

**ABIOTIC STRESS RESPONSES IN COFFEE (*Coffea* spp.): INTEGRATING
PHYSIOLOGICAL, BIOCHEMICAL, AND MOLECULAR MECHANISMS FOR
CLIMATE RESILIENCE**

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<https://doi.org/10.35410/IJAEB.2026.1045>

Received: 20 March 2026/Published: 29 April 2026

ABSTRACT

Coffee (*Coffea* spp.) is a globally important perennial crop that supports millions of livelihoods and contributes significantly to the agricultural economy of tropical and subtropical regions. However, coffee production is increasingly threatened by abiotic stresses such as drought, heat, cold, salinity, and nutrient deficiency, which are exacerbated by climate change. These stressors disrupt key physiological processes including photosynthesis, water relations, and growth, leading to reduced yield and bean quality. At the biochemical level, stress induces oxidative damage through the overproduction of reactive oxygen species, triggering antioxidant defense systems, osmolyte accumulation, and secondary metabolite synthesis. At the molecular level, coffee plants respond through complex regulatory networks involving stress-responsive genes, signal transduction pathways, transcription factors, and multi-omics mechanisms. This review synthesizes current knowledge on physiological, biochemical, and molecular responses of coffee to abiotic stress and highlights key adaptation and tolerance mechanisms. In addition, it examines management and mitigation strategies, including agronomic practices, breeding approaches, and biotechnological tools for improving stress resilience. Understanding these integrated responses is essential for developing climate-resilient coffee production systems and ensuring long-term sustainability under changing environmental conditions.

Keywords: Coffee (*Coffea arabica*, *Coffea canephora*), Abiotic stress, Climate change, Stress tolerance, Molecular responses.

1. INTRODUCTION

Coffee (*Coffea* spp.) is one of the world's leading perennial crops, with significant economic value (DaMatta & Ramalho, 2006). Coffee is one of the agricultural products that provide income for millions of farmers worldwide, particularly those living in tropical or subtropical countries. The coffee business is critical in supplying income through exports, creating rural jobs and agricultural incomes, and supporting the full global value chain, which includes coffee production, processing, commerce, roasting, and consumption. Global coffee production is dominated by two commercially important species: *Coffea arabica* L. and *Coffea canephora* Pierre ex A. Froehner, commonly known as Arabica and Robusta coffee, respectively (DaMatta et al., 2025; Ramalho et al., 2025). Robusta coffee is widely known for its greater vigor, higher productivity, and comparatively better tolerance to various environmental

constraints, while Arabica coffee is highly valued for its superior beverage quality and accounts for a significant portion of specialty coffee markets (Bilen et al., 2022; Borgo et al., 2024).

Despite its global economic importance, coffee is extremely vulnerable to environmental change. Both *C. Arabica* and *C. Canephora* require relatively particular climatic conditions to thrive. *C. Arabica* is extremely vulnerable to high temperatures, dryness, and irregular rainfall, unlike *C. Canephora* has higher heat tolerance, but it is still vulnerable to drought, salt, nitrogen deficiencies, and other adverse conditions (Ahmed et al., 2021; DaMatta et al., 2025; Ramalho et al., 2025). However, climate change has exacerbated these issues for coffee by increasing the frequency of droughts, heatwaves, variable precipitation, and other adverse meteorological conditions in coffee-producing countries (Bilen et al., 2022; Ovalle-Rivera et al., 2015). Furthermore, these phenomena endanger coffee output, quality, and geographical dispersion, as indicated by the expected detrimental impact of climate change on Arabica coffee areas (Bunn et al., 2015; Chemura et al., 2021; Ovalle-Rivera et al., 2015).

The term “abiotic stress” is used to describe any negative impact on plants by environmental factors other than living organisms. For coffee plants, abiotic stresses comprise drought, heat, cold, salinity, too much light, and lack or excess of nutrients (Borgo et al., 2024; Ramalho et al., 2025). Abiotic stresses affect vital processes such as photosynthesis, stomata opening, transpiration, water absorption, nutrient movement, and carbon fixation (Avila et al., 2020; DaMatta et al., 2025). Drought stress leads to lower water potential in leaves, stomata conductance, and photosynthesis, whereas high temperatures may lead to reduced membrane stability, enzyme function, reproduction, and fruit filling (Marques et al., 2024; Ramalho et al., 2018). Similarly, salinity and nutrient stress adversely affect ionic balance, osmoregulation, and metabolism, which results in poor growth and productivity (Borgo et al., 2024).

On the biochemical level, stress frequently results in an overproduction of reactive oxygen species, leading to oxidative damage of lipids, proteins, nucleic acids, and cell membranes. To defend against these effects, coffee plants rely on their antioxidant mechanisms, which involve the activity of enzyme-based antioxidants, as well as non-enzyme-based antioxidants like superoxide dismutase, catalase, peroxidases, ascorbic acid, glutathione, phenolics, and other molecules (Borgo et al., 2024; Ramalho et al., 2025). Compatible osmolytes, such as proline and soluble sugars, might be synthesized under stressful conditions, regulating water status and preserving metabolism (Avila et al., 2020; Kullachonphuri et al., 2025). The above biochemical changes have been linked to physiological resistance and could be utilized as stress-tolerant genotypic screening criteria.

