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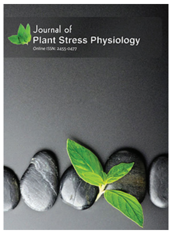

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Role of phytohormones and secondary metabolites in mitigating stressors of selected crop plants

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ABSTRACT

Crop plants are continuously threatened as climate change imposes abiotic stressors that limit crop growth and yield. Abiotic stress includes drought, high salt concentration and excessive heat. Phytohormones which act as messengers, play a central part in coordinating adaptive responses to these environmental stressors. Plants often employ phytohormones, such as cytokinins (CKs), auxins (AUX), ethylene (ET), salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), brassinosteroids (BRs) and gibberellins (GAs), in their strategic response to stress. The review of original research works in the last ten years specifically highlights the involvement of plant hormones in enabling some crop plants to withstand environmental stressors. This study explored the active roles of secondary metabolites, which are by-products of plant metabolism in conferring stress tolerance on crop plants. These secondary metabolites are flavonoids and phenolic compounds that act as antioxidants, scavenging reactive oxygen and nitrogen species thereby protecting plant cells from oxidative damage during stress. The phytohormonal signaling and secondary metabolite production enhance crop plants' overall stress tolerance and adaptation to harsh environmental conditions. We provide a summary of studies from 2014 to 2024 reporting the ability of these phytochemicals to mitigate the effects of climate-induced stressors.

KEYWORDS: Plant stress, Phytohormones, Secondary metabolites, Climate change, Crop stress

INTRODUCTION

Stress is a term used to describe one of the extracellular factors that adversely affects the development and growth of plants, including crop yield and quality. Plants are confined to a single location for the duration of their whole life cycle, making them susceptible to various stress conditions which can be either biotic or abiotic. Environmental stressors result in physiological, biochemical, and molecular alterations that ultimately manifest as a reduction in development and crop output.

Abiotic stress is any adverse effect on living things, including plants, animals, and microbes, brought on by a non-living component of the environment. Numerous abiotic factors, such as light, temperature, dryness, salinity of the soil, polluted air, and mechanical injury, can result in abiotic stress, which directly affects plant performance and yield (Jiang *et al.*, 2022). The top three harmful abiotic stressors are heat (high temperatures), salt (high salinity), and drought (poor water supply). Other organisms including symbionts, parasites, diseases, herbivores, and competitors are examples of biotic environmental influences. Under the demands of a constantly expanding human population and climate change, these risks are probably going to get even more serious.

Abiotic stressors are a constant hazard to plants due to environmental changes. Abiotic stressors primarily cause plants to produce more reactive oxygen species (ROS), adversely affect plant antioxidant defenses and make it more difficult for plants to survive under stressful conditions (Talbia *et al.*, 2020). Abiotic stress affects virtually all biological, biochemical, and molecular functions of plants from the earliest stage of seed germination through maturity. This could ultimately result in serious losses in the economic output of crop plants. In response to abiotic challenges, plants use diverse techniques to promote growth and productivity in challenging conditions. These include responses to different stimuli in the physiological and biochemical domains, as well as structural and developmental pattern alteration (growth adaptability). Additionally, plants have devised complex processes to survive stress conditions and to perceive environmental signals with an appropriate reaction.

Phytohormone is frequently used to explain substances derived from plant biosynthetic pathways. These substances can mediate development and growth responses under normal and stressful circumstances, acting at the site of their synthesis and/or being transported to another site within a plant (Peleg & Blumwald, 2011). A group of phytohormones responds to stress in various synergistic and antagonistic ways. Examples include salicylic acid, jasmonic acid, ethylene, abscisic acid, brassinosteroids, auxins, cytokinins, and gibberellins (Mauch-Mani & Mauch, 2005; Wang *et al.*, 2020). It is well recognized that phytohormones play important roles in controlling the mechanisms by which plants adjust to a drought environment using diverse cell signaling processes at the molecular level.

Plants produce organic substances that do not directly contribute to their development and growth. These substances are classified as secondary metabolites (SMs) since they result from primary metabolism. The long-term impacts of the SMs on plant development and survival in challenging settings have been documented (Agostini-Costa *et al.*, 2012). The creation of secondary metabolites, however, is the primary mechanism by which plants demonstrate a high level of tolerance to attacks. Plants experience drought stress and change SM production because of insufficient water or a higher transpiration rate. Numerous SMs play a critical function in assisting plants under drought and other environmental stress to adapt and increase their chances of survival. The build-up of SMs improves plant stress tolerance and plays significant protective functions in abiotic stress tolerance.

