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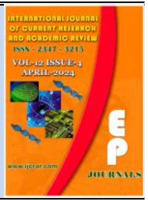

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Phytohormone as one of the Mediators under Water Deficit: A Review Article

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Abstract

Climate change is resulting in abiotic stress, including drought and high temperatures, which are affecting the development and production of coffee plants. Drought, a significant environmental stressor, has a detrimental effect on plant growth and productivity, posing a risk to global food security. It diminishes the moisture content in the soil, thereby restricting plant growth and productivity. The objective of this paper is to review the role of Abscisic Acid on coffee under water deficit. Plants have developed adaptive mechanisms to cope with drought stress, including the presence of a crucial phytohormone, Abscisic Acid. Abscisic Acid serves as a key mediator of drought and holds a crucial position in plant growth, development, and reactions to environmental pressures. It serves as a pivotal hormone in enhancing the plant's ability to tolerate abiotic stresses such as heat, cold, salt, drought, and high levels of irradiance. It regulates plant growth, stress responses, and physiological processes, safeguarding plants against abiotic stresses like drought. Furthermore, it activates stress-responsive genes, stomata closure, and regulates plant growth. Abscisic Acid levels increase during drought stress due to gene expression changes and enzymes responsible for Abscisic Acid biosynthesis. Hence, Abscisic Acid serves as a mechanism for drought tolerance in coffee, and research should be concentrated on addressing the existing gaps.

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Keywords

Coffee, Biosynthesis, Drought, Stomatal closure, Morphological changes.

Introduction

Global climate change is leading to more erratic weather patterns, with abiotic stressors like drought and high temperatures significantly impacting the growth and production of coffee plants. Drought, specifically, results in water scarcity and stress for coffee plants, making it a major challenge for rain-fed agriculture, particularly in the face of changing climate conditions (Pinheiro *et al.*, 2005). The lack of water due to drought stress hinders the plant's ability to absorb water from the soil through its roots, ultimately stunting growth and reducing productivity (Rubin *et al.*, 2017). These challenges are anticipated to become more prevalent in various coffee producing regions as the global climate continues to evolve. Additionally, the expansion of coffee cultivation into less favorable areas, characterized by water scarcity and unsuitable temperatures, poses a significant obstacle to achieving high coffee yields (DaMatta and Ramalho, 2006).

Plants have developed various adaptive strategies to detect stress stimuli and react to these signals using specific mechanisms. They have also developed a diverse range of morpho-physiological, metabolic, and molecular mechanisms to withstand the effects of drought stress, whether it is for a short or long duration (Ali *et al.*, 2020). Abscisic Acid (ABA) and ethylene are crucial plant hormones that play a vital role in regulating plant growth, stress responses, and physiological processes (Müller and Hasanuzzaman, 2021). ABA is a very important agent in the mechanisms of resistance and adaptation in plants against various abiotic stress conditions (Li *et al.*, 2010; Bakhsh *et al.*, 2011; Vu *et al.*, 2015). ABA, acts as a central regulator that safeguards plants against abiotic stresses such as drought (Cotta *et al.*, 2014). It controls the expression of stress-responsive genes, regulates stomatal closure, and modulates vegetative growth.

ABA is utmost importance in enhancing the plant's ability to tolerate abiotic stresses, including heat, cold, salt, drought, and high irradiance (Taylor *et al.*, 2000l; Pospisilova *et al.*, 2009). Additionally, it acts as an important signaling mediator for plants' adaptive response to a variety of environmental stresses regulating many physiological processes, including bud dormancy, seed germination and stomatal development (Finkelstein *et al.*, 2002; Planes *et al.*, 2015) and transcriptional and post-transcriptional regulation of stress responsive gene expression (Ali *et al.*, 2020). Elevated levels of ABA in water-deprived plants could serve as a chemical cue that initiates a cascade of cellular responses, such as the activation of genes associated with enhancing plant resilience to drought conditions (Gao *et al.*, 2004). Therefore, the objective of this paper is to review the role of Abscisic Acid (ABA) on coffee under water deficit.

