



Review Article

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CONTROLLING STRESS RESPONSES IN FRUIT CROPS THROUGH THE INFLUENCE OF PLANT HORMONES

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Abstract Abiotic stress, impaired by climate change, poses a significant threat to global fruit crop production, with less than 3.5% of the world's land considered free from such stressors. The ensuing morphological, physiological, and biochemical changes in plants under abiotic stress are explored, underscoring the importance of addressing these challenges for sustainable agriculture. The postharvest diseases induced by pathogens emphasize the role of fruit resistance and intricate defense signaling pathways. Anthocyanins emerge as crucial compounds in mitigating stress-induced damage, with a focus on their chelating properties and diverse functions. Plant hormones' modulation of anthocyanin production is investigated, shedding light on the potential of hormones like abscisic acid, jasmonic acid, cytokinin, gibberellic acid, and ethylene in enhancing stress resistance. The involvement of Gibberellins in plant defense mechanisms and the significance of Salicylic acid in stress response are discussed, providing valuable insights into hormonal regulation under different stress conditions. The responses of fruit crops to temperature, water, salt, and heavy metal stress highlight the complex interactions and adaptations crucial for survival. It highlights the importance of understanding hormonal control mechanisms for enhancing crop resilience and sustainability in the face of global agricultural challenges. Further research is needed to unravel signaling pathways and molecular networks, paving the way for innovative approaches in crop breeding, genetic engineering, and precision agriculture to ensure food security amidst changing environmental conditions.

Keywords: abiotic stress; signalling pathways; heavy metals; salt stress; hormones

Introduction

Various ecological stressors can significantly impact fruit crops, broadly categorized into two types, biotic and abiotic, based on their origin. Parasites, bacteria, viruses, nematodes, insects, and weeds initiate biotic stress. On the other hand, abiotic stress is often linked to environmental factors like geography, climate, and soil conditions, which influence plant growth and productivity (Kochar et al., 2020). According to the FAO's "The State of Food and Agriculture 2007," less than 3.5% of the world's land area is considered devoid of abiotic stress and suitable for cultivation. With the ongoing impact of climate change leading to a continuous decline in crop yields, concerns regarding these stressors are escalating (Minhas et al., 2017). To withstand the detrimental impact of abiotic stressors on growth and development, plants must activate protective mechanisms, enabling them to thrive in challenging environmental conditions. Abiotic stressors have the potential to significantly diminish fruit and vegetable yields, sometimes by as much as 70%. In response to such stress, plants may undergo morphological alterations at the molecular, physiological, biochemical, and molecular levels (Rao et al., 2016). These changes encompass reduced shoot and root development, loss of flowers,

diminished fruit setting, and distorted fruit shape. Furthermore, stress can affect nutrient levels and their content, along with rates of photosynthesis, respiration, water loss, and absorption. Effectively addressing these challenges within agricultural practices is imperative to ensure sustainable fruit crop production amid the escalating environmental pressures (Nora et al., 2012).

Postharvest diseases resulting from pathogen infections significantly contribute to fruit loss, carrying notable economic implications. Recent research suggests that bolstering fruit resistance against pathogens is an effective strategy for preventing and managing diseases post-harvest (Chen et al., 2023; Zhang et al., 2021). Examining the dynamics within fruit-pathogen interactions has revealed that fruits promptly recognize pathogens, triggering a sophisticated and finely tuned network of hormone-mediated defense signaling pathways (Peng et al., 2018). Downstream of this signaling network, regulating a diverse set of genes takes place, emphasizing the production of pathogenesis-related (PR) amino acids, synthesis of phytoalexins, and establishing external barriers (Zhang et al., 2021). Anthocyanins play a vital role in averting the generation of hydroxyl radicals by chelating ferrous

ions, effectively neutralizing hydrogen peroxide and superoxide produced due to trauma, sudden temperature fluctuations, or intense sunlight ([Agati et al., 2020](#)). These compounds can also create complexes with metalloids elements such as boron (B) and germanium (Ge), exhibiting characteristics of both metals and nonmetals. Furthermore, anthocyanins can retard leaf senescence and extend leaf lifespan, particularly in plants cultivated in low-nutrient environments ([Jezeq et al., 2023](#)).