SMs typically give plants a distinct flavor and odour that attract pollinators and seed dispersers. Terpenoids, flavonoids, and steroids have a significant influence on olfactory attractants, according to studies on *Mentha spp.* and *Linaria vulgaris* (Nazem *et al.*, 2019). Additionally, a significant amount of SMs, which are composed of volatile chemicals known as chemo-attractants, are released by plants from their roots. Plants produce these substances as an adaptive response to various biotic and abiotic stressors. Flavonoids, terpenoids, and phenolic substances assist in intolerance to different stimuli. Cold, desiccation, intense light, metal toxicity, lack of nutrients, insect and disease attack, senescence, salt, and UV light cause them to produce SMs (Davies *et al.*, 2018).

The metabolism and physiology of plants depend on water. It is essential for the movement of nutrients and metabolites along the various regions of the plant. Plants experience drought stress due to high transpiration rates and the unavailability of water, which causes a drop in water potential and turgor pressure. As a result, changes are made to some crucial physiological processes, such as the biosynthesis of SMs (Ashraf *et al.*, 2018). This changed SM synthesis aids plants in developing drought resilience (Verma & Shukla, 2015). Plants experience oxidative stress due to drought, which causes them to produce reactive oxygen species (ROS). Plants can scavenge ROS by utilizing flavonoids and polyphenols, which are natural antioxidants (Treml & Smejkal, 2016). SMs act as antioxidants and cell wall-strengthening elements in stressed plants, by lowering the membrane lipid peroxidation and modifying the cell wall. This article summarizes recent research works on the role of plant hormones and SMs in mitigating drought, heat and salinity stress of crop plants. Interventions to increase target plant hormones and metabolites could be helpful in improving crop yield under unfavorable climatic conditions.

PHYTOHORMONES AND SECONDARY METABOLITES

Phytohormones

Phytohormones are chemical messengers and signaling components that contribute to almost all aspects of plant growth and development. They work in a communication network that enables plants to adapt to constantly changing environmental and climatic conditions (Ullah *et al.*, 2018; Bittner *et al.*, 2022). For a plant to function normally, phytohormones impact various physiological processes, including growth and development, reproduction, longevity, and death. Phytohormones categories include salicylates (SA), auxins, cytokinins (CK), brassinosteroids (BR), jasmonates (JA), ethylene (ET), abscisic acid (ABA), gibberellins (Ga), and strigolacones (SL) (Wang *et al.*, 2019, 2022). Phytohormones also play a key role in defense signaling and as essential transducers. They start a signaling cascade that triggers the stress response and activates the response mechanism.

Secondary Metabolites

Plant secondary metabolites (SMs) are derived from primary metabolites produced by plants because of various physiological changes. The SMs considerably increase plant growth and survival under different environmental conditions and serve as significant plant metabolites (Kliebenstein, 2013; Chaudhary *et al.*, 2018). Secondary metabolites are specialized substances that are not directly necessary for basic plant metabolism but for plants to survive in the environment due to their structural and chemical diversity and greater diversity than primary metabolites. The three chemically separate primary classes of secondary metabolites are as follows: phenolic substance, terpenes and nitrogen compounds. Phenolics (such as phenolic acids, coumarins, lignans, stilbenes, flavonoids, tannins, and lignin), Terpenes (such as plant volatiles, cardiac glycosides, carotenoids, and sterols), and Nitrogen-containing substances (such as alkaloids and glucosinolates). In harsh settings, secondary metabolites have a long-lasting impact on plant development and survival (Agostini-Costa *et al.*, 2012). Figure 1 shows the three main classification of secondary metabolites in plants.

Phytohormones and Secondary Metabolites in Abiotic Stress Conditions

Abiotic stress is any adverse effect on living things, including plants, animals, and microbes, brought on by a non-living

