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Influence Of Cold Stress on Abscisic Acid Production in Plants

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ABSTRACT:

The mode of action of Abscisic acid (ABA) and its connections to adapt cold stress in particular have captured the attention of plant hormone researchers for more than a decade. Abiotic stresses are the main risk to agriculture productivity which is needed to feed the growing population of the world in coming decades. Being a significant phytohormone, ABA is crucial in responding to a variety of challenges, including high and low temperatures, drought, thermal or heat stress, heavy metal and radiation stress. Stress situations cause plants to slow down their growth and development, which ultimately has an impact on the output. There is a lot of proof that ABA moves around inside plants. In reaction to dry soil conditions, ABA has been proposed as a root-derived signalling chemical that causes stomatal closures. Additionally, it has been claimed that ABA produced in vegetative tissues is transferred to seeds. Because it has a large impact on the endogenous hormone concentration at the site of action, ABA transport is a key mechanism in physiological responses. Additionally, ABA is a significant messenger that functions as a signalling mediator to control how plants respond adaptively to various environmental stresses. Additionally, a variety of developmental stages are explained in depth, including stomata closure, seed dormancy, and seed germination. Endogenous ABA levels are increased in many plants as a result of cold stress. The function of ABA at low temperatures will be discussed in this review. ABA transportation in plants, ABA biosynthesis in plants, the pathway from IPP to ABA production, the use of ABA in plants, and the site of ABA biosynthesis are all discussed in current review.

KEYWORDS: ABA discovery, ABA synthesis, Cold stress, Role of ABA, Transport of ABA

1. INTRODUCTION

Abiotic stressors affect plants in a variety of ways, including increased salinity, low temperatures (chilling and freezing), high temperatures (heat), and a lack of water (drought or dehydration). These stressors are the main factor that drastically lowers crop production. (Mahajan & Tuteja, 2005; Roelofs, Aarts, Schat, & Van Straalen, 2008; Tuteja, 2007; Yadav et al., 2020). Throughout plant's life cycle, the phytohormone abscisic acid functions as a signal molecule to regulate a variety of processes. Plants are sensitive to abiotic stress, such as cold, salt, drought, and injury, and they adjust accordingly. (Mahajan & Tuteja, 2005; Shariatipour & Heidari, 2018; Swamy & Smith, 1999; Tuteja, 2007). ABA known as a stress hormone (Mauch-Mani & Mauch, 2005; Yoshida, Christmann, Yamaguchi-Shinozaki, Grill, & Fernie, 2019; J. Zhang, Jia, Yang, & Ismail, 2006) which was discovered and categorized as a plant hormone for the first time by Frederick T. Addicott and Larry A. Davis in the 1940s. They were researching 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 & Addicott, 1972). Abscisic acid (ABA or abscisin II) is a hormone that plants make, but only in extremely small amounts (Davis & Addicott, 1972; Schwartz & Zeevaart, 2010). It is understood that a number of transcription factors regulate how the ABA sensitive genes are

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expressed. (Fujita, Fujita, Shinozaki, & Yamaguchi-Shinozaki, 2011; Xiong, Schumaker, & Zhu, 2002). A 15-C weak acid is abscisic acid. (Finkelsteina & Rockb, 2002) Early in the 1960s, it was identified as a growth inhibitor by its accumulation in the leaves of photoperiodically induced dormant sycamore trees and abscising cotton fruit. (Cutler, Rodriguez, Finkelstein, & Abrams, 2010; Nakabayashi, Okamoto, Koshiba, Kamiya, & Nambara, 2005; Wasilewska et al., 2008). Stress-responsive genes can be expressed in one of two ways: ABA-dependent or ABA-independent. (Chinnusamy, Schumaker, & Zhu, 2004; Ding, Avramova, & Fromm, 2011; Tuteja, 2007; Yang et al., 2011). From embryogenesis onward, hormones control the growth and development of plants (Méndez-Hernández et al., 2019) controlling organ size and pathogen protection (Bürger & Chory, 2019; Shigenaga & Argueso, 2016), stress tolerance (J. Feng et al., 2015; Ku, Sintaha, Cheung, & Lam, 2018) and for reproduction (Pierre-Jerome, Drapek, & Benfey, 2018). ABA is involved in a number of developmental processes in plants, including bud and seed dormancy, control of organ size, and stomatal closure. (Kishor, Tiozon, Fernie, & Sreenivasulu, 2022; Liu et al., 2022). It is crucial in how the body reacts to environmental challenges like cold tolerance, drought, and soil salinity. (A. Kumar & Verma, 2018), tolerance to heavy metal ions and freezing temperature (Capelle et al., 2010; Gull, Lone, & Wani, 2019).