The global agricultural challenges arising from abiotic stressors, such as floods, low temperatures, high salinity, nutrient deficiencies, and heavy metal pollution, are expected to exacerbate due to ongoing climate change and human activities ([Salim Akhter et al., 2021](#)). Plant hormones, which govern various aspects of plant life, including responses to abiotic and biotic stressors, are essential small molecules ([Ahmed et al., 2023](#)). Numerous studies have established the modulating effect of plant hormones on anthocyanin production, enhancing stress resistance ([Wang et al., 2018b](#)). Phytohormones like abscisic acid, jasmonic acid, cytokinin, gibberellic acid, and ethylene specifically mediate foliar anthocyanin accumulation and stress response ([Iqbal et al., 2022](#); [An et al., 2018a](#)). This review explores the role of plant hormones in anthocyanin biosynthesis and the mechanisms by which crop hormones mediate anthocyanin accumulation, contributing to abiotic stress tolerance. The review encourages further research into plant hormones regulating anthocyanin biosynthesis to enhance plant stress resilience, providing recommendations for crop production. Future investigations are needed to determine whether plant hormones can increase anthocyanin levels, improving plant stress resistance.

Impact of Plant Growth Regulators on Fruit Crops

Plant Growth Regulators (PGRs) are crucial in shaping the growth and development of apples, strawberries, and grapes, influencing critical aspects such as fruit size, quality, yield, maturity, and shelf life ([Bons & Kaur, 2019](#)).

Apple

Naphthaleneacetic acid (NAA), a synthetic auxin commonly used for apples, proves effective in thinning excess fruit, reducing pre-harvest drop, and enhancing fruit shape. Administered at specific stages, such as petal fall or 7-10 mm fruit size, it plays a crucial role in thinning, with additional applications 3-4 weeks before harvest to control drop ([Ozkan, 2016](#)). 6-Benzyladenine (BA), identified as a synthetic cytokinin, stimulates cell division and is applied at 10-12 mm fruit size, either independently or in conjunction with NAA, particularly benefiting spur-type cultivars in augmenting fruit size ([Sebek, 2015](#)). Ethephon (Ethrel), releasing ethylene, promotes fruit ripening, color development, and abscission when applied 2-4 weeks before harvest, contributing to advanced maturity and facilitating mechanical harvesting ([Goldental-Cohen et al.,](#)

[2017](#)). Aminoethoxyvinylglycine (AVG), functioning as an ethylene production inhibitor, demonstrates its utility by delaying fruit ripening, softening, and drop when applied 4-6 weeks before harvest, thereby extending the harvest window and improving overall fruit quality ([Liu et al., 2022](#)). Despite the positive impacts of PGRs, careful adherence to recommended doses and practices for each apple variety is crucial, as they may have potential adverse effects such as reduced fruit firmness, flavor, and storability. Thus, a reasonable and cautious approach to using PGRs is imperative for optimal outcomes.

Strawberry

Gibberellic acid (GA3), a natural hormone frequently employed for strawberries, is applied during flowering or fruit set to enhance fruit size, weight, and firmness while mitigating malformation and senescence ([Rana et al., 2020](#)). Naphthaleneacetic acid (NAA), a synthetic auxin, proves beneficial for low-pollination conditions by enhancing fruit set, size, and shape, typically applied at early or full bloom ([Milić et al., 2016](#)). Triacantanol (TRIA), a fatty alcohol, stimulates photosynthesis, respiration, and translocation, contributing to improved fruit yield, quality, and sugar content when applied at pre-bloom or post-bloom ([Shahbaz et al., 2013](#)). Chlormequat chloride (CCC), a growth retardant, enhances fruit uniformity and color by reducing plant height and increasing branching, with application recommended at the vegetative stage or early flowering ([Koutroubas & Damalas, 2016](#)). However, the effects of PGRs vary among strawberry varieties, necessitating adherence to recommended doses and practices for each cultivar. Despite their positive impacts, PGRs may have drawbacks, such as a potential reduction in fruit flavor, aroma, and juice content, emphasizing the need for a cautious and reasonable approach to their utilization.

Grapes

Gibberellic acid (GA3), a natural hormone commonly used for grapes, enhances berry size and elongation, reduces cluster compactness, and delays ripening ([Dokoozlian & Peacock, 2001](#)). Forchlorfenuron (CPPU), a synthetic cytokinin, is utilized to boost berry size, weight, and sugar content, particularly in seedless grape varieties ([Maoz et al., 2014](#)). Ethephon (Ethrel) aids in color enhancement by releasing ethylene, a hormone that stimulates pigment accumulation in red and black grapes, applied at veraison ([Leão et al., 2014](#)). Abscisic acid (ABA), another natural hormone, is strategically applied around veraison or post-veraison to expedite and enhance grape coloring, especially in warmer climates ([Cantín et al., 2007](#)). It is imperative to adhere to recommended doses and practices tailored to each grape variety, as PGRs may exert varied effects. While offering benefits, PGRs should be cautiously used due to potential drawbacks, such as reduced fruit firmness, shelf life, and flavor.