General about Abscisic Acid

Phytohormones play a crucial role in regulating plant growth and mitigating environmental stresses like drought, which can have a negative impact on crop yield and global food security (Ali *et al.*, 2020). Several physiological assessments of these clones have indicated the significance of the following traits: maintaining an optimal water status through deep rooting, effective control of transpiration through stomatal regulation, and preservation of leaf area (DaMatta *et al.*, 2003; Pinheiro *et al.*, 2005). Additionally, biochemical traits such as enhanced tolerance to oxidative stress have been observed (Lima *et al.*, 2002; Pinheiro *et al.*, 2004).

Plant development heavily relies on Abscisic acid (ABA), which can alter various physiological and biochemical pathways in response to environmental stresses, especially drought (Chaves *et al.*, 2003; Wag and Kumar, 2015). Moreover, ABA is crucial for the synthesis of biomolecules, senescence, seed germination, stomatal closure, and modification of root architecture (Trivedi *et al.*, 2016; Gonzalez *et al.*, 2021). ABA, a key hormone, regulates various aspects of plant development, stomata closure, proline synthesis, and seed maturation, including drought responsive gene expression (Bhaskara *et al.*, 2015; Lim *et al.*, 2015 and Ghate *et al.*, 2019).

Plants exhibit increased ABA levels under drought stress, influenced by gene expression and ABA biosynthesis enzymes. ABA is a key mediator of drought and regulates plant growth and responses (Zhu, 2002; Boominathan *et al.*, 2004; Kim *et al.*, 2010). Abscisic acid (ABA) is a crucial signal for plants to respond to drought, triggering physiological processes like stomatal closure, root system modulation, and gene expression activation (Muhammad *et al.*, 2002). ABA, a hormone, plays a crucial role in plant physiological and molecular responses to drought, with protein kinases positively regulating signaling, metabolism, and transport (Fujita *et al.*, 2009). It is a potential root-shoot communication tool during water scarcity, and drought-tolerant genotypes can stimulate ABA production in susceptible scions under severe conditions through citrus reciprocal grafting experiments (Santana-Vieira *et al.*, 2016; Vishwakarma *et al.*, 2017). According to certain reports, ABA has been implicated in the synthesis of betaine in plants when they are subjected to environmental stresses (Nakamura *et al.*, 2001; Saneoka *et al.*, 2001). A well-documented benefit of ABA in relation to flowering is the phenomenon known as drought escape.

This mechanism allows plants to preemptively flower early in order to produce seeds before the onset of severe drought conditions, thus minimizing potential damage (Franks, 2011; Gupta *et al.*, 2020). The early flowering process is marked by an elevation in ABA levels as a response to water stress (Sherrard and Maherali, 2006; Shavrukov *et al.*, 2017).

Role of Abscisic Acid

Root growth modification

The plant's root system serves the purpose of firmly securing the plant in the soil, while also extracting water and minerals from its surroundings. This enables the plant to grow and undergo various developmental processes (Hong *et al.*, 2013). ABA alters root structure, growth pattern, and restricts growth, linked to environmental changes and controlling lateral root emergence (De Smet *et al.*, 2003; Liang *et al.*, 2007; Hong *et al.*, 2013; Benderradji *et al.*, 2021). The role of ABA in maintaining root meristem in Medicago truncatula mutants is utmost importance, and its absence is vital for promoting root growth during periods of drought (Liang *et al.*, 2007; Fang and Xiong, 2015). ABA is crucial for stress-related responses and plant growth, can adapt to drought conditions, with the shoot and root systems of a tolerant clone increasing ABA concentrations in leaves (Silva *et al.*, 2018).

According to the reports by Zhao *et al.*, (2015) and Daszkowska (2016), ABA improves hydraulic conductivity, promotes root cell elongation, aids plant recovery from water scarcity, and regulates root growth through interaction with plant hormones, acting as a messenger.

Stomatal closure

ABA is known to protect plants from drought damage by inducing stomata closure to reduce water loss via transpiration (Li *et al.*, 2000) and increasing hydraulic conductance for water movement from roots to leaves (Zhang *et al.*, 1995). ABA regulates stomatal closure, reducing water loss during drought stress by lowering transpiration rate, as demonstrated by Daszkowska, (2016); Trivedi *et al.*, (2016); Gonzalez *et al.*, (2021). During periods of drought, the regulation of stomatal conductance by ABA helps to reduce transpiration and conserve water, signaling a lack of soil moisture.