One major environmental factor that restricts its growth and dissemination is thought to be cold stress. (L. J. Chen et al., 2014; Fan et al., 2014; Peng et al., 2019; Shi & Yang, 2014). Abscisic acid regulates a variety of plant physiological systems. (K. Chen et al., 2020; Singh & Roychoudhury, 2023). Increased level of ABA is observed under several stresses such drought, cold, light in the water, and temperature (Gao et al., 2011; Swamy & Smith, 1999) (Gao 2011). Abscisic acid plays a significant function in plant physiology. Spermatophyta and Pteridophya are two higher plants where ABA has been found. (Hirai, 2018).

The overall plant stress response system is initially described in this review article, then, it is described how transcription factors and ABA react to handle stress. It is also discussed how cold stress affects plant abscisic acid synthesis and how the ABA biosynthesis pathway is regulated.

ABA TRANSPORT OR TRANSPORTER:

The transport of ABA is crucial for determining endogenous hormone concentrations at the site of action, making it a crucial mechanism in physiological reactions. (Seo & Koshiba, 2011). When the plant receives ABA therapy on its roots, an increased ABA content in leaves can be promptly found after the administration of ABA. (Agrawal et al., 2001) demonstrating that plants have an effective transport mechanism for ABA. The permeable nature of ABA to the cell membrane has previously led people to believe that ABA transport is a diffusive mechanism. (Ye, Jia, & Zhang, 2012). But unlike Auxin, another plant hormone that is known to be transported over long distances by a complex mechanism, ABA should not be transported purely by diffusive process. (Daeter & Hartung, 1993; Jiang & Hartung, 2008; Wilkinson & Davies, 1997).

There is strong evidence that ABA is transported inside of plants. In reaction to dry soil conditions, ABA has been proposed as a root-derived signaling chemical that causes stomatal closure. Additionally, it has been claimed that ABA is transmitted to seeds from vegetative tissues (Seo & Koshiba, 2011). Identification of the transporters that facilitate ABA uptake into the cells at the site of action (guard cells) and ABA export from the cells at the site of ABA production (vascular tissue) (Kuromori, Seo, & Shinozaki, 2018; Seo & Koshiba, 2011).

At the root apex, ABA can migrate laterally. (Pilet, 1975) According to Hartung, Sauter, and Hose (2002), ABA is a hormonal stress signal that travels up the xylem from the root (Hartung, Sauter, & Hose, 2002). Global effects on plants are caused by ABA transfer between cells and organs. (Ikegami, Okamoto, Seo, & Koshiba, 2009) discovered that during water shortages, isotope-labeled ABA travels from leaves to roots, and that ABA can only accumulate when leaves and roots are subjected to restricting water independently. Additional research has validated that ABA is produced in leaves and subsequently transferred to other organs (F.-P. Zhang et al., 2018). As a result, an essential component of ABA activity in the overall plant's systemic stress responses is the movement of ABA across cells, tissues, and organs.

ABA BIOSYNTHESIS PATHWAY:

ABA-deficient mutants have partially disclosed the ABA production process. Due to their early seed germination and wilted appearance, mutants deficient in ABA biosynthesis have been identified in a number of

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plant species, including maize (Zea mays), tomato (Lycopersicon esculentum), tobacco (Nicotiana tabacum), potato (Solanum tuberosum), barley (Hordeum vulgare), and Arabidopsis. Before the molecular identities of the damaged genes were known, profiling ABA biosynthetic intermediates in conjunction with feeding trials using these mutants showed a primary route for ABA synthesis. These experiments demonstrated that the synthesis of ABA in higher plants occurs via a "indirect" method involving cleavage of a C40 carotenoid precursor, followed by a two-step conversion of the intermediate xanthoxin to ABA via ABA-aldehyde (Finkelsteina & Rockb, 2002; Schwartz, Qin, & Zeevaart, 2003; Seo & Koshiba, 2002; Taylor, Burbidge, & Thompson, 2000). One of the two important new discoveries in ABA biosynthesis is that IPP is produced from mevalonate in the cytosol for sterol synthesis, but that IPP is produced from pyruvate and glyceraldehyde phosphate for terpenoid biosynthesis in chloroplast (Rohmer, 1999; Rohmer, Knani, Simonin, Sutter, & Sahm, 1993).