The involvement of GA in crop defensive reaction

The role of Gibberellins (GAs) in plant defensive responses has gained prominence despite their primary recognition as phytohormones crucial for plant reproductive organ development, flowering, leaf growth, and stem elongation (Hyun et al., 2016). Recent research has unveiled the pivotal involvement of GAs in plant defense mechanisms under stressful conditions. Investigations have revealed the essential role of GA signaling and metabolism in responding to environmental stressors. Particularly noteworthy is the identified interaction between ABA and GA signaling, where the DREB2 gene represses GA signaling, potentially leading to impaired growth in rice displaying GA deficiency symptoms. Exogenous GA has proven effective in restoring average growth under such stress conditions (Claeys et al., 2012). Furthermore, the synthesis of crucial GA biosynthesis genes, significantly reduced in plants exposed to stress, especially salt stress, underscores the intricate interplay between GA and stress responses. This realization emphasizes the potential of GAs as vital regulators in a plant's ability to navigate challenging environmental conditions. Unraveling the molecular mechanisms orchestrating the crosstalk between GA signaling and stress pathways not only provides avenues for targeted strategies in crop enhancement and stress resilience but also imparts valuable insights for innovative agricultural practices aimed at bolstering plant resilience and productivity amid adverse environmental challenges (Shah et al., 2021).

Role of Salicylic acid in plant defense response

The plant defense response involving Salicylic acid (SA) is significant in the context of its synthesis through the phenylalanine pathway (An & Mou, 2011). SA, along with its chemical counterparts, is employed in the pharmaceutical field to produce medications such as codeine, morphine, digitalis, and taxol-like compounds. SA levels in various crops range from 1 mg to 1 kg of vegetative tissue (Ahmad and Prasad, 2012b). Plants rely on SA for various essential processes, including seed development, seedling growth, metabolism, stomatal opening, and senescence. SA contributes to plant tolerance against external stressors such as salt-induced stress and cold and heavy metal strain (Chen et al., 2016). Additionally, it enhances the antioxidant system to preserve transpiration, which is crucial in promoting the generation of acute responses (HR) or systemically established resistance. SA influences biological processes such as thermogenesis, ion intake, and stress-induced cell death. The intricate actions and interactions of hormones in fruit crops are pivotal for stress tolerance.

Hormonal Responses to Temperature Stress

The development of plants is significantly influenced by temperature, in conjunction with moisture levels. Under favorable conditions, plants may display accelerated growth and earlier flowering. Cold-grown plants typically exhibit more upright leaves, while those cultivated in warm and wet conditions often

have a higher prevalence of horizontal to downward leaves (Ravi et al., 2013). In the case of bananas, irrespective of yield or bunch size, optimal growth is hindered in subtropical regions compared to tropical regions. The ideal temperatures for optimal growth range around 21-22°C, with extremes above 38 or 39°C and below 9 or 10°C proving detrimental. Exposure to temperatures exceeding 38 degrees Celsius can lead to sunburn, resulting in chlorophyll degradation and hindering banana development. The fruit may undergo morphological and physiological changes to withstand stress, enabling it to avoid or postpone desiccation, particularly in arid or semi-arid zones (Ravi & Vaganan, 2016). For optimal fruit growth, custard apple trees require a warm and humid environment during blooming, tolerating temperatures ranging from extremely cold (below 0°C) to high temperatures (up to 40°C). Exposure to soil temperatures at ten °C can induce substantial freezing damage, impacting cell wall stability (Pfleiderer et al., 2019).

Hormonal Growth Response to Water Stress

Research conducted by Farooq et al. (2009a, 2009b) indicates that the extent and duration of water stress can substantially impact agricultural production, ranging from 13% to 94% across different crops. Essential for regular metabolic functions and membrane transport systems, plants are highly dependent on moisture. As fruits and nuts are typically marketed by fresh weight, water content predominantly influences their yield (Marcelis et al., 1998). Drought effects become evident in wet and arid or semi-tropic conditions when roots lack sufficient moisture or when transpiration rates increase with temperature (Mubarik et al., 2021). Challenging circumstances, including insufficient precipitation, heightened wind speed, inadequate moisture storage, and varying water accessibility, impede the expression of genetic traits in agricultural plants (Sinha and Watson, 2007). In response to water stress, plants employ physical, physiological, and biochemical responses, encompassing changes in water use effectiveness, leaf characteristics, osmotic adjustments, and stress adaptation mechanisms (Sinha and Watson, 2007). Drought significantly reduces yields (Medici et al., 2014), while floods similarly harm fruit crops, creating a reduced respiration zone around soil roots and increasing susceptibility to soil-borne diseases (Issarakraisila et al., 2007). Consequently, extensive research has been conducted to explore the impact of various hormones on water stress management in fruit plants.