Elevated levels of ABA trigger the closure of stomata in plants (Kim *et al.*, 2010; Li *et al.*, 2017). Previous studies have also been demonstrated that drought escape induced by water stress depends on ABA (Muhammed *et al.*, 2022). The role of ABA in controlling stomatal conductance (*gs*) is strongly supported by many experiments and experimental approaches in *Arabidopsis thaliana* (Osakabe *et al.*, 2014). ABA, when applied to leaves, can cause stomata to close, a process that helps maintain turgor and growth in plants during water scarcity (Wright, 1969; Jones and Mansfield, 1970). The closure of stomata induced by ABA appears to be part of a series of integrated responses throughout the plant which helps to maintain turgor and growth when water is in short supply (Mansfield *et al.*, 1978).

Leaf chlorophyll content and quantum efficiency of photosystem

ABA foliar application reduced Arabica coffee seedling growth and physiology traits, but enhanced drought tolerance by increasing leaf chlorophyll value and Fv/Fm. The application of ABA improved Arabica coffee seedlings' drought tolerance by increasing leaf chlorophyll content and photosystem quantum efficiency. The highest chlorophyll content was achieved with 100 mgL^{-1} of ABA (Vu *et al.*, 2020). The study by Anbarasi *et al.*, (2015) in Suaeda maritima plant found that the application of ABA increased chlorophyll a, chlorophyll b, and total chlorophyll. The study found that photosystem II quantum efficiency (Fv/Fm) decreased with water deficit duration, with the lowest value in the control. After re-watering, Fv/Fm increased, but higher values were also observed in ABA treatments (Vu *et al.*, 2020). The research validates the discovery made by Wang *et al.*, (2010), which states that ABA pre-treatment enhances the Fv/Fm ratio in cucumber seedlings. This suggests that coffee plants exhibit elevated Fv/Fm values when subjected to water stress conditions.

Relative water content, wilting point and ion leakage

The utilization of ABA improved the ability of coffee seedlings to withstand drought by augmenting the relative water content in the leaf in Arabica coffee seedlings. Moreover, the implementation of ABA amplified the relative water content in the soil and postponed the onset of wilting point during water scarcity conditions (Vu *et al.*, 2020). Research shows that applying ABA to coffee seedlings' leaves increased relative water content, indicating a potential impact on plant water status and tissue metabolic activity, thereby affecting growth (Figure 1A) (Ashraf, 2010; Lu *et al.*, 2010; Vu *et al.*, 2020). Agarwal *et al.*, (2005) study found that external application of ABA increased water content in wheat leaves under water stress. The study found that the highest relative water content in coffee leaf was found in 100 mgL^{-1} of ABA. The control leaf had higher relative water content after re-watering but still lower than the treatments. ABA application improved drought tolerance by delaying wilting point start times (Vu *et al.*, 2020).

Electrolyte leakage is a correlated factor associated with various abiotic stresses. The previous investigation reveals that the application of ABA resulted in a notable reduction in the relative ion leakage. Research shows foliar spraying with ABA reduces ion leakage in wheat plants and improves stress tolerance in tomato seedlings, with the lowest value observed in 100 mgL^{-1} ABA treatment (Hala and Ghadas, 2009; Vu *et al.*, 2015). The study found that the control treatment had the highest relative ion leakage, while the lowest value was found in 100 mgL^{-1} of ABA treatment (Vu *et al.*, 2020) (Figure 1B).

Figure.1 Effect of ABA concentrations on relative water content in the leaf of Arabica coffee seedlings in water deficit condition (A) and on relative ion leakage (B). Vertical bars represents ± SD, n=8.