The second innovation involved obtaining conclusive evidence that carotenoids could be converted into ABA by cell-free systems by employing carotenoids that had been biosynthetically tagged (Cowan & Richardson, 1993; Milborrow & Lee, 1997; Richardson & Cowan, 1996). The first phase that is more specifically connected to the ABA synthesis process is the epoxidation of zeaxanthin and antheraxanthin to violaxanthin, which happens in plastids. This mechanism is catalyzed by zeaxanthin epoxidase (ZEP), whose molecular identity was first found in tobacco(Marin et al., 1996). Before violaxanthin transforms into 9-cis-epoxycaroteniod, it goes through a variety of structural modifications. Important epoxycarotenoid 9-cis neoxanthin is broken down oxidatively by the enzyme 9-cis-epoxycarotenoid dioxygenase (NCED) to create the C15 intermediate xanthoxin (Schwartz, Tan, Gage, Zeevaart, & McCarty, 1997).

After that, the resulting xanthoxin is transferred to the cytosol, where it steps with ABA-aldehyde to form ABA (Cheng et al., 2002; González-Guzmán et al., 2002; Raz, Bergervoet, & Koornneef, 2001; Rook et al., 2001). Abamine, the first specialized inhibitor of ABA production, has been developed and patented. This enables the management of endogenous ABA levels (Awan et al., 2017; Dejonghe, Okamoto, & Cutler, 2018).

Synthesis: virtually all cells with chloroplasts and amyloplasts (Bhatla, A. Lal, & Kalra, 2018).

Precursor: 40-C carotenoid intermediates (Manzi et al., 2015).

Locations: Plastids and cytosol (Dong, Park, & Hwang, 2015; Ma et al., 2018).

Pathways: Isoprenoid Pathway (IPP)(Milborrow, 2001; Wani & Kumar, 2015).

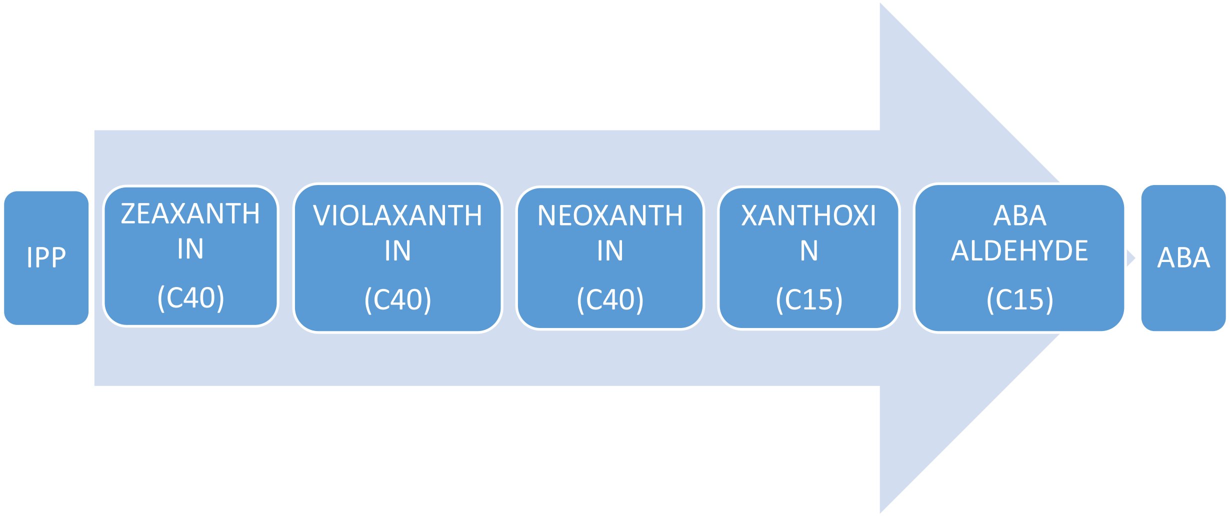

Fig:1 Abscisic acid (ABA) is produced by plants, Pathway from IPP to ABA Production.

