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THE ROLE OF ABSCISIC ACID IN INDUCING COLD TOLERANCE IN PLANTS

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Abstract *Abscisic acid's (ABA) mode of action and its connections to adaptations to cold have captured plant hormone researchers' attention for over a decade. Abiotic stress is the main risk to agriculture productivity needed to feed the globe in the next decades. A significant phytohormone, ABA, is crucial in responding to various challenges, including high and low temperatures, drought, thermal or heat stress, and heavy metal and radiation stress. Stress situations cause plants to slow down their growth and development, ultimately impacting the output. There is a lot of proof that ABA moves around inside plants. In reaction to dry soil conditions, As a growth hormone ABA is an important biochemical that causes stomata closures. It has been claimed that ABA produced in morphological plant body parts is transferred to seeds. The transport of ABA is a crucial mechanism in physiological responses because it significantly determines an endogenous concentration of ABA action sites. ABA is a significant messenger that is a signaling mediator to control how plants respond adaptively to various environmental stressors. It is described in detail that several plant exposures elevated ABA endogenous levels under cold stress. In our present discussion, the role of ABA in low temperatures will be our main focus. ABA transportation in plants, the biosynthetic pathway of ABA in plants, the Pathway from IPP to ABA Production, the ABA functions in plants, and the location of biosynthesis. The review also deals with the production of ABA in plants under cold stress.*

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Introduction

Abiotic stressors affect plants in a variety of ways, including increased salinity (salinity), low temperatures, chilling and freezing, high temperatures (heat), and a lack of water (drought or dehydration). These stressors are the main factor drastically lowering crop production (Mahajan and Tuteja, 2005; Roelofs et al., 2008; Tuteja, 2007; Yadav et al., 2020). The phytohormone abscisic acid is a signal to control many activities throughout a plant's life cycle. Adaptively plants perceive and respond to abiotic stress imposed by cold, drought, salt, and wounding (Mahajan and Tuteja, 2005; Shariatipour and Heidari, 2018; Swamy and Smith, 1999; Tuteja, 2007). Abscisic acid is also a stress hormone (Mauch-Mani and Mauch, 2005; Yoshida et al., 2019; Zhang et al., 2006). Abscisic acid was discovered and categorized as a plant hormone for the first time by Frederick and his colleagues in the 1940s. They researched substances that lead to cotton bolls' abscission (shedding). The chemicals Abscisin I and Abscisin II were isolated. Abscisic acid (ABA) is the current name for abscisin II (Davis and Addicott, 1972). Abscisic acid (ABA or abscisin II) is a hormone that plants make in extremely small amounts. It is known that transcription factors control the expression of ABA-sensitive genes. (Fujita et al., 2011; Xiong et al., 2002). ABA is weak acid that has 15pH (Finkelsteina and Rockb, 2002). In the early 1960s, ABA was discovered as a growth inhibitor, addition in abscising cotton fruit and photoperiodically induced dormant leaves of sycamore plant (Cutler et al., 2010; Nakabayashi et al., 2005; Wasilewska et al., 2008). ABA-dependent and ABA-independent are two ways of expressing stress-responsive genes (Chinnusamy et al., 2004; Ding et al., 2011; Tuteja, 2007; Yang et al., 2011).
From embryogenesis onward, the hormones regulate the plant's development and growth (Méndez-Hernández et al., 2019). Controlling the size of the organ and pathogenic organisms (Bürger and Chory, 2019; Shigenaga and Argueso, 2016), stress tolerance (Feng et al., 2015; Ku et al., 2018), and then the reproduction development (Pierre-Jerome et al., 2018). Abscisic acid is important for the various