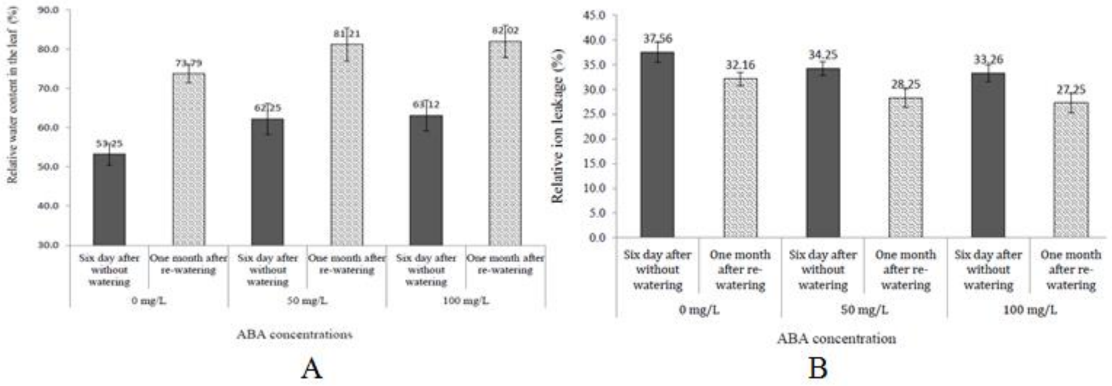


Figure.2 (A) Effect of ABA concentrations on growth characteristics of Arabica coffee seedlings in the watering condition. Where PH is Plant height (cm), LL is Leaf length (cm), LW is Leaf width (cm), LA is Leaf area (dm^2) and $SPAD^z$ is the value of leaf chlorophyll content. (B) ABA content in leaves, floral bud, roots at rainy period (May18th), at the dry period (August18th) and after rain in the re-watering period (August 28th).

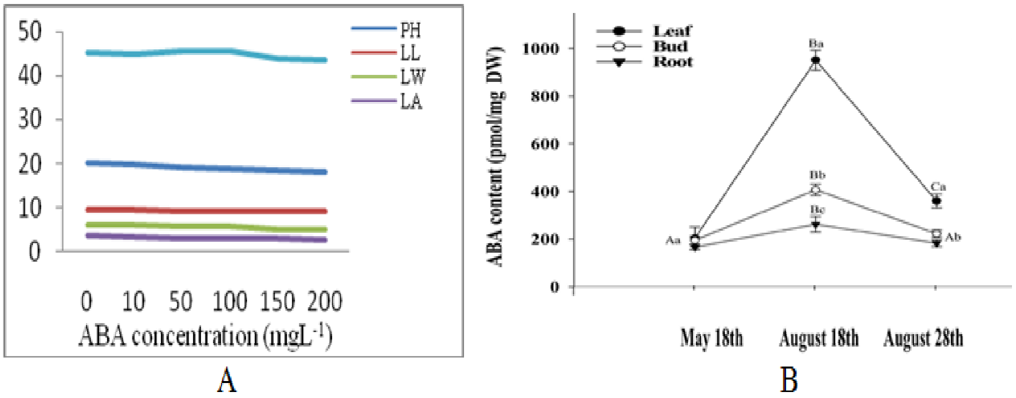
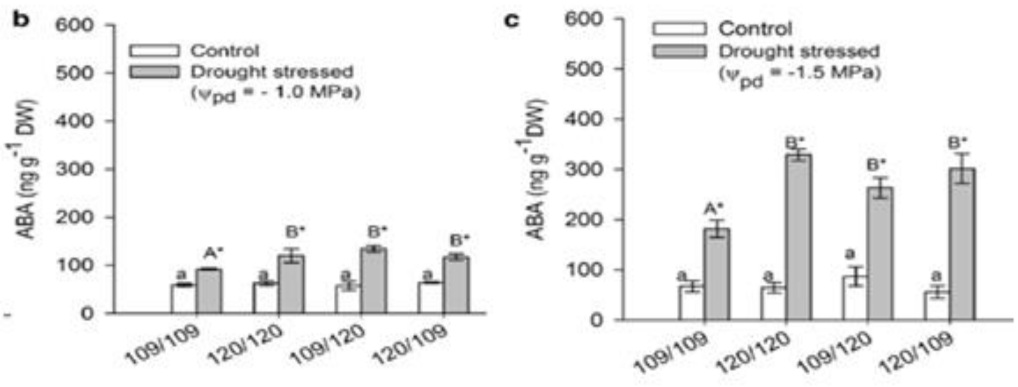


Figure.3 Response of clones and grafts to water deficit. ABA concentrations from leaf tissue collected in plants under irrigated condition and submitted to a water deficit of (**b**) Ψpd=-1.0 MPa, and (**c**) Ψpd=-1.5 MPa.