Hormonal Responses to Salt Stress

The accumulation of excess chlorine from sodium chloride (NaCl) leads to soil salinity, as highlighted by Munns and Tester (2008). Elevated concentrations of unnecessary minerals soluble in irrigation water challenge proper plant growth and reproduction (Hussain et al., 2020). When the salt concentration in irrigation water exceeds a certain threshold, it

adversely affects osmotic forces, ion intake, water exchange, transpiration, photosynthesis, protein synthesis, nucleic acid production, enzyme activity, and overall plant health (Raga et al., 2016). Plants exhibit varying tolerance levels to salt stress, categorizing them into two groups: (i) halophytes, capable of surviving and reproducing even at salt levels as high as 200 mM NaCl, and (ii) glycophytes, unable to thrive in salty conditions. Indicators of glycophyte stress include reduced leaf area and growth, yellowing, edge, and tip burning, delayed leaf senescence, stem decline, wilting, injury, and leaf scorching (Bernstein et al., 2004). Severe aridity leads to salt accumulation in young leaves, disrupting normal photosynthesis through pigment loss and inhibiting the Calvin cycle enzyme (Acosta-Motos et al., 2017). The most sensitive or tolerant types may exhibit structural anomalies such as larger leaf size, increased chloride accumulation, and reduced Mg²⁺ concentration.

Hormonal Growth Responses to Heavy Metal Stress

Metal ions play indispensable roles in the growth and survival of all living organisms. The components of living organisms are categorized as significant, minor, or trace elements based on their importance in proper biological functioning. Plants absorbing excessive microelements like lead, zinc, copper, and magnesium may face detrimental consequences (Page & Feller, 2015). Iron, copper, and other metals, including precious metals, mercury, lead, and aluminum, conduct redox reactions, influencing enzymatic functions in plant cells. Transition metals, such as iron and copper, containing unpaired electron pairs diminish the efficacy of oxygen catalysis. Heavy metal poisoning threatens natural ecosystems and agricultural systems (Edelstein & Ben-Hur, 2018). These chemicals are essential for plant development and growth at trace levels, playing a crucial role in metabolism by initiating various digestion-related processes (Roy and McDonald, 2015). Elevated concentrations of metallic elements can have adverse effects on biological functions, leading to reduced biomass growth, photosynthesis rates (Rodriguez et al., 2012), nutritional uptake (Vernay et al., 2007), or water loss relations (Mukhopadhyay and Mondal, 2015). Excessive levels can induce cell toxicity by generating reactive oxygen species (ROS), diminishing antioxidant function, and causing significant tissue damage (Rui and Zhen, 2016). Prior research has demonstrated that plant growth-promoting phytohormones can enhance protection by mitigating the effects of toxic substances in crops (Agami and Mohamed, 2013). Studies have shown that significant metal usage increases crops' ABA (abscisic acid) content. Heavy metals like zinc, aluminum, nickel, and cadmium have been shown to elevate ABA concentrations in crops (Fediuc et al., 2005). Hsu and Kao (2007) observed that ABA

modulates and enhances cadmium tolerance in rice seedlings at temperatures above freezing (30/35°C).

Conclusion

In summary, the responses of fruit crops to stress are undeniably influenced by the intricate interplay of various plant hormones. This dynamic interaction among hormones, including abscisic acid, ethylene, gibberellic acid, and jasmonic acid, is pivotal in triggering a cascade of molecular events that empower fruit crops to withstand and adapt to diverse stressors. Understanding these regulatory mechanisms advances our comprehension of plant physiology and bears significant implications for agricultural practices. Exploring the nuances of stress response regulation presents a promising avenue to leverage this knowledge for enhancing crop resilience and productivity. Researchers and agriculturists can formulate targeted strategies to modulate hormone levels, thereby boosting stress tolerance in fruit crops by unraveling intricate signaling pathways and molecular networks. This endeavor can contribute to adopting sustainable agricultural practices and developing robust crop varieties that thrive in various environmental conditions.

Moreover, given the unprecedented challenges climate change poses to global agriculture, understanding the regulatory mechanisms of stress responses becomes increasingly crucial. Insights derived from studying the impact of plant hormones on stress regulation open doors to innovative approaches in crop breeding, genetic engineering, and precision agriculture. Leveraging this knowledge is imperative for ensuring food security and mitigating the impact of environmental stresses on fruit crop production. Regulating stress responses in fruit crops represents a captivating research domain with profound implications for agricultural sustainability. As we delve deeper into unravelling hormonal control mechanisms, the potential to enhance crop resilience and adaptability becomes more tangible. Through collaborative efforts across scientific disciplines and the implementation of innovative agricultural strategies, we can envision a future where fruit crops not only withstand environmental stresses but thrive in the face of adversity.

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Declaration

Conflict of interest

There is no conflict of interest among the authors.

Data Availability statement

All authenticated data have been included in the manuscript.

Ethics approval and consent to participate

These aspects are not applicable in this paper.

Consent for publication

Not applicable

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