developmental processes in the plant, for example, organ size regulation, bud and seed dormancy, and stomatal closure (Kishor et al., 2022; Liu et al., 2022). How the body reacts to environmental changes like cold tolerance, drought, and soil salinity is crucial (Kumar and Verma, 2018), as tolerance to heavy ionic metals and freezing (Capelle et al., 2010; Gull et al., 2019). One main environmental component which restricts its growth and dissemination is thought to be cold stress. (Chen et al., 2014; Fan et al., 2014; Peng et al., 2019; Shi and Yang, 2014). An organic hormone Abscisic acid, regulates different plant physiological systems (Chen et al., 2020; Singh and Roychoudhury, 2023). Increased levels of ABA are caused by several stressors, such as drought, cold, temperature, and light in the water (Gao et al., 2011; Swamy and Smith, 1999). Abscisic acid, which was shown to be a hormone in plants, shows a significant function in plant physiology. Pteridophya and Spermatophyta are two higher plants where ABA has been found (Hirai, 2018). Several important plant activities are controlled by a plant hormone known as ABA, such as seed germination (Sah et al., 2016), abiotic stress tolerance, and development (Hubbard et al., 2010; Lee and Luan, 2012). Overall plant stress response system is initially described in this review article, after which the function of abscisic acid and regulatory transcription factors are discussed in the stress tolerance. It also discusses how cold stress affects plant ABA synthesis and how the pathways of abscisic acid biosynthesis are controlled.

ABA Transport or Transporter

The transport of ABA is crucial for determining endogenous hormone concentrations at the specific site where the action occurs, making it an essential mechanism in physiological reactions (Seo and Koshiba, 2011). When the plant receives ABA therapy on its roots, increased abscisic acid concentration in leaves can be promptly found after administration of abscisic acid (Agrawal et al., 2001), demonstrating that plants have an effective transport mechanism for ABA. The porous nature of ABA to the cell membrane has previously led people to believe that ABA transport is a diffusive mechanism (Ye et al., 2012). But unlike Auxin, which is a plant hormone that is transported over long distances through a complex mechanism by a diffusive process, abscisic acid should not be transported purely (Daeter and Hartung, 1993; Jiang and Hartung, 2008; Wilkinson and Davies, 1997). Strong evidence suggests that ABA is transported inside plants. In reaction to dry soil conditions, abscisic acid is proposed as a root-derived signaling chemical that causes stomatal occlusion. Additionally, it claimed that abscisic produced in plant tissues is transferred to the seeds (Seo and Koshiba, 2011). Identification of transporters that facilitate ABA, Guard cells are the site of action where the abscisic acid uptake into the cell and ABA export from vascular tissue, which is the production site of abscisic acid (Kuromori et al., 2018; Seo and Koshiba, 2011). At the root apex, abscisic acid can migrate laterally (Pilet, 1975). According to Hartung and his colleagues, abscisic acid is a stress signal hormone that travels from the root toward the xylem (Hartung et al., 2002). Global effects on plants are caused by ABA transfer between cells and organs (Ikegami et al., 2009), it is discovered that during water shortages, the ABA travels from leaves to roots. Abscisic acid can only accumulate when roots and leaves both are subjected to restricting water independently. Additional research has validated that abscisic acid is produced in the leaves and then transferred to other parts (Zhang et al., 2018). Therefore, an essential component of ABA activity in plants' overall systemic stress responses is the movement of the abscisic acid across organs, cells, and tissues.

ABA Biosynthesis pathway

The mechanism of abscisic acid production was revealed in part by ABA-deficient mutants. Mutant deficiency in the biosynthesis of ABA was found in a variety of plant species, including Arabidopsis, tomato (Nicotiana tabacum), maize (*Zea mays*), tobacco (Nicotiana tabacum), barley (Hordeum vulgare), and potato (Solanum tuberosum), due to their early seed germination and the plants' wilted appearance. Profiling of ABA biosynthetic intermediates and feeding assays utilizing these mutants revealed a main route for ABA production. First, the molecular identity of impacted genes was established. These investigations revealed that the "indirect" mechanism of C40 carotenoid precursor cleavage, xanthoxin to ABA through ABA-aldehyde intermediate conversion followed by two steps, results in the synthesis of the ABA in higher plants (Finkelsteina and Rockb, 2002; Schwartz et al., 2003; Seo and Koshiba, 2002; Taylor et al., 2000). The discovery that mevalonate is converted in the IPP for sterol synthesis in the cytosol, but terpenoid biosynthesis in chloroplast employs IPP synthesized from glyceraldehyde phosphate and pyruvate, one of the two significant breakthroughs in ABA biosynthesis (Rohmer, 1999; Rohmer et al., 1993).