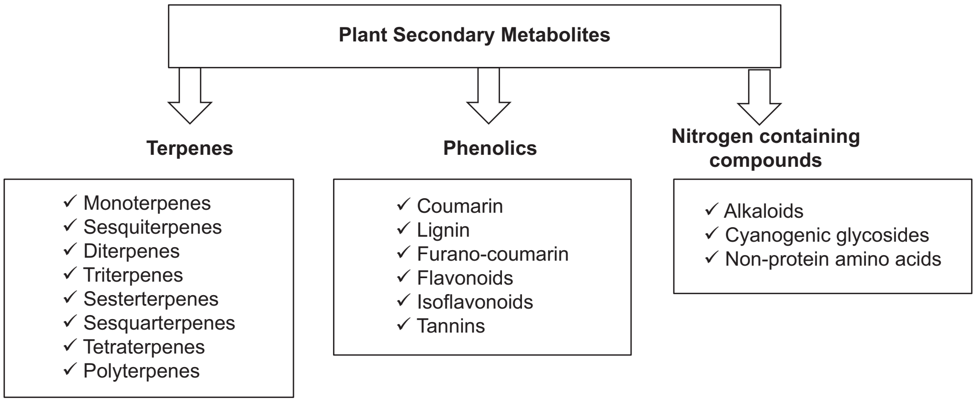

Figure 1: Secondary metabolites in plants (Nawrot-Chorabik *et al.*, 2022)

component of the environment. Numerous abiotic factors, including light, temperature, dryness, soil salinity, polluted air, and mechanical injury, can result in abiotic stress, which directly affects plant performance and yield (Jiang *et al.*, 2022). Phytohormones can mediate development and growth responses under normal and stressful circumstances, acting at the site of their synthesis and/or being transported to another site within a plant (Peleg & Blumwald, 2011). Secondary metabolites - flavonoids and phenolic compounds act as antioxidants, scavenging nitrogen species and reactive oxygen thereby protecting plant cells from oxidative damage during stress. The combination of phytohormonal signaling and secondary metabolite production enhances crop plants' overall stress tolerance and adaptation to harsh environmental conditions.

Phytohormones and Secondary Metabolites in Drought Stress Tolerance of Crop Plants

In a study by Zhang *et al.* (2020a, b), the effect of abscisic acid (ABA) on the resistance to drought of two sweet potato cultivars was investigated in which one was drought-tolerant while the other was drought-sensitive. It showed that early drought stress resulted in osmotic injury in the leaves and fibrous roots of the cultivars. The potato cultivar that was drought-tolerant under drought stress showed lesser relative electricity conductivity, malondialdehyde (MDA) content in its leaves and fibrous roots while an increase in soluble sugar content, free amino acids, and antioxidant enzymes -catalase, superoxide dismutase, and ascorbate peroxidase was observed in both leaves and fibrous roots in comparison to the drought-sensitive cultivar. However, the study revealed the application of 150 μmol/L ABA during exposure of the drought-tolerant cultivar to early drought increased the relative water content of the leaves, chlorophyll, soluble sugar, proline, gibberellic acid-3, indole-3-acetic acid, and antioxidant enzyme activities. However, there was a reduction in the relative electrical conductivity and MDA content in leaves on all sampling days. More so, in the fibrous roots, ABA application increased the level of free amino acids, and proline and tested antioxidant enzymes, lowering MDA and relative electrical conductivity. It was reported that the application of ABA to the drought-sensitive potato cultivar caused a greater increase in the percentages of some of the parameters in the leaves and fibrous roots when compared to the drought-tolerant cultivar. Hence, the application of ABA can significantly improve the ability of the potato cultivar to withstand drought stress. The principle is by stimulating an increase in the level of plant hormones such as IAA, gibberellic acid and increasing antioxidant levels.

According to a study by Li *et al.* (2023), the application of ABA has been shown to significantly enhance the ability of tomato seedlings to withstand both cold and drought conditions. This is achieved through some physiological adjustments that help the plants cope with these stresses more effectively. The study found that ABA treatment delayed the onset of wilting in tomato seedlings when exposed to drought conditions. This delay is critical as it allows the plants more time to access and utilize available water resources, prolonging their survival during water scarcity. ABA achieves this by reducing the rate of transpiration, which is the process of water loss through the leaves. As the concentration of ABA increases, the transpiration rate decreases significantly. This reduction in water loss is further supported by an increase in stomatal diffusive resistance, meaning that the stomata (tiny openings on the leaf surface) close more tightly, thereby conserving water (Vu *et al.*, 2015). In addition to its effects on drought tolerance, ABA also plays a vital role in protecting tomato seedlings from cold stress. The study highlighted that ABA application reduced the relative ion leakage and chilling injury index in tomato seedlings subjected to low temperatures. Ion leakage is an indicator of cell membrane damage caused by cold stress. By lowering ion leakage, ABA helps maintain the integrity of cell membranes, which is essential for preserving cell function under cold conditions. The chilling injury index is another measure of cold damage, and its reduction further indicates that ABA-treated seedlings are better equipped to handle low temperatures (Vu *et al.*, 2015). Another critical finding from the study is that ABA helps maintain the quality of tomato seedlings under both low-temperature and water-deficient conditions. The hormone achieves this by preserving the relative water content of the seedlings. Even though there is a natural decline in water content during periods without irrigation, ABA-treated seedlings showed a less dramatic drop in water content. This preservation of water within the plant tissues is crucial for maintaining turgor pressure, which is necessary for the seedlings' structural integrity and overall health (Vu *et al.*, 2015).

