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Plant Growth Regulators in Abiotic Stress Resilience of Plants: A Review

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

In recent decades, the global demand for vegetables has surged alongside population growth. However, biotic and abiotic stresses increasingly hinder seed germination, growth and yields. Plant growth regulators (PGRs) acting as chemical messengers are crucial in regulating plant development and responses to environmental stresses. Key phytohormones like abscisic acid, ethylene, salicylic acid and jasmonic acid play pivotal role in stress responses of vegetable crops. These hormones enable plants to sense and adapt to adverse conditions such as drought, salinity and extremities of temperatures. Through enzyme activation and hormone synthesis, plants enhance their resilience to stressors. The growth regulators initiate/activate a cascade event either on their own or by evolving a cross - talk within them that final recruits various transcription factors those in turn activate or suppress a variety of genes. The vital role of PGRs in mitigating stress impacts on vegetable crops, highlighting their potential in agricultural sustainability in future.

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1. INTRODUCTION

Plants require essential resources such as sunlight, water, carbon dioxide and minerals for their growth and development. Insufficient availability of these inputs can induce stress in plants, leading to reduced growth and lower crop yields. Despite adverse environmental conditions, plants can experience stress and may adjust itself by slowing down their growth [1]. Given climate change and population growth, increasing agricultural productivity is critical, with a projected 70 per cent rise in output needed by mid-century to meet global demands amid significant climate variability impacting horticultural crop production [2].

Plants, being stationary, face challenges from environmental changes caused by human activities or seasonal shifts, including drought, waterlogging, salinity, extreme temperatures, presence of heavy metals and solar radiation, all of which hinder optimal growth. These factors contribute to global decline in biomass and yields [3-5]. In severe conditions, different abiotic stresses can overlap, exacerbating their effects, such as the combined impact of salt stress and drought under extreme temperatures [6].

Both abiotic and biotic stresses being major constraints on agricultural productivity, salt, drought and heat stress, particularly are widespread and crucial in affecting plant growth and development [7]. Conventional breeding methods, due to their complexity in developing stress-tolerant traits, often show limited efficacy, necessitating advancements to meet global food demands. Phytohormones have emerged as a promising alternative for cultivating productive and climate-resilient crops, leveraging plants' efficient sensing, signaling and response mechanisms to combat stress [8].

Phytohormones released by plants act as chemical messengers to regulate responses, growth and development under environmental stresses, especially in horticultural plants [9,10]. They play a crucial role in coordinating various signal transduction pathways under abiotic stresses [11,12], modulating both internal and external stimuli to induce significant changes in plant development. Research on phytohormones as signaling molecules in enhancing abiotic stress resistance has been extensively studied in horticultural plants [13,14].

2. ABIOTIC STRESS

Abiotic stress refers to the detrimental impact of non-living factors on living organisms within a specific habitat includes extreme temperatures (cold and heat), salinity, drought (lack of water), waterlogging (excess water) and radiation (high UV and visible light intensity) impact. Variables such as temperature, drought, nutrients, salinity, water availability, light and flooding are critical for optimizing plant growth and development. These factors can cause significant yield losses in major crops, exacerbated by climate change, thereby jeopardizing food security. Abiotic stress alters the physiological, morphological, biochemical and metabolic processes of plants, directly impacting their growth, development and productivity. Salinity, drought, heat and cold are particularly significant stressors affecting crop production, resulting in substantial yield reductions and up to 70 per cent decrease in biomass production [15,16].

3. PLANT GROWTH REGULATOR (PGR) AND THEIR ROLE IN ABIOTIC STREES

The term "hormone" is derived from a Greek word meaning “to arouse or stimulate or enhance an activity" [17].

“Plant growth regulators are generally defined as organic compounds, other than nutrients, that in small concentrations, affect the physiological processes of plants” [18].

“At present, nine types of PHs have been identified including auxins, the first phytohormone discovered, salicylates (SA), ethylene (ET), cytokinins (CKs), gibberellins (GAs), brassinosteroids (BRs), jasmonates (JA), abscisic acid (ABA) and strigolactones (SL), the last PHs to be discovered. Among these plant hormone (PH), ABA, SA, ET and JA have been recognized to have a central role in the plant’s responses to environmental stresses” [7].