Recent developments in molecular biology and omics technologies have increased understanding of coffee's responses to abiotic stress. Transcriptomic studies have shown that *C. arabica* and *C. canephora* activate complex gene regulatory networks under drought, heat, and combined stress conditions, involving stress-responsive genes, transcription factors, heat shock proteins, antioxidant-related genes, lipid metabolism, and hormone signaling pathways. In particular, combined heat and drought stress may generate more complex molecular responses than separate stress variables, implying that investigating single stresses alone would not fully understand coffee tolerance mechanisms (Marques et al., 2024). This is especially important in field situations, where coffee plants are frequently subjected to various concurrent or sequential stressors.

While several works have assessed effects of drought, heat, salinity, and other abiotic stresses on coffee plants, there still exists a dearth of literature in this regard. While some studies

emphasize physiological parameters, specific varieties of coffee, or specific environmental stresses, only a few have attempted to study the physiology, biochemistry, and molecular aspects of these effects together (Ahmed et al., 2021; Borgo et al., 2024; Marques et al., 2024). Furthermore, while a majority of studies tend to concentrate on the response to stress of the Arabica variety of coffee, there are very few comparative works dealing with Robusta and other *Coffea* genetic stocks (Bilen et al., 2022; DaMatta et al., 2025; Kullachonphuri et al., 2025).

Therefore, a thorough synthesis of current research is required to understand how coffee plants perceive, respond to, and tolerate abiotic challenges at the physiological, biochemical, and molecular levels. Such synthesis can aid in the identification of essential tolerance features, research gaps, and crop enhancement potential in response to changing climatic conditions. This review aims to integrate existing knowledge about physiological, biochemical, and molecular responses to abiotic stressors, as well as to identify future research prospects.

2. MAJOR ABIOTIC STRESSES AFFECTING COFFEE

A variety of abiotic stressors that alter plant growth, physiology, and productivity are putting further strain on coffee production. These stresses, mostly caused by climatic variability and poor soil conditions, affect both *Coffea arabica* and *Coffea canephora*, however their susceptibility varies by species and genotype (DaMatta et al., 2025; Ramalho et al., 2025). Drought, heat, cold, salinity, and nutrient shortage are five of the most important abiotic elements influencing coffee production. Each of these stresses has distinct but often interrelated effects on plant performance, resulting in reduced yield quantity and quality. A concise review of these major stresses is provided below.

1. Drought Stress

Stress induced by drought is characterized by limited water availability, thereby leading to inadequate hydration of the plant cells, metabolic disorders, and restriction of growth activities. In coffee, stress caused by drought is considered among the critical bottlenecks, especially in areas that practice rainfed farming due to climatic variability (DaMatta et al., 2025). Drought stress in coffee plants reduces leaf water potential, stomatal closure, and photosynthetic activity, reducing carbon uptake and biomass buildup (Avila et al., 2020; Ramalho et al., 2018). Prolonged water scarcity can impede blooming, fruit formation, and bean development, resulting in significant output losses and poor bean quality (Borgo et al., 2024). *C. arabica* is generally more drought-sensitive than *C. canephora*, while tolerance varies by cultivar and is impacted by root architecture, stomatal behavior, and osmotic adjustment capability (DaMatta et al., 2025).

2. Heat Stress

Heat stress arises when temperatures surpass the temperature limits favorable for plant growth, causing disturbances in cell structure, enzymatic activities, and physiological processes. *Coffea arabica* is especially susceptible to heat stress, with ideal growing temperatures ranging from 18 to 24 °C (DaMatta et al., 2025).

The adverse effects of heat stress on coffee plants include disruption of photosynthetic processes, cell membrane stability, and reproductive functions (Ramalho et al., 2018). Heat stress may induce fast development phases, thus decrease the duration of grain filling and shrinking the size of beans (Bilen et al., 2022). In extreme cases, heat stress causes flower abortions, low fruit yields, and enhanced pest and pathogen attacks (DaMatta et al., 2025).

Climate change will likely cause more frequent heat stress events, affecting traditional coffee production areas and necessitating the relocation of cultivation sites to high-altitude locations (Chemura et al., 2021).

3. Cold Stress

Cold stress can be defined as the damage inflicted by subzero (chilling stress) or freezing temperature levels on the metabolic processes and structural integrity of plants. Generally, coffee is sensitive to cold, with *C. arabica* being affected physiologically by low temperatures of less than 10–12 °C (DaMatta et al., 2025). Chloroplast damage, decreased enzyme function, and an increase in oxidative stress due to excessive amounts of reactive oxygen species (ROS) are the consequences of cold stress among coffee plants (Ramalho et al., 2018). Leaf scorch, defoliation, and death of coffee plants may occur due to the occurrence of chilling/frost events, leading to substantial yield losses (Borgo et al., 2024). In climates characterized by the presence of cold periods, cold stress is considered a key threat to coffee viability.

4. Salinity Stress

Salt stress is caused by the buildup of soluble salts, primarily Na⁺ and Cl⁻ ions, in the soil to a concentration that adversely impacts plant growth and physiological activities. While coffee is usually not grown in soils with high salt concentrations, salt stress is increasingly becoming a problem for irrigation systems and degraded soils with contaminated water sources (Borgo et al., 2024).

Coffee plants experiencing salinity stress experience osmotic stress, ion toxicity, and mineral imbalance, which ultimately hinder water absorption, photosynthesis, and other physiological processes (Borgo et al., 2024). The excess of sodium ions interferes with cellular ion balance and makes the absorption of important minerals like potassium and calcium difficult. Ultimately, plant growth is limited, leaves become chlorotic, and yield production is decreased. Coffee plants generally have a low tolerance level to salt stress; however, some genotypes are partly tolerant to salt stress through the process of ion exclusion and compartmentalization.