Drought stress is a significant challenge for agriculture, particularly for crops like peanuts (*Arachis hypogaea* L.), which are crucial for food security in many parts of the world. Recent studies have focused on understanding the physiological and molecular mechanisms that enable certain peanut cultivars to tolerate drought conditions better than others. According to a study by Jiang *et al.* (2022), BARI2011, a peanut cultivar, was identified as one of the most drought-resistant varieties. This study selected six different peanut varieties based on their ability to produce and withstand drought stress. Among these, BARI2011 showed the highest capacity for water retention under drought conditions, indicating its superior drought tolerance. This trait was attributed to the cultivar's ability to maintain higher leaf water content, primarily through effective stomatal regulation, which minimizes water loss during drought periods (Guo *et al.*, 2022). The study further explored the molecular responses of these peanut cultivars to drought stress, focusing on the expression of genes related to bioactive compounds such as flavonoids, phenols, and anthocyanins. According to Jiang *et al.* (2022), while most genes linked to flavonoid biosynthesis were either downregulated or remained at normal levels, BARI2011 exhibited a significant accumulation of phenols, anthocyanins, and flavonols, particularly in its leaves and roots. These compounds are known for their antioxidant properties, which help to protect the plants from oxidative stress induced by drought conditions. This accumulation suggests that BARI2011 not only conserves water effectively but also enhances its oxidative stress defense mechanisms, contributing to its overall drought resilience (Guo *et al.*, 2022).

More so, the study drew comparisons between peanuts and sorghum, another drought-resistant crop. It was observed that in sorghum, water stress led to an increase in flavone, flavanone, and 3-deoxyanthocyanidin content, particularly in tannin-free genotypes. This increase in bioactive compounds under drought conditions enhanced the functional potential of sorghum, highlighting a similar pattern of drought response across different plant species. The findings suggest that both peanuts and sorghum utilize a combination of water conservation strategies and bioactive compound accumulation to mitigate the effects of drought. Further, comparative transcriptome analysis between drought-tolerant and drought-sensitive peanut varieties revealed that the number of differentially expressed genes (DEGs) varied significantly. In drought-tolerant varieties like BARI2011, the number of DEGs was lower, and the changes in gene expression were more stable. This stability indicates a robust molecular response different from the more dynamic and less stable gene expression patterns observed in drought-sensitive varieties. The difference in gene expression suggests that drought-tolerant varieties can maintain homeostasis more effectively under stress, which is crucial for their survival during prolonged drought conditions. The ability of BARI2011 to retain water and accumulate protective bioactive compounds under drought stress positions it as a valuable cultivar for breeding programs aimed at improving drought resilience in peanuts. These insights have implications for peanut cultivation and offer broader lessons for enhancing drought tolerance in other crops.

Under drought stress, plant often synthesize SMs by diverting pyruvate which is a product of the glycolysis pathway and other intermediates through various pathways including the shikimic acid pathway, malonic acid pathway, mevalonic acid pathway and Methylerythritol Phosphate Pathway (MEP) as shown in Figure 2.

Phytohormones and Secondary Metabolites in Heat Stress Tolerance of Crop Plants

According to a study by Suliman *et al.* (2024), the application of Benzylaminopurine (BAP), a type of cytokinin, has been shown to improve the resilience of tomato plants under