The second innovation was using biosynthetically labeled carotenoids to acquire concrete proof that carotenoids transform into ABA by cell-free systems (Cowan and Richardson, 1993; Milborrow and Lee, 1997; Richardson and Cowan, 1996). The oxidation of antheraxanthin and zeaxanthin to violaxanthin, which takes place in the plastids, is the first step more specifically related to the ABA production process. The molecular identity of Zeaxanthin epoxidase (ZEP) was originally discovered in tobacco, catalyzing this process (Marin et al., 1996). Violaxanthin undergoes several structural changes before becoming 9-cis-epoxycaroteniod. NCED (9-cis-epoxycarotenoid dioxygenase) oxidatively breaks down important epoxy carotenoid 9-cis neoxanthin to produce the C15 intermediate xanthoxin. The resultant xanthoxin is moved towards the cytosol, where it experiences a step reaction with ABA-aldehyde to become abscisic acid (Cheng et al., 2002; González-Guzmán et al., 2002; Raz et al., 2001; Rook et al., 2001). The first specific ABA biosynthesis inhibitor, Abamine, has been created, developed, and patented. This allows for the control of the endogenous abscisic acid levels. (Awan et al., 2017; Dejonghe et al., 2018). **Synthesis:** All cells have chloroplasts and amyloplasts (Bhatla et al., 2018). **Precursor:** 40-C carotenoid intermediates(Manzi et al., 2015). **Locations:** Plastids and cytosol(Dong et al., 2015; Ma et al., 2018). **Pathways:** Isoprenoid Pathway (IPP)(Milborrow, 2001; Wani and Kumar, 2015).

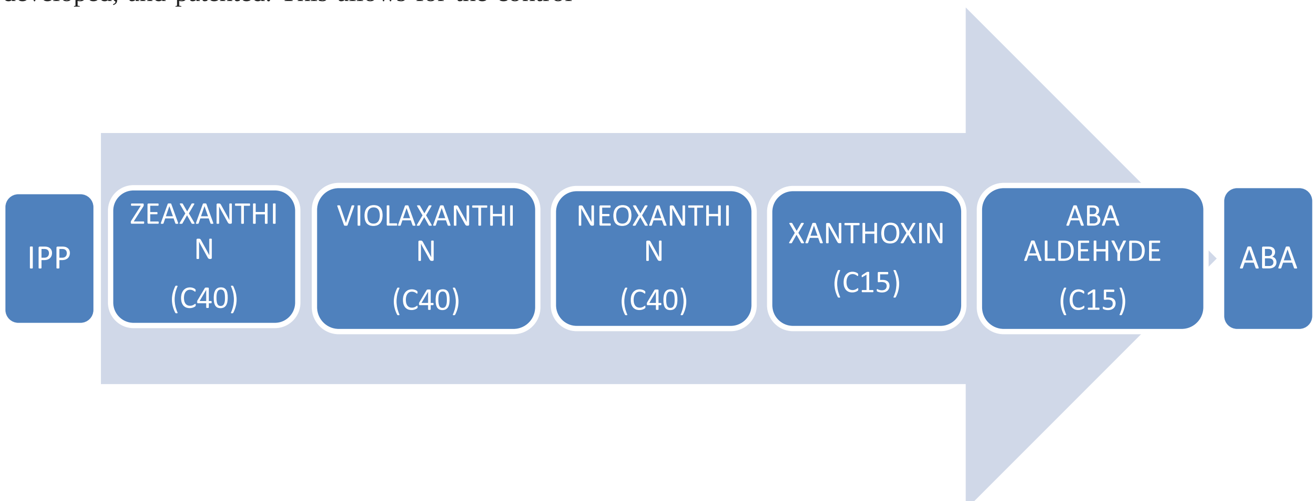

Fig:1 Abscisic acid (ABA) Biosynthesis in the plant, Pathway starting from IPP to ABA.