“Plant growth regulators (PGRs) play crucial role in the physiological processes governing plant growth and development. The modulation of endogenous hormone levels in response to biotic and abiotic stresses significantly influences plant growth. Increasing the application of growth regulators can enhance yields and improve crop nutrition by mitigating stress impacts. PGRs contribute to stress tolerance by promoting seed germination, seedling growth, photosynthesis, root development and antioxidant enzyme activity, while reducing reactive oxygen species, malonaldehyde and electrolyte leakage. Recent research underscores the importance of various phytohormones like melatonin (MEL), Gamma-aminobutyric acid (GABA), jasmonic acid (JA), salicylic acid (SA), brassinosteroids (BRs) and strigolactones (SLs) in enhancing abiotic stress resilience in horticultural plants. Besides their developmental roles, these hormones serve as pivotal mediators in plant responses to stress conditions. Phytohormones act as signaling molecules influencing diverse cellular and developmental processes. They can regulate multiple processes individually or synergistically, illustrating their versatality in plant biology" [19,20,14].

In short, phytohormones such as ABA, SA, JA and ET, among others like auxins, gibberellins (GA) and cytokinins (CK), are pivotal in orchestrating plant defense mechanisms against both pathogens and abiotic stresses. ABA, for instance, is particularly crucial in conferring plant resilience to abiotic stresses such as drought, salinity, cold, heat and mechanical damage, by modulating various physiological processes [21].

3.1 Abscisic Acid (ABA)

ABA, initially discovered in young cotton fruits 60 years ago, has since been identified in various plant species and mosses. Its functions include involvement in maturation processes, acquisition of desiccation tolerance and regulation of seed dormancy. Additionally, ABA plays a crucial role in plant development and responses to both biotic and abiotic stresses [22].

ABA serves as the primary hormone enabling plants to tolerate abiotic stresses, particularly salinity and drought. It is observed that salinity, drought and low temperatures enhance the biosynthesis of ABA. Additionally, genes responsible for encoding essential enzymes in ABA biosynthesis may undergo catabolism once the stressful conditions subside [23]. During abiotic stress, including drought, low temperatures and salinity, plant cells undergo dehydration. In response to stress, plants employ diverse strategies involving rapid physiological adjustments such as closing of stomata (Fig. 2) to prevent water loss, altering developmental patterns and undergoing biochemical changes in the expression and accumulation of various proteins associated with stress tolerance.

In higher plants, ABA plays a crucial role in governing multiple physiological processes, such as seed development and plant adaptation to various environmental stresses. In situations of water and saline stress, ABA facilitates the maintenance of water balance within the plant by regulating stomatal opening. During drought, there is an elevation in ABA concentrations within the leaves. This rise in ABA levels functions as a signaling mechanism, amplifying the initial stress signal and initiating subsequent signaling cascades [24]. Synthesis of ABA in roots and its translocation to leaves is a response mechanism to soil water scarcity. A well-established function of ABA is its ability to induce stomatal closure, thereby preventing desiccation [25]. The function of ABA extends even beyond salinity tolerance to various stressors, encompassing the regulation of water balance and osmotic stress tolerance in plants. Research suggests that ABA induces the expression of genes associated with abiotic stress through both dependent and independent pathways, as demonstrated by numerous experiments [26].

3.2 Ethylene (ET)

Ethylene, existing in gaseous form, plays pivotal roles in various morpho-physiological processes crucial for plant development. These include triggering the triple response in germinating seeds, regulating flower development, initiating fruit ripening and prompting plant responses to environmental cues. Additionally, ethylene governs a multitude of stress-related biochemical reactions in plants subjected to diverse abiotic stresses, including heat, drought, chilling, salinity, heavy metals, water-logging, flooding or submerged conditions [27]. An evident correlation exists between elevated levels of ethylene and exposure to freezing and cold stress in Arabidopsis [28]. The regulation of ethylene homeostasis proves essential for enhancing tolerance to suboptimal temperature stresses like chilling and freezing. Moreover, heightened ethylene levels contribute to salt stress tolerance, as observed in salt-tolerant Arabidopsis plants. ETIO1 (ethylene overproducer 1) plays a beneficial role in salt stress by positively influencing Na^+/K^+ balance and the production of reactive oxygen species (ROS) [29].