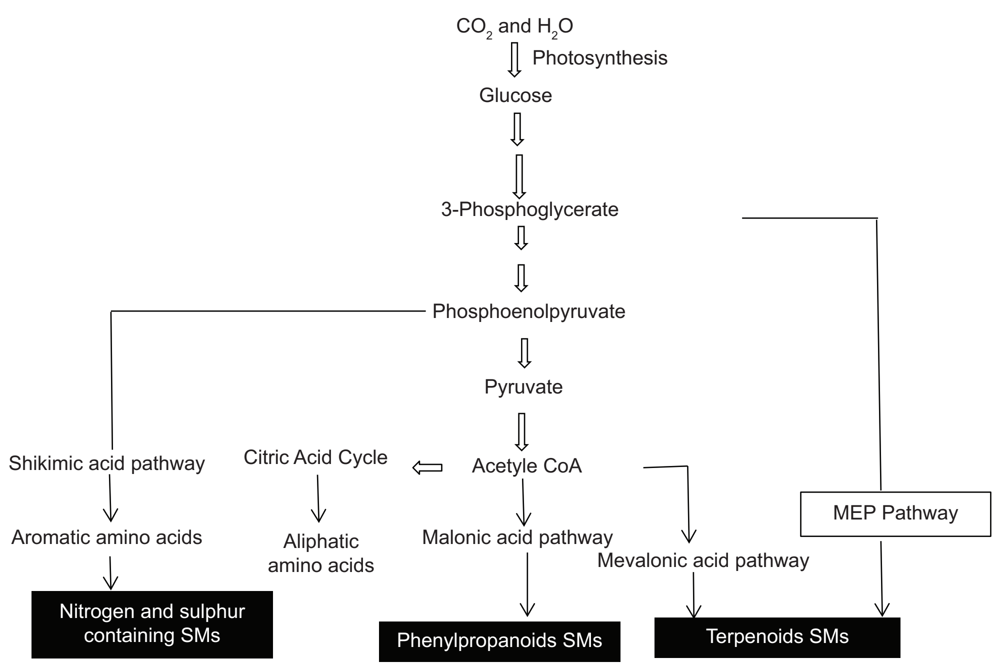

Figure 2: Biosynthesis of secondary metabolites in plants under drought stress (Jogawat *et al.*, 2021)

heat stress. The study revealed that when tomato plants were treated with BAP at concentrations of 300-600 ppm, there was a notable improvement in their physiological and biochemical responses. Specifically, higher concentrations of BAP increased chlorophyll content and proline levels, which are crucial for maintaining plant health under stressful conditions. Furthermore, BAP application enhanced antioxidant enzyme activities, and protected plants from oxidative stress induced by high temperatures (Suliman *et al.*, 2024). In addition to these biochemical improvements, the study found that BAP moderately improved fruit quality by increasing the levels of ascorbic acid and enhancing the maturity of the fruits. However, it also reduced the total soluble solids (TSS) and acidity of the fruits, indicating a complex interaction between BAP application and fruit quality traits (Suliman *et al.*, 2024). These findings suggest that the application of BAP could be a viable strategy to mitigate the adverse effects of heat stress in tomato cultivation, particularly in areas facing increasing temperatures due to climate change. Moreover, the study highlighted that the efficacy of BAP in enhancing heat tolerance and improving fruit quality varied among different tomato genotypes, emphasizing the need for genotype-specific strategies in crop management.

Another phytohormone, gibberellic acid (GA3), has also been studied for its role in alleviating heat stress in tomatoes. Foliar application of GA3 at a concentration of 75 mg L^{-1} has been reported to significantly mitigate the detrimental effects of heat stress, promoting better plant growth and physiological responses. This exogenous application of GA3 improves the general health of tomato plants under heat stress, contributing to increased productivity and resilience against high temperatures. In addition to phytohormones, secondary metabolites such as alkaloids, phenolic acids, and flavonoids play a crucial role in the heat stress tolerance of tomatoes. Another study by Yang *et al.* (2022), indicated that the NOR-like1 gene significantly influences the expression of metabolic pathways during various developmental stages, with flavonoids being particularly affected. These secondary metabolites are critical for enhancing the antioxidant capacity of tomatoes, which is directly linked to slower overripening and extended shelf-life. Moreover, the presence of phenolics and alkaloids contributes to both biotic and abiotic stress resistance, making tomatoes more resilient to environmental challenges. The study further identifies key regulatory genes involved in the synthesis of these secondary metabolites. For instance, genes like Ami in the arginine and proline metabolic pathways, PAL, C_4H, 4CL, and CAD in the phenylpropane synthesis, and CHS, FLS, F_3H, F_30H, and C_4H in the flavonoid pathway have significant regulatory effects on the accumulation of these vital compounds. The enhanced accumulation of these metabolites under heat-stress conditions helps to protect the tomato plants by strengthening their antioxidant defense mechanisms and improving their overall stress tolerance.