5. Nutrient Deficiency

Nutrient deficiency happens where essential macronutrients or micronutrients are deficient in amounts necessary for healthy growth and development of the plant. Coffee cultivation is considered highly demanding in nutrients, such as nitrogen, phosphorous, potassium, calcium, magnesium, and micronutrients to achieve high yields (DaMatta et al., 2025).

Deficiency in essential nutrients may show through symptoms like chlorosis, growth retardation, poor root growth, and decrease in leaf area. For instance, deficiency in nitrogen causes chlorophyll depletion and photosynthetic efficiency impairment, while potassium deficiency affects stomatal closure, hence, resistance against drought stress (Borgo et al., 2024). Other consequences of nutrient deficiencies include problems in flowering and fruit development, and quality of beans produced, which results in lower yields and poor economics. In many regions where coffee is grown, nutrient deficiency has been associated with soil degradation, inefficient fertilizer use, and climate effects (DaMatta et al., 2025).

Table 1. Major Abiotic Stresses Affecting Coffee

Stress Type	Definition	Key Physiological Effects	Impact on Coffee Production
Drought	Water deficit	Stomatal closure, reduced photosynthesis	Reduced yield and bean size
Heat	High temperature stress	Enzyme denaturation, membrane instability	Reduced quality and reproductive failure
Cold	Low temperature stress	ROS accumulation, chlorosis	Leaf damage and plant death
Salinity	High salt concentration	Ion toxicity, osmotic stress	Growth reduction and chlorosis
Nutrient deficiency	Lack of essential nutrients	Reduced chlorophyll, poor growth	Low productivity and poor bean quality

3. PHYSIOLOGICAL RESPONSES TO ABIOTIC STRESS

Abiotic stresses significantly impair coffee growth and productivity by disrupting fundamental physiological processes, including biomass accumulation, photosynthetic performance, stomatal regulation, plant water status, and reproductive development. The magnitude of these effects depends on stress type, intensity, duration, developmental stage, and genotype.

In general, *Coffea arabica* exhibits greater sensitivity to environmental stress than *Coffea canephora*, although substantial intra-specific variability exists (DaMatta et al., 2025; Ramalho et al., 2025). Physiological traits such as stomatal conductance, photosynthetic rate, relative water content, and water-use efficiency are widely recognized as reliable indicators for screening stress tolerance in coffee (Avila et al., 2020; Chekol et al., 2024).

A. Growth and Biomass Changes

Growth inhibition is among the first and most apparent responses to abiotic stress by coffee plants. Growth inhibition of plant height, leaf area, internode length, and biomass production have been shown to occur due to exposure to drought, heat, salinity, or nutrient deficiency (DaMatta et al., 2025).

Shoot growth inhibition is usually more pronounced than root growth inhibition in response to drought, and thus, the root/shoot ratio is increased (Avila et al., 2020). Such a strategy can be considered an adaptive mechanism that helps to increase water uptake from the soil. Drought tolerant genotypes with more extensive or deep roots have been described because of their higher water intake potential.

Leaf area decrease is another adaptive mechanism aimed at reducing water loss through transpiration; nevertheless, too much restriction may decrease light interception and photosynthesis and negatively affect biomass production and yield (Borgo et al., 2024).

Similarly, heat stress inhibits growth due to the increased respiration, instability of cell membrane structures, and accelerated development. The combined effects of drought and heat have proven to be more destructive than the isolated stresses (Marques et al., 2024; Ramalho et al., 2025).

B. Photosynthesis and Gas Exchange

Photosynthesis is vulnerable to abiotic stress and usually determines plant productivity reduction in coffee. Drought results in stomata closing that affects transpiration while limiting CO₂ uptake by leaves and lowering photosynthetic carbon assimilation. While the regulation of stomata may increase water use efficiency, their sustained closure causes a decrease in photosynthesis, growth, and reproduction.

The impact of abiotic stress on photosynthesis occurs due to both stomata limitations as well as non-stomatal limitations such as lower Rubisco activity and electron transfer, as well as chloroplast damage (Ramalho et al., 2018; Marques et al., 2024). Chlorophyll reduction and changes in chlorophyll fluorescence indicate the damages to the photosynthetic system. The high levels of excitations under severe stress can cause photoinhibition and oxidation of chloroplasts.

Heat stress exacerbates these effects by interfering with enzyme stability and metabolic activities, whereas drought-induced oxidative stress further reduces photosynthetic efficiency. These mechanisms work together to limit carbon uptake and plant growth under stress circumstances (DaMatta et al., 2025).

C. Water Relations

Water relationships play an essential role in coffee's adaptation to drought and heat stresses. Parameters such as relative water content, leaf water potential, transpiration, and water-use efficiency can be helpful in assessing the hydration state and physiological performance of plants (Avila et al., 2020).

In cases of water deficit, dehydration leads to lower values of leaf water potential and relative water content, causing dehydration, loss of turgidity, and disruption of metabolic processes. The response of coffee plants to these conditions includes changes in stomata conductance, decreased transpiration, and osmotic adjustment aimed at maintaining cellular hydration. Those genotypes that have the ability to maintain relatively high levels of relative water content are more resistant to drought (Silva et al., 2022; Chekol et al., 2024).

