA moves through the apoplastic space (Kramer, 2006). At this stage, the pH in the apoplast remains at 5.0-6.0. This pH gradient condition suggests active transport mechanism of apoplastic ABA in cells. However, stoma are closed due to a flux of ABA in well-watered conditions by changing acidic pH to alkaline pH conditions. A little alkalinisation in xylem sap may result in stomatal closure (Wilkinson & Davies, 1997) and might influence leaf growth (Bacon et al., 1998). Apoplastic pH rises to about 7.0 when plants are under water stress conditions, which enables a moderately large percentage of ABA-H to move over extended distances across the apoplast (Wilkinson & Davies, 2002). The transportation of ABA is required to induce ABA signalling under stress conditions. The distribution of ABA is a concern to environmental conditions. Under normal circumstances, ABA concentration in leaves is higher than in roots and stems (Bahrun et al., 2002).

Intercellular Transport of ABA to Stomatal Movement

ABA is a key controller of stomatal movement in guard cells under water scarcity. Several studies have focussed on the signal transduction pathways underlying the ABA-regulated stomatal aperture. ABA is primarily localised in chloroplast and vascular tissue. From here, it is transported to sites of action in guard cells during water shortage (Seo & Koshiba, 2002). Drought-induced pH changes in different parts of the leaves of a plant (Islam et al., 2011) control a complex distribution of ABA throughout the various cells of the leaves. Then ABA gathers in guard cells and persuades stomatal closure (Jahan et al., 2016). Water stress leads to an increment of ABA content in the apoplast but not in the mesophyll cells (Wang & Jia, 1995). Interestingly, ABA translocates from mesophyll and vascular cells to the guard cells to close stomata under stress conditions, but under non-stress conditions, stomatal movement is unaffected by the ABA although both mesophyll and vascular cells contain plentiful ABA content. Drought stress increases ABA content in the mesophyll and vascular cells of leaves and ABA-induced secondary signalling metabolites (Jahan et al., 2016; Munemasa et al., 2007). More prominently, ABA build-up in guard cells seems to protect plants against drought stress (Okuma et al., 2011).

Cross Talk Between ABA and Methyl Jasmonate Acid in Signalling Pathways

Guard cells are specialised cells that control gas exchange and water movement to respond to numerous types of stress due to climate change through the closing and opening of stomatal pores (Kim et al., 2010; Okuma et al., 2011; Jahan et al., 2014). Plants synthesise ABA in response to consequences of climate change and prove the transduction of ABA to guard cells through production of second messengers, for example, cytosolic $Ca2^+$, nitric oxide (NO) and reactive oxygen species (ROS) in guard cells (Murata et al., 2015). A plant hormone, jasmonate, regulates stomatal opening in reaction to diverse stimuli such as senescence, wounding and pathogen attacks in plants (Turner et al., 2002). MeJA stimulates ROS intervention in guard cells like ABA under different climate change conditions such as water stress, wounding, salinity and insect attacks (Tsonev et al., 1998; Suhita et al., 2004). Similarities observed in different stomatal aperture experiments involved the NAD(P)H oxidase inhibitor, diphenyleneiodonium (Tsonev et al., 1998). Two NAD(P)H oxidases, AtrbohD and AtrbohF, link methyl jasmonate acid (MeJA) and ROS for signalling in guard cells, proving that MeJA and ABA function in the similar signalling way to persuade stomatal closure. Furthermore, both ABA and MeJA stimulate NO synthase (NOS) guard cells during NO-induced stomatal closure, which indicates a similar path of ABA and MeJA in the signalling force of stomatal closure (Desikan et al., 2002; Sasaki-Sekimoto et al., 2005). As a result, MeJA- and ABA-induced stomatal closure is due to the production of ROS and NO in guard cells through the stimulation of $Ca2^+$ from intracellular stores to the cytosol (Desikan et al., 2002). MeJA does not induce stomatal closure in the *abi2-1* mutant, an ABA-insensitive mutant; this suggests that a protein phosphatase 2C links with MeJA core components in ABA regulation in receptor complexes (Munemasa et al., 2007; Desikan et al., 2002; Murata et al., 2001). ABA and MeJA signalling might affect ABA receptor developments to control downstream signal mechanisms.