It has been shown that tomatoes with higher antioxidant capacities exhibit slower overripening and fruits with similar inherited backgrounds can be stored for longer than fruits with lower antioxidant capacities, and that phenolics and alkaloids also play a major role in biotic-biotic resistance (Yang *et al.*, 2022).

Phytohormones and Secondary Metabolites in Salinity Stress Tolerance of Crop Plants

The study on salinity stress in sorghum reveals how salicylic acid (SA) plays a crucial role in mitigating the negative impacts of salinity on plant growth. Salinity stress leads to increased levels of sodium (Na) and chlorine (Cl), and adversely affects the nutrient content and dry matter of sorghum roots and shoots. Specifically, salinity increases Na and Cl concentrations while reducing essential nutrients like nitrogen (N), phosphorus (P), potassium (K), and iron (Fe) (Ahmed *et al.*, 2019). This results in reduced plant growth and dry weights of roots and shoots. However, the application of SA has been shown to counteract these adverse effects. SA not only reduces the Na and Cl concentrations in sorghum but also enhances the nutrient content and dry matter of the plant. SA's beneficial effects are more pronounced in roots than in shoots, and its application under both saline and non-saline conditions significantly improves plant growth and nutrient absorption. For instance, under salt stress, a specific concentration of SA (150 mg/L) was found to be most effective in promoting growth and mitigating salinity-induced damage. Under non-saline conditions, a concentration of 100 mg/L SA proved beneficial in enhancing sorghum growth and dry matter production (Dehnavi *et al.*, 2022).

According to a study by Ren *et al.* (2022), the mixture of flavonoid chemicals in sorghum contributes to its great tolerance to abiotic stress. Plants can withstand both biotic and abiotic stress with the help of flavonoids, generated by the phenylpropanoid pathway. Stress from salt caused notable changes in proteins and secondary metabolites, as well as differentially regulated gene expression (Dehnavi *et al.*, 2019). A comparison of two sorghum cultivars, HN and GZ, was conducted with varying salt treatments (0, 24, 48, and 72). In the pathway of flavonoid biosynthesis, four important genes and seven important secondary metabolites were found and enriched. Also, 12 important proteins that are abundant in the route leading to the manufacture of phenylpropanoids were discovered. Multiomics analyses revealed that the sorghum resistance to salt stress is largely due to the flavonoid biosynthesis pathway, and that the gene LOC8066840, which codes for the production of epicatechin and the protein C5XED0, may be the main regulator of sorghum resistance to salt stress.

RECOMMENDATIONS FOR FUTURE RESEARCH

All previously done research involving how plant hormones and SMs enable crop plants to survive harsh environmental and climatic conditions including heat, drought and salinity stress have only shown their positive impact on the growth of treated seeds or seedlings and how some plants have been able to stimulate pathways for the biosynthesis of relevant plant hormones and SMs. However, there is paucity of research on how these treatments affect the offspring of treated crops. Research should progress to determine whether improvements in the performance of crop plants under stress conditions as a result of hormone and SMs stimulation extend to other generations of the crop plant.

CONCLUSION

Abiotic stressors include conditions brought on by light, temperature, dryness, salinity of the soil, pollution in the environment, and mechanical injury. Heat, salt, and drought are the three most harmful abiotic stressors on plants, which significantly lower productivity. Reactive oxygen species (ROS) are produced in plants in response to abiotic stressors, which have an impact on their survival and functionality. Stress has a profound impact on crop plants, but these plants can develop intricate mechanisms, including phytohormones and secondary metabolites, to cope with these challenges and ensure their survival and growth by biochemically stimulating flavonoid biosynthesis pathway, enhancing nutrient content and dry matter of crop plants, activating arginine and proline metabolic pathways and accumulating phenols, anthocyanin, and flavonoids. Enhancing these pathways through the incorporation of target hormones and metabolites could improve the performance of sweet potatoes, tomatoes, peas and sorghum during adverse climatic conditions. Research efforts to aid the transfer of stress tolerance characteristics of parent crops (post-treatment with hormones) to offspring could be helpful to achieve continuity of crop performance.

AUTHORS' CONTRIBUTIONS

MEK led the review team and decided on the topic and areas to be covered in the review, provided guidance for the compilation of information and reviewed the manuscript. OEF collected original research works used in the review and wrote the manuscript. AAA supported in providing access to research papers, edited and revised the manuscript while KOK supported in planning the methodology for the review and reviewed the article.

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