Water-use efficiency is an indicator showing the correlation between photosynthetic assimilation and water loss by plants. During moderate water stress, optimal water-use efficiency can be achieved through partial stomatal closure; during severe drought, photosynthesis and water-use efficiency decrease significantly (Tounekti et al., 2018; DaMatta et al., 2025).

These physiological indices are often utilized in breeding programs as selection traits of drought resistance.

D. Yield and Productivity Impacts

The result of abiotic stress on coffee yield occurs through interference with both vegetative and reproductive stages of growth. Flowering is associated with inhibition in flowering induction, abortion, and synchronization. Abiotic stress during fruiting results in reduced bean sizes and yield of coffee beans (Borgo et al., 2024). Heat stress will interfere with pollination, fertilization, and filling of grains.

Inhibition in photosynthetic rate results in reduced synthesis of carbohydrates, thus interfering with fruit development and filling of the beans. Since there needs to be a consistent source of carbon for coffee fruit development, photosynthesis will be key in determining yield and quality of the beans (DaMatta et al., 2025).

Continuous exposure of plants to abiotic stress may lead to reduced vigor of the plant and decreased productivity in more than one cycle. In the context of climate change, increasing temperature and rainfall patterns are likely to make coffee growing areas inappropriate especially for Arabica coffee. Therefore, abiotic stress becomes both physiological and socio-economic (Bilen et al., 2022; Chemura et al., 2021).

4. BIOCHEMICAL RESPONSES

Coffee plants adapt to abiotic stress through biochemical responses that maintain cellular integrity, metabolic balance, and stress tolerance. Drought, heat, salinity, and nutritional imbalance cause considerable metabolic reprogramming in coffee plants, resulting in oxidative stress, osmotic imbalance, protein instability, and membrane disruption. These alterations activate protective biochemical systems such as ROS control, antioxidant defense activation, osmolyte accumulation, and secondary metabolite synthesis (Ramalho et al., 2025; Borgo et al., 2024).

A. Reactive Oxygen Species and Oxidative Stress

One of the most common stresses in plants is associated with an increase in the synthesis of reactive oxygen species, such as H_2O_2 , O_2^- , $\bullet OH$, and singlet oxygen. While ROS molecules can act as signals for normal physiological processes, their excessive production during abiotic stress results in damage to proteins, lipids, nucleic acids, and cell organelles (Ramalho et al., 2018; Marques et al., 2024).

The key factors inducing oxidative stress in coffee plants are drought and heat stress. The former causes the closure of stomata that reduces the availability of CO_2 in the cells. Consequently, there is a higher amount of excitation energy in the chloroplasts and a higher level of ROS production. Heat stress additionally contributes to the instability of protein molecules and membrane permeability (Marques et al., 2024; Ramalho et al., 2025).

Hydrogen peroxide and superoxide radicals have both signaling and damaging properties, while the latter are very reactive substances produced by chloroplasts, mitochondria, and peroxisomes. When not removed from the plant cells efficiently, reactive oxygen species cause lipid peroxidation, loss of integrity of membranes, breakdown of chlorophyll, and decrease of photosynthetic efficiency.

B. Antioxidant Defense Systems

Antioxidant systems are employed by coffee plants to cope with oxidative stress through both enzymatic and non-enzymatic reactions that contribute to ROS regulation and cell protection during stress situations (Borgo et al., 2024; Ramalho et al., 2025).

Superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) belong to enzyme antioxidants. Superoxide dismutase works as a main protector because it reduces the harmful effect of superoxide radicals turning them to hydrogen peroxide that further gets degraded to water and oxygen molecules by the action of CAT and

POD. Increased activity of these enzymes positively correlated with resistance to drought, low temperatures, and joint effects on the coffee (Ramalho et al., 2018; Avila et al., 2020).

There are other antioxidants not linked to the enzyme system. These substances can include ascorbate, glutathione, carotenoids, tocopherols, phenolics, and flavonoids. Ascorbate–glutathione cycle plays an essential role since it helps continuously regenerate antioxidants and detoxify hydrogen peroxide.

A ratio between ROS formation and the antioxidant ability is critical when dealing with stress because only those coffee genotypes possessing highly developed antioxidant systems are able to sustain cellular membranes, photosynthesis, and metabolism. Thus, antioxidant activity is considered one of the biochemical indicators of stress tolerance in coffee.

C. Osmolyte Accumulation

The accumulation of osmolytes is an important adaptation process by which coffee plants can manage water balance when subjected to drought and salt stresses. Osmolytes are small compatible solutes that have protein stabilization ability, lipid bilayer stabilization, and maintenance of osmotic potentials while maintaining metabolic activity (Avila et al., 2020).

Proline belongs to the group of osmolytes studied the most intensely in plants. It helps in achieving osmotic adjustment, ROS scavenging, stabilization of membranes and cellular proteins, among others. Increased proline production and accumulation are common traits among drought-stressed coffee plants and are generally linked with better stress tolerance.

Soluble sugars such as glucose, fructose, and sucrose are also included among osmolytes. Their functions include osmoprotection, energy storage, and cellular structure support in addition to playing signaling role. They play a vital role in cell turgor maintenance and protection of cellular compartments during dehydration.

Nonetheless, care must be taken when interpreting osmolyte accumulation. For instance, high amounts of proline or other soluble sugars in plants may not necessarily indicate adaptation, but rather injury resulting from the stress condition. This means that osmolyte measurements should always be considered together with physiological responses (Chekol et al., 2024).