Mechanism of ABA biosynthesis: Amyloplast and chloroplast are both plastids that contain chlorophyll (Borowitzka, 1976; Chloroplast; Sadali et al., 2019). It is known as amyloplast, which retains starch. (Borowitzka, 1976; Solymosi and Keresztes, 2012). ABA's precursor is C40 Zeaxanthin (Duckham et al., 1991; WAN, 2004). Zeaxanthin produces and synthesizes the ABA hormone Abscisic acid (Iuchi et al., 2001). The initial synthesis stage of the ABA takes place in plastids, while in the cytosol, the latter stage occurs (Dong et al., 2015; Tarkowská and Strnad, 2018). Two organelles are involved: plastids and cytosol(Jarvis and López-Juez, 2013). IPP is the route involved in generating ABA (isoprenoid pathway) Zeazanthin is the starting point because it is ABA's predecessor. Rather than Neoxanthin C40, 40-Carbon Precursor is transformed into Violaxanthin C40 (Seo and Marion-Poll, 2019). All three intermediates are formed in the plastids. After forming, neoxanthin diffuses into the plastid and cytoplasm, transforming it into xanthoxin C15, a 15-carbon intermediate (Xu et al., 2013). ABA is also 15-Carbon compound (Dobrev and Vankova, 2012; Shah et al., 2022; Taylor et al., 2005). It suggests that Xanthoxin will aid in synthesizing and manufacturing ABA (Parry and Horgan, 1991; Seo and Koshiba, 2002; Xiong and Zhu, 2003). Xanthoxin is transformed into ABA aldehyde C15, ultimately into ABA (Benderradji et al., 2021; Jia et al., 2022; North et al., 2007; Taylor et al., 2000). Aldehydic group is therefore removed to create ABA, which is once more a 15-Carbon compound (Milborrow, 2001; Parry and Horgan, 1991). Final step is catalyzed into the cytosol (Ma et al., 2018; Seo and Koshiba, 2011).

Locations and timing of Abscisic acid biosynthesis:

ABA is produced synthetically in almost all plant parts, including the stems, leaves, roots, and flowers (Jiang and Hartung, 2008). ABA-glucose-ester, an inactive form, is produced when glucose is conjugated to uridine diphosphate glucosyltransferase and stored in mesophyll (chlorenchyma) cells. In reaction to abiotic stress, the chlorenchyma discharges salt stress, water, heat, and cold (Zhang et al., 2021). When plant tissues dry out, roots come into contact with compacted soil (DeJong-Hughes et al., 2001). Green fruits are synthesized at the start of the winter season (Bhatla et al., 2018). synthesized in developing seeds to create dormancy (Ali et al., 2022; Gu et al., 2010; Le Page-Degivry et al., 1990). Rapid mobile movement within the leaf makes it possible for the phloem to reach the roots from the leaves (Hoad, 1995; Jiang and Hartung, 2008). Lateral root development is altered through root accumulation, improving stress response (Duan et al., 2013). Accumulation of abscisic acid can hasten lengthening of the root hair (Zhang et al., 2019). Almost all cells with chloroplasts or amyloplasts generate ABA (Howitt and Pogson, 2006; Li and Yuan, 2013). When under stress, ABA is produced in the roots and transferred towards the leaves, but leaves can also synthesize ABA (Kuromori et al., 2018; Thompson et al., 2007).

Functions of ABA Plants

An optically active sesquiterpenoid ABA ($C_{15}H_{20}O_4$), asymmetric carbon of atom at position C-1 (Cutler et al., 2010). The primary controllers of the development and plant growth are phytohormones, and to abiotic stress, the mediator's responses (Sreenivasulu et al., 2012). Absicsic acid (ABA), one of many phytohormones, is an important regulator that coordinates a variety of tasks in plants and resistance to plants under environmental stresses (Finkelstein, 2013; Wani and Kumar, 2015), Enabling plants to adjust the various stress conditions. When the environment is hostile, ABA levels in plants rise through ABA biosynthesis. (Ng et al., 2014)