Mechanism of ABA biosynthesis: Amyloplast and chloroplast are both plastids that contain chlorophyll (Borowitzka, 1976; Chloroplast; Sadali, Sowden, Ling, & Jarvis, 2019). It is known as amyloplast, which retains starch (Borowitzka, 1976; Solymosi & Keresztes, 2012). ABA's precursor is C40 Zeaxanthin (Duckham, Linforth,

& Taylor, 1991; WAN, 2004). Zeaxanthin is responsible to production and synthesis of ABA hormone that is Abscisic acid (Iuchi et al., 2001). The first stage of the synthesis of ABA occurs in plastids, while the later stage occurs in the cytosol (Dong et al., 2015; Tarkowská & Strnad, 2018). Two organelles plastids and cytosol are involved (Jarvis & López-Juez, 2013).

IPP is the name of the route that is involved in the generation of ABA (isoprenoid pathway). Zeazanthin is the starting point because it is ABA's predecessor. Rather than Neoxanthin C40, 40-Carbon Precursor is transformed to Violaxanthin C40 (Seo & Marion-Poll, 2019). All three intermediate they are formed in the plastids.

After forming, neoxanthin diffuses into the plastid and cytoplasm where it is transformed into xanthoxin C15, a 15-carbon intermediate (Xu, Kim, & Hwang, 2013). Absicsic acid is also a 15-Carbon compound (Dobrev & Vankova, 2012; Shah, Li, Jiang, Fahad, & Hassan, 2022; Taylor, Sonneveld, Bugg, & Thompson, 2005). It implies that Xanthoxin will aid in the synthesis and manufacturing of ABA (Parry & Horgan, 1991; Seo & Koshiba, 2002; Xiong & Zhu, 2003).

Xanthoxin is transformed into ABA aldehyde C15, which is ultimately transformed into ABA (Benderradji, Saibi, & Brini, 2021; Jia et al., 2022; North et al., 2007; Taylor et al., 2000). In order to create ABA, which is again a 15-Carbon compound, the aldehydic group is therefore removed (Milborrow, 2001; Parry & Horgan, 1991). Final step is catalyzed into the cytosol (Ma et al., 2018; Seo & Koshiba, 2011).

LOCATIONS AND TIMING OF ABA BIOSYNTHESIS:

ABA produced synthetically in almost all plant parts, including the roots, flowers, leaves, and stems (Jiang & 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 environmental stress, such as cold, heat, water, and salt stress, and discharged by the chlorenchyma (Y. Zhang et al., 2021). It is released when plant tissues dry out and when roots come into contact with compacted soil (DeJong-Hughes, Moncrief, Voorhees, & Swan, 2001). At the start of the winter season, green fruits are synthesized (Bhatla et al., 2018). It is synthesized in developing seeds to create dormancy (Ali, Qanmber, Li, & Wang, 2022; Gu, Liu, Feng, Suttle, & Gibbons, 2010; Le Page-Degivry, Barthe, & Garello, 1990).

Movement of this mobile hormone within the leaf, from the leaves to the roots through the phloem is possible (Hoad, 1995; Jiang & Hartung, 2008) (jiang 2008). Its development in the lateral roots is altered by its accumulation in the roots, which improves the stress response (Duan et al., 2013). Accumulation of ABA can hasten the lengthening of root hair (Fei Zhang, Wang, Zou, Wu, & Kuča, 2019). Almost all cells with chloroplasts or amyloplasts generate ABA (Howitt & Pogson, 2006; L. Li & Yuan, 2013). When under stress, ABA is produced in the roots and transferred to the leaves, but the leaves can also synthesis ABA (Kuromori et al., 2018; Thompson et al., 2007).

ABA FUNCTIONS IN PLANTS:

Sesquiterpene having the chemical formula $C15H20O4$ called ABA has an optically active, asymmetric carbon atom at position C-1'.(Cutler et al., 2010). Phytohormones are the main regulators of plant growth and development as well as the mediators of reactions to environmental stress (Sreenivasulu, Harshavardhan, Govind, Seiler, & Kohli, 2012). Absicsic acid (ABA), One of the many phytohormones plays a critical role in controlling abiotic stress tolerance in plants and orchestrates a number of functions (Finkelstein, 2013; Wani & Kumar, 2015), enabling plants to adjust to different stresses. When the environment is hostile, ABA levels in plants rise through ABA biosynthesis (Ng, Melcher, Teh, & Xu, 2014)