D. Secondary Metabolites

Secondary metabolites serve as an essential factor in the process of plants' defense and adaptation to stress and are important for stress tolerance and coffee quality. Phenolic compounds, flavonoids, and other specialized metabolites are involved in antioxidant reactions, cellular protection, and stress signaling in coffee (Ahmed et al., 2021; Borgo et al., 2024). As active antioxidants, phenols remove reactive oxygen species and stabilize cell membranes. Additionally, these compounds protect plants from UV rays and serve as stress signaling factors. Flavonoids belong to phenolics and play a critical role in protecting plants from light damage, drought, heat, and oxidative stress.

Moreover, abiotic stress may affect the biochemical content of coffee beans, which affects beverage quality. The environmental conditions, stress intensity, and cultivation techniques of a coffee plantation influence the content of secondary metabolites and their impact on beverage taste and aroma in *Coffea arabica* and *Coffea canephora* (Ahmed et al., 2021).

Overall, biochemical responses—such as ROS modulation, antioxidant defense activation, osmolyte accumulation, and secondary metabolite production—are closely linked to physiological processes and play an important part in coffee stress tolerance. These processes

work together to preserve cellular homeostasis, decrease oxidative damage, and prolong plant performance under harsh environmental conditions. Understanding these metabolic pathways is critical for increasing stress tolerance by breeding, management, and biotechnology techniques.

5. MOLECULAR RESPONSES

The molecular biology of coffee in reaction to abiotic stresses consists of a series of coordinated actions that include stress sensing, signal transduction, transcriptional regulation, and metabolic regulation. This makes it possible for plants to respond to abiotic stressors to initiate defense responses against drought, heat, and salinity stresses. Stress tolerance in Arabica coffee (*Coffea arabica*) and Robusta coffee (*Coffea canephora*) has been found to be mediated by complex regulatory systems including stress responsive genes, phytohormone signals, Ca-based signaling, transcription factors, and post-translational regulation (Marques et al., 2024; Ramalho et al., 2025).

A. Stress-Responsive Genes

The regulation of stress-induced genes plays a vital role in plants' ability to adapt to unfavorable environmental conditions. Drought and heat stress in coffee plants activate genes involved in osmotic regulation, antioxidative mechanisms, membrane stability, protein synthesis, and cell repair (Marques et al., 2024; Ramalho et al., 2025).

Gene families induced by drought conditions include ABA signaling, aquaporin, late embryogenesis abundant (LEA), dehydrins, and osmoprotectant metabolism. Collectively, these genes participate in processes such as stomata closure, water transport, cell protection, and recovery after stress.

Heat shock proteins (HSPs) comprise yet another group of stress-induced proteins. HSPs act as chaperones and help stabilize proteins and avoid protein aggregation and refolding under high-temperature stress conditions. Their regulation is often mediated by heat shock transcription factors and is necessary to maintain cellular activities under heat stress (Dündar et al., 2024; Li et al., 2025).

It should be noted that according to transcriptomics data, the interaction of drought and heat stress causes more significant and complex gene expression than a single type of stress. Therefore, studying the interplay between different types of stress under field conditions is important (Marques et al., 2024).

B. Signal Transduction Pathways

A signal transduction pathway connects stress sensing with subsequent gene activation and other physiological events. In the case of coffee, hormonal and secondary messenger signaling pathways play a role in the process of environmental stress signal transduction and enable a rapid response from the cells (Ramalho et al., 2025).

Signaling by abscisic acid (ABA) is critical in plant stress responses. Elevated concentrations of ABA cause stomatal closure and reduced transpiration while activating stress responsive genes responsible for osmotic regulation and protection. ABA signaling also involves interaction with ROS, calcium signaling, and protein kinases (Khan, 2025).

Ca²⁺ signaling represents yet another crucial signaling pathway. An increase in the concentration of calcium ions serves as a secondary messenger, triggering subsequent reactions

through calcium-binding proteins, kinases, and transcription factors. The latter affect stomata functioning, ROS, ion transport, and gene expression (Naz et al., 2024; Zhang, 2025).

The described mechanisms are interconnected. Cross-regulation of ABA, calcium, and ROS signaling allows for integrating several stresses signaling pathways into one, which is especially important in coffee growing because both drought and temperature stresses happen at the same time (Marques et al., 2024; Ramalho et al., 2025).

C. Transcription Factors

Transcription factors (TFs) play an important role in gene expression and are crucial components in stress response coordination. In the coffee plant and other crops, transcription factor families like MYB, WRKY, NAC, DREB/ERF, and bZIP control pathways related to drought, heat, salinity, and oxidative stress (Khosro et al., 2022; Zhang, 2025).

The MYB transcription factors are important regulators of osmotic response, antioxidation, secondary metabolism, and abscisic acid (ABA) signaling. They participate in processes like stomata regulation, osmolyte production, and removal of reactive oxygen species (ROS), which are essential for drought and heat resistance.

The WRKY transcription factors control stress-response genes through interactions with hormonal signaling pathways and metabolic pathways such as sugar metabolism and ROS regulation. Such actions become important in the coffee plant since balancing the levels of carbon and antioxidants is necessary for stress resilience.

The NAC transcription factors serve as stress signal integrators and control processes like root growth, senescence, osmotic acclimation, and stress-inducible gene expression. The interactions of NAC transcription factors with ABA and ROS signaling pathways underscore their role in stress adaptation (Chen, 2025).