In the past, Abscisic acid was formerly thought a factor in abscission (Schwartz and Zeevaart, 2010), which is how the name was given. Based on current knowledge, only a few plants are known to exhibit this. Moreover, ABA-mediated signaling is essential for plants to respond to abiotic stress and plant diseases (Milborrow, 2001; Nambara and Marion-Poll, 2005; Pérez-Clemente et al., 2013). Several plant pathogenic fungi also synthesize ABA, although they do it in a different way than plants do (Lievens et al., 2017; Siewers et al., 2004; Spence and Bais, 2015). Abscisic acid contributes to the signaling of nutrients by modulating nitrate's controllable effects on seedlings' root branching (Signora et al., 2001). More recently, it has become evident that hormonal signaling and nutrient-based interactions interact significantly(Krouk et al., 2011). Such as concentrations of nitrate influence signaling, auxin transport, cytokinin, and ethylene production. Cytokinins, auxin, ethylene, and the ABA all mutually affect nitrogen intake and assimilation. This results in a cycle where nutrients govern hormone levels, controlling growth and nutrient uptake. Auxin, cytokinin, and ABA signaling interactions, as well as soil nitrogen and phosphate levels, all have a role in controlling root branching, which directly influences availability to nutrients of soil (Brady et al., 2003).

In reaction to the lower the potential of soil water (related to the dehydrated soil), Also in the roots the ABA is produced (Munns and Sharp, 1993). Any other circumstances that could put the plant under stress. ABA quickly changes the stomatal guard cells' osmotic potential in leaves, causing stomata to close and guard cells to shrink (Mishra et al., 2006). Under the low water supply, the abscisic acid-induced stomatal closure prevents further leaf loss of water by reducing vaporization (water evaporates from the stomata). Based on leaf area, a strong linear association between the Stomatal resistance (conductance) and the leaves' ABA content was discovered (Steuer et al., 1988). ABA inhibits seed germination in opposition to gibberellin (Ye and Zhang, 2012). Additionally, ABA reduces seed dormancy loss (Sano and Marion-Poll, 2021). Plants is sensitive or oversensitive to abscisic acid display abnormalities in germination and seed dormancy (Daszkowska-Golec et al., 2013; Feng et al., 2014; Huang et al., 2016), Stomatal regulation(Pei et al., 1998) and further mutants have dark or yellow leaves that have reduced growth. These mutations demonstrate the importance of ABA in early embryo development and seed germination. Additionally, ABA has different concentration-dependent effects on primary root growth, promoting the growth at nanomolar concentrations while inhibiting it at micromolar concentrations. Mechanically, the promotion has been linked with the differentiation of repressed stem cells and decreased cell division in the quiescent center (QC), which maintains the meristem and promotes growth (Zhang et al., 2010). Most studies above concentrate on how high abscisic acid levels impede growth. However, even plants with enough water show limited development, indicating that low abscisic acid levels in plants without stress encourage growth. Studies on maize and tomatoes show the failure to suppress ethylene synthesis causes the limited growth of abscisic acid-deficient plants, demonstrating yet other antagonistic interaction between ethylene and ABA (Sharp et al., 2000; Spollen et al., 2000)

Low temperature affects the ABA production in plant

The ability of ABA to modulate responses to environmental challenges like cold, salt, and dehydration during vegetative growth plays a crucial role(Brandt et al., 2012; Qin et al., 2011; Yamaguchi-Shinozaki and Shinozaki, 2006). Compare all stresses, and all these stresses cause oxidative stress and cellular osmotic, however these have different effects, and as a result, proper reactions are not the same. Abscisic acid is also involved in the response to hypoxic stress caused by flooding, which lowers the levels of ABA-flooded plants' shoots and the submerged tissues (Hsu et al., 2011). Plants increase downstream gene expression under low-temperature conditions via ABA-dependent and ABA-independent ways. In the Arabidopsis, the expression level abscisic acid-responsive transcript factors ABF4 and ABF1 was prompted under low-temperature conditions(Choi et al., 2000). Two signaling pathways are ABA-independent and ABA-dependent, providing a complex arrangement of interactions, in a shown manner by a contrast expression of stress-induced gene in response mutants and ABA production (Brandt et al., 2012; Cutler et al., 2010; Yamaguchi-Shinozaki and Shinozaki, 2006). A short photoperiod with a low temperature 10 °C in some varieties of grasses and trees increases a plant's freezing tolerance or cold acclimation over time (Ensminger et al., 2006; Malyshev et al., 2014). This could previously explain the finding that abscisic acid enhanced roots' ability to tolerate hypoxic stress but not in the shoots(Ellis et al., 1999). Winter annuals' freezing tolerance rises by 10°C during this phase, spring annuals' by 2-8°C, and tree verities' by 20-200°C (Gusta et al., 2005; O'Brien et al., 2020). Exogenous ABA administration significantly enhanced proline levels and soluble sugar, which improved the retention of water (Deng et al., 2005; Huang et al., 2015) and decreased peroxidation of membrane lipid, effectively treating membrane of the cell damage (Huang et al., 2015; Zhou and Guo, 2005) as well as enhanced photosynthesis(He et al., 2008).