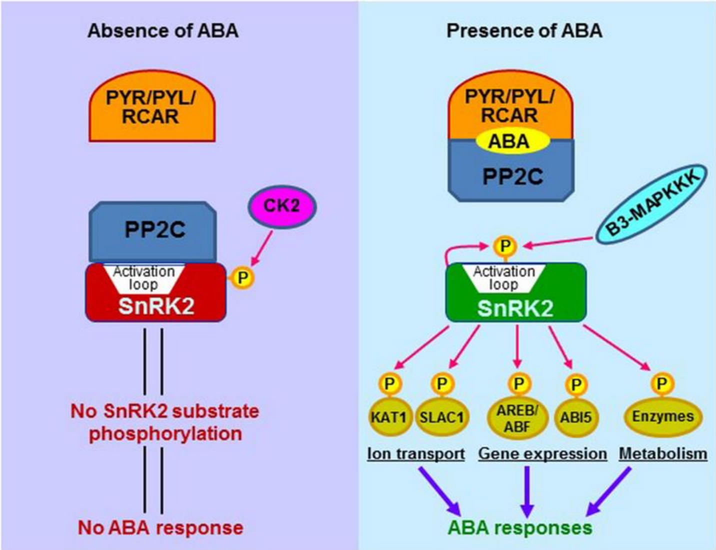

Fig. 1. ABA Signalling mechanism

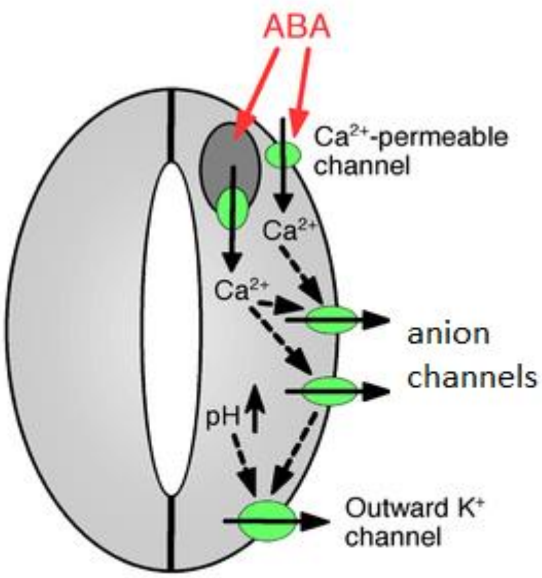

Fig. 2. ABA effect on stomatal closure

"The biosynthesis of ET has been quantified in various plant tissues, wilting flowers and ripening fruits in plants exposed to abiotic stresses" [30]. "The underlying mechanism for ET biosynthesis gets initiated with S-Adenosyl methionine (SAM), which is the precursor of ET and is usually synthesized in large concentrations in various crops. An enzyme called 1- aminocyclopropane-1-carboxylic acid (ACC) synthase catalyzes the first chain reaction to convert SAM to ACC and methylthioadenosine (MTA), which subsequently gets recycled to L-methionine. Owing to this recycling, L-methionine levels remain unchanged even when ethylene biosynthesis is at its peak. Moreover, the ET biosynthesis pathway is affected by ACC synthase enzyme, which is extremely labile and tends to limit biosynthetic rate and rises proportionally as that of ethylene levels in tissues, flowers and fruits" [31].

3.3 Salicylic Acid (SA)

"Among phenolic endogenous growth regulators, salicylic acid is one of the most vital growth regulators and has been characterized in almost all plant species belonging to diverse groups.

However, in plants subjected to salinity and osmotic stresses, the SA role remained somewhat ambiguous in various plant species depending on the intensity and duration of osmotic stress. The exogenous application of SA could alleviate the adverse effects of salinity" [32]. "During the 1960s, SA was synthesized from cinnamic acid (CA) by two biosynthetic pathways. One pathway involves a side chain of CA, which undergoes decarboxylation to produce benzoic acid, which is then subjected to 2-hydroxylation leading to the synthesis of SA in crops including tobacco. However, it postulated that some other enzymes involved in this pathway are still unknown. The second pathway of SA biosynthesis involves CA, which gets subjected to 2-hydroxylation, leading to ocoumaric acid production, which is subsequently decarboxylated to biosynthesize SA. Trans-cinnamate-4- hydroxylate enzyme is responsible for catalyzing this reaction. This pathway was first studied in seedlings of peas" [7].

3.4 Jasmonates (JA)

Jasmonates are a broad group, which are covering various compounds, such as jasmonic acids (JAs), jasmonic acid methyl ester (JAME), precursor of the JAs; octadecanoid cis (+) 12 oxophytodienoic acid (OPDA), amino acid conjugates and metabolites such as 12-OH-JA and 11-OH-JA and often these compounds are involved in plant responses to biotic and abiotic stresses. Jasmonates are found throughout the plant body; however, shoot apex, root tips, immature fruits and young leaves like tender growing parts show remarkably high concentrations. The synthesizing pathway of JAs is said to be via the octadecanoid pathway, starting at linolenic acid and terminating at (+)-7-epi-JAs.