Abscisic Acid Signalling in Glutathione Functions on Guard Cells

Abscisic acid stimulates different physiological processes of a plant in stress conditions (Finkelstein et al., 2002). ABA features on GSH variation in guard cells of Arabidopsis (Okuma et al., 2011; Jahan et al., 2014). Water stress promotes the primary gathering of ABA that generates ROS creation, which might adjust GSH biosynthesis in plants (Murata et al., 2015). ABA signalling in GSH was studied earlier in guard cells of the Arabidopsis plants (Jahan et al., 2008; Jahan et al., 2011; Okuma et al., 2011; Munemasa et al., 2013). The Arabidopsis mutant, GLUTATHIONE S-TRANSFERASE U17 (AtGSTU17), stores a greater amount of ABA in the presence of GSH (Cheng et al., 2013). Therefore, the functions of GSH with ABA in plants would be a critical aspect for the plants' ability to cope with climate change conditions (Cheng et al., 2013). ABA affects GSH content in ratio to GSSG, GR activity and γ-ECS transcript levels in maize genotypes (Okuma et al., 2011; Cheng et al., 2013). Glutathione peroxidase3 (*atgpx3*) controls H2O2 homeostasis in ABA-mediated stomatal movement (Miao et al., 2006), which suggests that ABA signalling with GSH is linked to the stomatal movement in guard cells of Arabidopsis (Okuma et al. 2011; Jahan et al., 2014). Therefore, GSH-deficient mutants, the *ch1-1* and cadmium sensitive mutant (*cad2-1*), exhibit a higher sensitivity to ABA than the wild types (Okuma et al., 2011; Jahan et al., 2011, 2008). In addition, Munemasa et al. (2013) confirm that GSH modulates the signalling compartment of ABA in guard cells.

It has been genetically and chemically confirmed that GSH does not affect ROS production in guard cells as well as the activation of $Ca2^+$ -permeable channel (ICa) (Akter et al., 2013; Okuma et al., 2011), which suggests that GSH might play a role in coupling H_2O_2 to downstream an ABA-induced signalling cascade in guard cells (Okuma et al. 2011). In a current development, Munemasa et al. (2013) stated that GSH depletion affects ROS signalling in apoplastic space rather than in the cytosol of guard cells during ABA-induced stomatal closure (Munemasa et al., 2013). Different studies have stated a similar result, that apoplastic ROS signals regulate stomatal movement (Hossain et al., 2013; An et al., 2008). Therefore, GSH-modulated ABA signalling of a GSH-deficient mutant (Jahan et al., 2008) is not conditional to the production of H_2O_2 in guard cells (Munemasa et al., 2013).

Abscisic Acid Signalling on Growth of Plants

Climate change is becoming a severe problem for plant growth in several regions of the world. Plants respond to drought conditions through intensely complicated mechanisms such as genetic and physiological processes (Chaves et al., 2003; Izanloo et al., 2008). Water stress influences plant growth and biomass production remarkably (Chaves et al., 2003; Hisao, 1973). The leaf area of *Leymus chinensis*, for instance, is significantly stimulated by rewatering compared to a short-term drought (Xu & Zhou, 2007). In another instance, tiller production of *Leymus chinensis* recovered after rewatering, suggesting that development of meristems of the tiller might play an important role in response to water stress conditions (Xu & Zhou, 2009). Water stress is closely related to the elevation of ABA in guard cells to close stomata (Jahan et al., 2016), which might reduce gas exchange through the opening of guard cells. Reactive oxygen species (ROS) increases during drought conditions because of the influence of ABA production (Jahan et al., 2008). Water application reduced ROS production in guard cells and the retrieval net photosynthetic and transpiration rate in plants (Okuma et al., 2011; Khairi et al., 2016). Low relative water content increased ROS production (Murata et al., 2015), which is also related to the ABA signalling for plant growth. Stoma closure due to drought conditions limits photosynthesis in plants (Chaves et al., 2003). Drought reduces light-dependent photosynthesis and stomatal conductance in plants (Peñuelas et al., 2004; Xu & Zhou, 2009). This was consistent with the results obtained by Nozulai et al. (2015) and Khaiti et al. (2016) in rice plants, where reduction of water content reduced plant physiological parameters. This result also suggests that ABA might have a significant role in gas exchange in drought conditions. In addition, Izanloo et al. (2008) stated that water stress declined quantum yield in the photosystem II, indicating a functional activity of ABA in regulating light reaction in plants. A defect of the light-harvesting mutant, *ch1-1*, led to higher sensitivity to ABA than was seen in wild types (Jahan et al., 2014, 2016). Therefore, *ch1-1* mutant plants are deficient in morphological, physiologic and yield parameters compared to wild types of the plant (Jahan et al., 2014, 2016). It is suggested that ABA controls growth and development of plants through multi-signalling waves.

CONCLUSION

Considering the latest documentation, it is clear that ABA has a distinct role in the hormonal signalling pathway in controlling physiological functions of plants. There is evidence that ABA modulates physiological changes in plants in the presence of stress conditions through a signalling network with other plant hormones as well as antioxidants. However, understanding the workings of the protocols of the gene that controls ABA function in plants needs further study. Further study and experimental proof are also necessary for understanding the role of ABA in different hormonal signalling cascades for a clearer picture of the ABA signalling-web on the growth and physiology of plants.

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