Other importance

Plants respond to environmental stress by activating the ABA signaling cascade, which activates ABA-responsive TFs and genes. ABA interacts with other hormones like auxin, gibberellins, cytokinin, ethylene, salicylic acid, and jasmonic acid, helping plants with stand abiotic stresses like drought. It regulates biochemical mechanisms for drought-prone plants (Liu *et al.*, 2007; Hwang *et al.*, 2019). ABA hormone regulates water deficiency in plants, affecting gene expression, proteins, and enzymatic activities, thereby governing plant responses to drought through intricate molecular signaling mechanisms (Chen *et al.*, 2020; Yu *et al.*, 2020; Muhammad *et al.*, 2022). It acts as a mediator of drought via enhanced osmolytes biosynthesis including proline, organic acids, and protective proteins (De Ollas *et al.*, 2015). ABA responsive-element binding protein (ABP9) enhances photosynthetic capacity under drought, while histone acetylation is crucial for ABA-mediated gene regulation. The mitogen-activated protein kinase (MAPK) signaling cascade plays a crucial role in drought regulation in plant species like rice, maize, and Arabidopsis (Sridha and Wu, 2002; Zhang *et al.*, 2008; Hamel *et al.*, 2012). The study found that moderate water deficits led to more pronounced differences in ABA content between tolerant and sensitive plants, suggesting that severe water deficits could induce ABA catabolism and contribute to drought tolerance in coffee plants. Increased ABA levels could minimize drought effects and improve photosynthetic performance (Silva *et al.*, 2010; Weng *et al.*, 2016).

The ethylene content and ACO activity decreased during rainy to dry periods, while ABA content increased, with different behaviors depending on each cultivar (López *et al.*, 2022). ABA levels in coffee genotypes increase during the dry period, possibly due to increased stomatal closure activity in leaves to cope with water restriction (Silva *et al.*, 2018). The study found that ABA content was higher in leaves and flower buds during the dry period for all genotypes, likely due to water deficit (McAdam and Brodribb, 2018). During the rainy period, coffee plants exhibited no water deficit stress and higher ethylene levels than ABA, while under water deficit stress, ethylene levels decreased and ABA production increased in Figure 2A and B (López *et al.*, 2022). Under moderate water deficit, grafting treatments showed up to three times higher levels of ABA, suggesting ABA is involved in increased drought tolerance, especially in early drought phases when using the 120 clone rootstock in Figure 3 b and c (Silva *et al.*, 2018). Stress response in plants is regulated by ABA and ethylene, influenced by stress duration, genetic potential, environmental conditions, and plant developmental stages (Müller and Hasanuzzaman, 2021).

The study reveals that tolerant coffee clones, both in shoots and roots, increase ABA content in leaves in response to drought, thereby improving drought tolerance in conilon coffee genotypes (Silva *et al.*, 2018), thereby enabling a progressive acclimation process and reducing oxidative damage. Studies on drought-tolerant coffee genotypes reveal a complex network of responses likely involving ABA and nitric oxide signaling pathways. Previous research suggests an active ABA signaling pathway in coffee leaves in response to drought (Marraccini *et al.*, 2012; Silva *et al.*, 2018).

Summary and Conclusion

Phytohormones play a vital role in the growth of plants and have the ability to alleviate environmental pressures such as drought, which can have a significant impact on crop production and global food security. These hormones facilitate the regulation of water levels, control the opening and closing of stomata, and ensure the maintenance of leaf area, ultimately enhancing the plant's ability to withstand oxidative stress. Abscisic acid (ABA) is a crucial phytohormone in plant development, influencing signal transduction, biomolecule synthesis, senescence, seed germination, and root architecture. Its role in drought tolerance is essential for plants to respond effectively to stress. ABA coordinates various functions, enabling plants to express stress-responsive genes, close stomata and regulate vegetative growth. Therefore, Abscisic Acid serves as a mechanism for drought tolerance in coffee. Therefore, the research should be concentrated on addressing the existing gaps.

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