During the plants development and growth, abscisic acid, a crucial phytohormone that controls numerous physiological and biochemical processes, plays an important part in stress tolerance (Fujii et al., 2009; Kim et al., 2016; Verslues and Zhu, 2005). According to an earlier study under cold stress in various plants, plants experience an ABA higher endogenous level (Li et al., 2016; Mantyla et al., 1995; Zhang et al., 2012). An increase in root shoot ratio effects from slightly raised ABA levels throughout the plant indicates mild water stress situations. According to the moisture gradients, these roots show positive "hydrotropism" (Moriwaki et al., 2013). The "core signaling pathway" is how ABA controls this reaction(Antoni et al., 2013). Exogenous abscisic acid therapy also increase plant cold tolerance (Fu et al., 2017; Kim et al., 2016; Kumar et al., 2008).

Changes in solute leakage, membrane fluidity, dysregulation of metabolic reactions, and damage in membrane caused by changes in enzyme properties are all symptoms of cold stress. An alternation of physiochemical characteristics of the important cellular elements like enzymes and membrane lipids describes cold stress. It ultimately produced reactive oxygen species (Welti et al., 2002). Since it occurs at the end of leaf development, cold-encouraged senescence in leaf is closely measured on different levels and aids in acclimatization. (Masclaux-Daubresse et al., 2007). Expression of the Abscisic acid biological synthesis genes selectively activated via cold stress in reproductive organs (Huang et al., 2022; Shi and Yang, 2014; Thakur et al., 2010). Abscisic acid is produced when the plant is under strain (Xiong and Zhu, 2003). Benzoic acid regulates several particular stress-responsive genes, ABA, an important stress hormone in plants, is implicated in the low-temperature response (Shi and Yang, 2014). Abscisic acid is a key stress hormone in the plants involved in cold stress responses by regulating specific stress-responsive genes (Heidarvand and Maali Amiri, 2010; Shi and Yang, 2014). In terminal buds, ABA is generated in anticipation of winter. As a result, plant growth is slowed, and leaf primordia are instructed to build scales to cover dormant buds during the colder months. Additionally, ABA prevents primary and secondary development in the vascular cambium, allowing the cells to adapt to the winter's cold by preventing cell division (Donno et al., 2015).

Conclusion

Studies of abscisic acid biological synthesis, ABA transportation throughout plants, ABA function, and cold stress effect on the ABA. In this study, we understand the biological synthesis mechanism of Abscisic acid in plants from C40 to C15. ABA levels are used to explore the ABA's function in development. These investigations have demonstrated that endogenous Abscisic acid plays a significant role in the induction of dormancy, prevention of germination, and regulation of the stomata. There are independent and redundant processes, several of which influence sensitivity to another signal, and mediate ABA signaling. However, under low temperature, ABA produced in apical buds also play an important role in plant growth and regulation. Under stress, production of the ABA increased. A biology system will be necessary to understand how these pathways are interrelated.

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Declarations

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All data generated or analyzed during the study are included in the manuscript.

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Regarding conflicts of interest, the authors state that their research was carried out independently without any affiliations or financial ties that could raise concerns about biases.