Although functional characterization of TFs in coffee is limited, transcriptome studies indicate that differential TF expression is an important predictor of stress tolerance variation among coffee genotypes (Marques et al., 2024).

D. Omics Approaches

The omics technologies have made it possible to study the response of coffee to various types of stress on the scale of genes, proteins, and metabolites. This is quite an important contribution since abiotic stress resistance is a polygenic trait.

The genomics allows analyzing the genome for diversity, evolution, and candidate genes for certain stress traits. For coffee, the narrow genetic base of *C. arabica* makes this approach especially valuable. Transcriptomics can be employed to find out differentially expressed genes under various types of stress. This allows studying pathways involved in the response to stress such as photosynthesis, antioxidative activity, hormones, and protein protection. Importantly, different combinations of stresses lead to more complicated transcriptional profiles than each stress on its own (Marques et al., 2024). Like transcriptomics, proteomics can reveal the mechanisms behind the response of the organism. Proteomics helps to detect which proteins are accumulated during stress response (Ramalho et al., 2025).

In general, there is an increasing application of the combined multi-omics approach to associate genetic variations with expression levels, functions of proteins, and metabolic consequences. This strategy allows researchers to obtain a broader perspective on stress

adaptation and enables the detection of robust markers for developing climate-tolerant coffee crops.

From a broader perspective, the molecular response of coffee plants to abiotic stresses consists of complex interactions between a variety of genes responsive to stress, signaling pathways, transcription factors, and omic-level events. This approach ensures physiological and biochemical adaptation through the regulation of water relations, antioxidant systems, proteostasis, and metabolism. However, further functional validation in the field is required.

Table 2. Physiological, Biochemical, and Molecular Responses

Level	Key Responses	Indicators / Examples
Physiological	Reduced photosynthesis	Stomatal conductance, CO ₂ assimilation
	Altered water relations	Relative water content, WUE
	Growth inhibition	Biomass, leaf area
Biochemical	ROS accumulation	H ₂ O ₂ , superoxide radicals
	Antioxidant defense	SOD, CAT, POD
	Osmolyte accumulation	Proline, soluble sugars
	Secondary metabolites	Phenolics, flavonoids
Molecular	Stress-responsive genes	LEA, aquaporins
	Signal transduction	ABA, Ca ²⁺ signaling
	Transcription factors	MYB, WRKY, NAC
	Omic regulation	Genomics, transcriptomics

6. ADAPTATION AND TOLERANCE MECHANISMS

Adaptation and tolerance in coffee consist of the coordinated responses of the plant’s morphology, physiology, biochemistry, and genetics in order to cope with stress factors. This contrasts with short-term stress response, which does not account for any coordination but only indicates the coping mechanism of plants. Tolerance in coffee is described as a combination of various factors including root morphology, leaf morphology, stomata function, photochemical activity, osmotic control, and genetics (Borgo et al., 2024; Marques et al., 2024; Ramalho et al., 2025). Resilience must be determined on the plant level, especially considering the exposure of coffee plants in fields to multiple types of stress.

A. Morphological Adaptations

Morphological adaptations are structural changes that improve stress reduction and resource efficiency. These adaptations are most visible in coffee's root systems and leaf morphology, which directly influence water intake, transpiration, and carbon assimilation.

Root system adjustments

Root morphology is critical for plants to tolerate drought and nutritional stress. In situations of water deficiency, coffee plants usually develop deeper and denser roots, thereby increasing the root-shoot ratio to improve access to moisture and facilitate better hydration of the plants (Sarzynski et al., 2024; de Souza et al., 2025). Deep rooting has been found to contribute to continued photosynthesis under drought stress.

For instance, *Coffea canephora* cultivars with greater resistance to drought have better developed and more efficient root structure after several cycles of drought. Development of roots is important in acquiring nutrients during poor soil quality but is hampered by severe stress owing to the limited carbon supply (DaMatta et al., 2025).

Leaf modifications

Traits related to the leaves play an equally important role in reducing the rate of water loss and maintaining homeostasis in terms of energy requirements. Under stress due to drought and temperature fluctuations, the leaves of coffee shrubs tend to shrink, their angle changes, and the cuticle gets thicker. At the same time, changes in the density of stomata help reduce water loss and prevent damage caused by high temperatures (Chekol et al., 2024; dos Santos et al., 2025).

Anatomical changes such as thicker cuticle and altered structure of the mesophyll are aimed at increasing water retention capacity. Such traits observed in *Coffea arabica* are considered good signs regarding the plant's resistance to drought (Rakocevic et al., 2024; dos Santos et al., 2025). Thermal tolerance of the leaves varies between different genotypes. Photosynthetic system flexibility and thermal safety margins provide evidence of the plasticity of thermotolerance of coffee plants.

B. Physiological Plasticity

Physiological plasticity is the adaptation potential of the coffee plant to modulate physiological processes based on the environmental variation. It involves the adjustment of stomata conductance, photosynthesis, transpiration, water-use efficiency, and physiological recovery following stress.

Stomatal regulation is an essential physiological strategy for adapting to drought. Partial stomatal closure minimizes water loss while allowing the assimilation of some carbon. Genotypes that achieve this optimization generally perform better under mild stress conditions (Avila et al., 2020). Severe stress levels cause significant reductions in both photosynthesis and growth rates.

Photosynthetic plasticity is an equally critical adaptation potential. Genotypes resistant to stress usually have higher chlorophyll content, efficient photosystems, and CO₂ assimilation during stress than susceptible genotypes (Chekol et al., 2024). Combined drought and heat stresses exhibit tolerance by regulating photosynthesis, antioxidant activity, and metabolism (Marques et al., 2024; Ramalho et al., 2025).