ABA was formerly thought to be a factor in abscission (Schwartz & Zeevaart, 2010), which is how the name was given. Only a few plants are known to exhibit this. Additionally, ABA-mediated signaling is crucial for plants to respond to environmental stress and plant diseases (Milborrow, 2001; Nambara & Marion-Poll, 2005; Pérez-Clemente et al., 2013). Some plant pathogenic fungi also synthesize ABA, although they do it in a different way than plants do (Lievens, Pollier, Goossens, Beyaert, & Staal, 2017; Siewers, Smedsgaard, & Tudzynski, 2004; Spence & Bais, 2015). By adjusting the nitrate's controllable effects on root branching, ABA contributes to the signaling of nutrients (Signora, De Smet, Foyer, & Zhang, 2001). Recently, it has been clear that there are important

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interactions between nutrient-based and hormonal signaling (Krouk et al., 2011). For instance, auxin transport and signaling, as well as the generation of cytokinin and ethylene, are all influenced by nitrate concentrations. The uptake and assimilation of nitrogen are both influenced by auxin, cytokinins, ethylene, and ABA in a reciprocal manner. This results in a cycle where nutrients govern hormone levels, which in turn control 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 soil nutrients (Brady, Sarkar, Bonetta, & McCourt, 2003).

In reaction to the lower soil water potential (which is related to the dry soil), abscisic acid is also produced in the roots(Munns & Sharp, 1993). Any other circumstances that could put the plant under stress. The osmotic potential of stomatal guard cells is quickly altered by ABA in leaves, where it causes stomata to close and the guard cells to contract(Mishra, Zhang, Deng, Zhao, & Wang, 2006). In times of low water supply, the ABA-induced stomatal closure prevents further water loss from the leaves by reducing transpiration (the evaporation of water out of the stomata). On a leaf area basis, a strong linear association between the leaves, ABA content and their conductance (stomatal resistance) was discovered (Steuer, Stuhlfauth, & Fock, 1988).

ABA inhibits seed germination in opposition to gibberellin (Ye & Zhang, 2012). Additionally, ABA reduces seed dormancy loss (Sano & Marion-Poll, 2021). Plants that are sensitive or hypersensitive to ABA display abnormalities in germination and seed dormancy. (Daszkowska-Golec et al., 2013; C. Z. Feng et al., 2014; Y. Huang, Feng, Ye, Wu, & Chen, 2016), stomatal regulation (Pei, Ghassemian, Kwak, McCourt, & Schroeder, 1998), and other mutants have leaves that are dark or yellow and have reduced growth. These alterations show the importance of ABA in seed germination and early embryo development. Additionally, ABA's effects on main root growth vary according on its concentration, boosting it at nanomolar levels while inhibiting it at micromolar ones. The promotion is thought to work by suppressing stem cell differentiation and reducing cell division in the quiescent center (QC), which together keep the meristem alive and encourage development (H. Zhang et al., 2010). The majority of the studies mentioned above concentrate on how high ABA levels impede growth. However, plants with adequate water supply exhibit limited growth, demonstrating that plants with minimal stress have low endogenous ABA levels, which promote growth. Studies on tomatoes and maize demonstrate yet another antagonistic relationship between ABA and ethylene, wherein failure to inhibit ethylene synthesis results in the stunted growth of ABA-deficient plants (Sharp, LeNoble, Else, Thorne, & Gherardi, 2000; Spollen, LeNoble, Samuels, Bernstein, & Sharp, 2000).

COLD STRESS EFFECT THE ABA PRODUCTION IN PLANT:

The ability of ABA to modulate responses to environmental challenges like cold, salt, and dehydration during vegetative growth is a crucial role (Brandt et al., 2012; Qin, Shinozaki, & Yamaguchi-Shinozaki, 2011; Yamaguchi-Shinozaki & Shinozaki, 2006). These stresses are comparable as they all result in cellular osmotic and oxidative stress, but because of their various consequences, the appropriate responses are different. The reaction to hypoxic stress brought on by flooding, which causes ABA levels to decrease in tissues that are submerged and increase in shoots of flooded plants, is also thought to include ABA (Hsu, Chou, Peng, Chou, & Shih, 2011). Under low temperature conditions, plants use ABA-dependent and ABA-independent mechanisms to enhance downstream gene expression. Low temperature conditions increased the expression of the ABA-responsive transcription factors ABF1 and ABF4 in Arabidopsis (Choi, Hong, Ha, Kang, & Kim, 2000). A comparison of stress-induced gene expression in ABA production and response mutants demonstrates the existence of both ABA-dependent and ABA-independent signaling pathways that provide a diverse array of interactions (Brandt et al., 2012; Cutler et al., 2010; Yamaguchi-Shinozaki & Shinozaki, 2006).

Temperatures below 10 °C with a short photoperiod in some species of trees and grasses increase a plant's freezing tolerance or cold acclimation over time (Ensminger, Busch, & Huner, 2006; Malyshev, Henry, & Kreyling, 2014). This could explain the earlier finding that exogenous ABA enhanced roots' ability to tolerate hypoxic stress but not shoots (Ellis, Dennis, & James Peacock, 1999). Winter annuals' freezing tolerance rises by 10°C during this phase, spring annuals' by 2-8°C, and tree species' by 20-200°C (Gusta, Trischuk, & Weiser, 2005; O'Brien et al., 2020). Exogenous ABA administration significantly enhanced soluble sugar and proline levels, which improved water retention (Deng et al., 2005; X. Huang, Chen, Yang, Li, & Wu, 2015), reduce the oxidation of membrane lipids to efficiently repair damaged cell membranes (X. Huang et al., 2015; Zhou & Guo, 2005) and enhanced photosynthesis (He, Xue, Tian, & Chen, 2008).

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Stress tolerance in plants is significantly influenced by ABA, a vital phytohormone that regulates a variety of vital physiological and biochemical processes (Fujii et al., 2009; Kim, Choi, Khan, Waqas, & Lee, 2016; Verslues & Zhu, 2005). According to a previous study, many plants produce more endogenous ABA in response to cold stress (X. Li, Tan, Jiang, & Liu, 2016; Mantyla, Lang, & Palva, 1995; Fan Zhang et al., 2012). An increase in the root shoot ratio results from slightly raised ABA levels throughout the entire plant, which are indicative of mild water stress situations. These roots exhibit positive "hydrotropism" in response to moisture gradients (Moriwaki, Miyazawa, Kobayashi, & Takahashi, 2013). The "core signaling pathway" is how ABA controls this reaction (Antoni et al., 2013) Additionally, exogenous ABA therapy could improve plant cold resistance (Fu et al., 2017; Kim et al., 2016; S. Kumar, Kaur, & Nayyar, 2008).

Cold stress manifests as solute leakage altered metabolic processes brought on by altered enzyme capabilities, alterations in membrane fluidity and eventual membrane damage. Changes in the physiochemical characteristics of vital biological elements such membrane lipids and enzymes are what define cold stress. Finally, reactive oxygen species were created as a result (Welti et al., 2002). Cold-induced leaf senescence is tightly regulated on many levels and can help with acclimation because it happens at the conclusion of leaf development (Masclaux-Daubresse et al., 2007). The expression of ABA biosynthesis genes is selectively activated by cold stress in reproductive organ (B. Huang, Fan, Cui, Li, & Guo, 2022; Shi & Yang, 2014; Thakur, Kumar, Malik, Berger, & Nayyar, 2010).

When a plant is under stress, ABA is produced (Xiong & Zhu, 2003). Alcoholic acid ABA, a significant stress hormone in plants, has been demonstrated to be involved in the cold stress response through the regulation of a number of specific stress-responsive genes (Shi & Yang, 2014). Benzoic acid through the regulation of a number of particular stress-responsive genes, ABA, a key stress hormone in plants, has been shown to be implicated in the cold stress response (Heidarvand & Maali Amiri, 2010; Shi & Yang, 2014). In terminal buds, ABA is generated in anticipation of winter. As a result, plant growth is slowed down, 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, Beccaro, Cerutti, Mellano, & Bounous, 2015).

CONCLUSION:

Studies of ABA synthesis, transportation in plant, its function, and its response during cold stress are discussed. In this study we understand biosynthesis mechanism of ABA in plant from C40 to C15. Benzoic acid through the regulation of a number of particular stress-responsive genes, ABA, a key stress hormone in plants, has been shown to be implicated in the cold stress response. These studies have shown that endogenous ABA is crucial for the regulation of stomata, the induction of dormancy, and the inhibition of germination. ABA signaling is mediated by redundant and separate pathways, some of which also affect susceptibility to other signals. However, in low temperature conditions, ABA production in terminal buds also plays a critical function in the regulation and growth of plants. When under stress, ABA production rises. It will probably be essential to use a systems biology approach to completely comprehend how these pathways are connected.

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