The ability to recover from stress is yet another adaptation potential. Coffee plants that effectively recover from stress by restoring their physiological processes after rehydration and/or temperature normalization are more productive in the long term. There is evidence that repetitive stress exposure triggers acclimation or stress memory responses, thus improving future tolerance to stress (de Souza et al., 2025).

Under combined stress situations, physiological adaptability becomes even more significant. Drought, for example, inhibits transpirational cooling, which raises leaf temperature, whereas heat stress promotes water loss. As a result, adequate tolerance necessitates coordinated management of water balance, heat protection, and oxidative stress control (Venancio et al., 2020; Ramalho et al., 2025).

C. Genetic Variability Among Species

Genetic diversity plays a crucial role in the development of tolerance against environmental stresses in coffee. The genus *Coffea* consists of different species with distinct adaptability to various forms of abiotic stresses. Cultivated species of *Coffea arabica* and *Coffea canephora* differ in adaptability to stress factors. While Arabica shows less adaptability to environmental stress factors, Robusta displays higher adaptability to drought and high temperatures (Borgo et al., 2024; DaMatta et al., 2025).

Still, considerable variation may be observed among species in terms of physiological and anatomical characteristics, including plant water use efficiency, stomatal conductance, chlorophyll retention and leaf anatomical features, which enables the selection of stress-tolerant genotypes of Arabica (Chekol et al., 2024; Coelho et al., 2022). However, Arabica is characterized by limited genetic diversity. On the contrary, *C. canephora* is genetically diverse and represents an essential source for plant breeding efforts due to its high diversity in terms of root morphology, stomatal activity, and recoverability (Kawuki et al., 2025; Ramalho et al., 2025).

Genotype by environment interactions also play a role, pointing to the importance of testing coffee genotypes across multiple locations. A genotype well-suited to an environment may not behave in the same way under different climates or soils, even considering future climate change projections (Borgo et al., 2024). Wild coffee varieties and lesser-known germplasms can serve as other sources of genes to breed coffee plants that can withstand environmental stresses. Modern genomics and population genetics have been instrumental in the discovery of adaptive genes, contributing to the development of new coffee breeds (Salojärvi et al., 2024).

Overall, adaptation and tolerance in coffee involve the combination of morphological characteristics, physiological plasticity, and genetic variability. The formation of roots, leaf adaptations, stomata control, photosynthesis efficiency, and recovery abilities together ensure a plant's ability to withstand stresses. These factors serve as essential targets in breeding, agronomy, and climate-resilient coffee farming practices.

7. MANAGEMENT AND MITIGATION STRATEGIES

Management and mitigation measures are critical for sustaining coffee production under growing abiotic stress. Given coffee's perennial nature and extended production cycle, effective adaptation necessitates a combination of short-term agronomic measures and long-term genetic and technological approaches. Irrigation, shade management, soil conservation, breeding, and biotechnology are all approaches that help to mitigate the effects of drought, heat, salinity, and nutrient stress. However, its efficacy is dependent on site-specific elements like as climate, soil conditions, coffee species, and management strategies. Recent research emphasizes that climate-resilient coffee production is dependent on integrated, climate-smart methods that combine

agronomy, genetics, and precision agriculture (Borgo et al., 2024; Patil et al., 2025; Ramalho et al., 2025).

A. Agronomic Practices

Agronomic interventions are some of the most direct and practical techniques to alleviating abiotic stress in coffee systems, with the goal of conserving soil moisture, regulating microclimate, increasing nutrient availability, and maintaining physiological performance.

Irrigation is a key strategy for alleviating drought stress, particularly in regions with irregular rainfall. Adequate water supply supports stomatal function, photosynthesis, nutrient transport, and reproductive development, especially during critical stages such as flowering and fruit filling (Byrareddy et al., 2021). Water deficit during flowering can disrupt synchronization and reduce fruit set, while stress during grain filling limits bean size and yield (Evasco & Marcelino, 2025; Reyes-Herrera et al., 2023). Thus, supplemental irrigation helps stabilize productivity and improve recovery following drought. However, inefficient water use may increase production costs and strain limited water resources. Sustainable irrigation practices—including drip and deficit irrigation, mulching, and improved soil organic matter—combined with precision irrigation technologies, can enhance water-use efficiency under climate variability.

Shade management is another important strategy for buffering climatic stress. Shade trees reduce solar radiation, moderate temperature, improve humidity, and enhance soil moisture retention, thereby mitigating both heat and drought stress. Agroforestry systems are widely recognized as climate-adaptive approaches that improve resilience and ecosystem services (Patil et al., 2025; Venancio et al., 2020). Moderate shade improves water-use efficiency and reduces canopy temperature, whereas excessive shade may limit photosynthesis and increase disease risk. Conversely, insufficient shade can lead to heat stress and photoinhibition, highlighting the need for site-specific optimization. Appropriate shade-tree selection, including species with deep roots or nitrogen-fixing capacity, can further enhance soil fertility and reduce competition, contributing to long-term system stability (Ayalew et al., 2025).

B. Breeding and Genetic Improvement

Breeding is a long-term method for increasing coffee resistance to abiotic stress, with modern programs focusing on qualities including drought and heat tolerance, yield stability, root performance, and quality (Bertrand et al., 2025; Kawuki et al., 2025).

Stress-tolerant varieties are essential for sustaining productivity under adverse conditions. Key traits include efficient root systems, stable stomatal regulation, high water-use efficiency, and the ability to maintain photosynthesis under stress (Ramalho et al., 2025). *Coffea canephora* serves as a valuable genetic resource due to its greater diversity and higher tolerance to heat and drought compared with *Coffea arabica*. Incorporating genetic variation from robusta, wild relatives, and interspecific hybrids is therefore critical for enhancing Arabica resilience (Salojärvi et al., 2024; Bertrand et al., 2025).

Rootstock-based approaches are also gaining attention. Grafting Arabica onto stress-tolerant rootstocks can improve water uptake, drought tolerance, and adaptation to marginal environments (Patil et al., 2025). Because stress tolerance is strongly influenced by genotype-by-environment interactions, multi-location trials and long-term evaluations are necessary to

identify stable, high-performing cultivars. In addition, genomic-assisted breeding approaches are enhancing selection efficiency in this long-cycle crop (Adunola et al., 2023).

C. Biotechnological Approaches

Biotechnological approaches supplement conventional breeding by speeding up the generation of stress-tolerant coffee types, which is especially crucial considering the crop's lengthy breeding cycle.

Genetic engineering offers potential for enhancing stress tolerance through targeted modification of genes associated with drought response, heat tolerance, antioxidant systems, and hormonal regulation. However, its application in coffee remains limited due to technical challenges, regulatory restrictions, and public acceptance issues. Emerging gene-editing technologies, such as CRISPR/Cas systems, provide more precise tools for trait improvement and hold promise for future applications once key stress-related genes are fully characterized.

Marker-assisted selection (MAS) enables early identification of desirable traits using DNA markers linked to stress tolerance, disease resistance, and productivity, thereby reducing breeding time and improving selection accuracy. Advances in coffee genomics—including genome sequencing and SNP marker development—have strengthened the use of MAS and genomic selection, particularly for complex traits such as drought tolerance that involve multiple genes and environmental interactions (Adunola et al., 2023). Genomic selection, which uses genome-wide markers to predict breeding values, is increasingly recognized as a powerful tool, although its effectiveness depends on integration with field validation and physiological screening.

Overall, effective management of abiotic stress in coffee requires an integrated approach combining agronomic practices, genetic improvement, and biotechnological innovation. While irrigation and shade management provide immediate field-level solutions, breeding and biotechnology offer long-term resilience, supporting climate-smart coffee production systems.

Table 3. Management and Mitigation Strategies

Strategy	Approach	Benefit
Irrigation	Drip irrigation, deficit irrigation	Maintains water availability
Shade management	Agroforestry systems	Reduces heat and drought stress
Soil management	Mulching, organic matter	Improves moisture retention
Breeding	Stress-tolerant varieties	Long-term resilience
Biotechnology	Marker-assisted selection	Faster trait improvement
Precision agriculture	Sensors, climate data	Efficient resource use

8. RESEARCH GAPS AND FUTURE DIRECTIONS

There have been considerable advancements made in terms of abiotic stress response mechanisms in coffee; however, there are still certain gaps that need to be addressed.

- First, research in this area has largely centered around single stressors under controlled laboratory conditions; however, the actual situation in the field is one where plants are often exposed to multiple or consecutive stresses such as drought and heat. Thus, future studies must focus more on multi-stress studies and field trials to more accurately assess stress tolerance.
- Second, there is a very strong bias in research towards the *Coffea arabica* variety, with fewer studies done on *Coffea canephora* and other wild or less commonly studied *Coffea* varieties. Considering the increased stress tolerance potential and genetic diversity of the latter varieties, this gap needs to be filled by comparative studies.
- Third, there is a lack of connection between known physiological and biochemical responses to stress and their molecular basis and behavior in the field.
- Fourth, there is a need for functional validation of the candidate genes and pathways involved. Research efforts must concentrate on gene function analysis, gene editing, and translational research to ensure knowledge is translated to practical use.
- Fifth, the interaction between genotypes and environments, along with the ability to withstand long-term stresses and recover from stresses, must be addressed. This issue is especially relevant in perennial crop species like coffee.

Finally, the integration of science into practice for smallholder farmers remains an unresolved challenge. Research efforts must be directed towards climate-smart agronomic practices and participatory plant breeding techniques.

9. CONCLUSIONS

Abiotic stress acts as a significant challenge to coffee production, affecting various physiological, biochemical, and molecular processes within the plants. The current review indicates that stress response within coffee plants is extremely complicated, being the result of interplay between physiological, biochemical, and molecular processes.

Physiological adaptation involves inhibition of photosynthesis, changes in water relations, and reduced growth and productivity. Biochemical adaptation includes activation of antioxidative system, osmolytes production, and synthesis of secondary metabolites aimed at overcoming the negative impact of oxidative stress on plants. The molecular regulation of stress response is achieved through coordinated gene expression, signal transduction pathways, and transcriptional regulation. Coffee adaptation to abiotic stress conditions and its ability to overcome these challenges rely upon combination of morphological features, physiological adaptation capacity, and genetic potential. The discussed processes can serve as a target for development of more resistant varieties and species through selection, breeding, and genetic improvement. Abiotic stress should be managed using multiple strategies, including breeding and modern biotechnology.

Overall, strengthening the link between fundamental research and practical application will be key to ensuring the long-term sustainability and resilience of global coffee production.

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