"The major plant organs of biosynthesizing Jasmonates are leaves and roots, while chloroplasts and peroxisomes are the subcellular primary sites of JAs biosynthesis. Reports showed that development of the embryo and reproductive organs, determination of sex, seed germination and seedling development, root growth, fruit ripening, leaf movements and senescence, gravitropism, the formation of the trichome and tubers are mediated" by JAs [33].

"Further, signaling related to defense mechanisms of insects or pathogen are driven wounding is mediated by jasmonates. JAs have a crucial role in abiotic stress tolerance; thus, studies were focused on these compounds because of their significant protective capacity on plants against stress" [34]. "For example, JAs-mediated plant responses are shown against drought stress, ozone stress, UV-stress, salinity stress, cold stress and temperature stress" [35].

3.5 Brassino Steroids (BRs)

"Brassinosteroids (BRs) are polyhydroxylated steroid PHs. They regulate several physiological and biochemical processes in the plant, such as cell elongation, cell division, photomorphogenesis, xylem differentiation, growth and reproduction" [36]. "The BRs exist in free and conjugated forms and nearly 69 and 5 conjugated and free BRs have been identified. The BRs are diverse in nature and biological activity. Among the BRs, brassinolide (BL) has been documented as the most active BR and it was isolated and purified from *Brassica napus* pollen" [37]. "The BRs are closely related to auxins, through the modulation of its transport, coordinating the tropic responses of plant organs and promoting lateral root primordial initiation during lateral root development. The endoplasmic reticulum most likely served as the site for BRs synthesis. The formation of a protein complex comprising enzymes (metabolon) to efficiently route the substrate to specified enzymes in a single biosynthetic pathway has been anticipated in plants only and BRs biosynthesis occurs through cyto-chrome P450 (CYP), a triterpenoid pathway" [38].

"Numerous studies have documented the abiotic stress tolerance in plants with exogenous application of BRs" [39]. Nevertheless, the BRs need in minimal quantity like other PHs. Therefore, plant responses to exogenous BRs treatment are concentration - dependent. A high BR application rate is found to inhibit the plant growth, while the opposite is observed at lower concentrations. The abiotic stresses enhanced ROS generation leading to oxidative stress, while BRs help regulates the cellular ROS level under stressful environments.

"For instance, 28-homobrassinolide application to *Brassica juncea* L. plants subjected to combined temperature and salt stress enhanced enzymatic antioxidant activities (SOD, CAT, APOX, DHAR and MDHAR) and ROS homeostasis" [40]. "Likewise, in *Lycopersicum esculentum*, BRs application ameliorated the supra optimal temperature-induced photosynthesis inhibition and augmented the carboxylation and activities of the antioxidant system" [41].

3.6 Polyamines (PA)

"Polyamines (PAs) are small aliphatic nitrogenous bases produced as a result of cellular metabolism. The PAs have no plant hormones, but due to their involvement in regulating several growth and development processes and responses to abiotic stress in plants, they have been proposed as a new category of plant growth regulators" [42]. "Initially, the ability of PAs to bind with anionic macromolecules was supposed to link with their biological functions, which lead to the consideration of PAs as polycations having distinctive structural roles. However, later may study demonstrated that PAs act as regulatory molecules in key cellular processes such as cell division, cell differentiation, DNA and protein synthesis and gene expression" [43].

"Furthermore, PAs are involved in various physiological processes in plants including embryogenesis, organogenesis, reproductive development, leaf senescence and fruit maturity. Several studies have reported the protective role of PAs against environmental stresses. Spermidine (Spd), spermine (Spm) and Putrescine (Put) are the major PAs in plants, while the role of cadaverine (Cad) and diamino propane (Dap) are less studied in plants. The PAs are present in conjugated (covalent and non-covalent bounded) or free form" [44].

"The main product of PAs biosynthetic pathway is Put, which serves as the precursor for Spm and Spd. In plants, Put biosynthesis occur in three different routes: via Arginine by arginine decarboxylase (ADC) (the most frequent route), via ornithine (Orn) by ornithine decarboxylase (ODC) and citrulline (Cit) by citrulline decarboxylase (CDC). The PAs catabolism is contingent on the action of diamine oxidase and PA oxidase and PAs metabolism is closely associated with several other metabolic pathways in plants. The H_2O_2 produced due to PA oxidation is involved in signal transduction and plant responses to biotic and environmental stresses" [45].

"The PA biosynthetic pathway is linked to ethylene synthesis, sharing the same precursor (S adenosyl methionine) and competing. Further, PAs metabolism is closely associated with nitric oxide generation, which triggers a signal transduction process related to plant growth. The distribution of PAs is organ and tissue-specific in plants. For instance, Put is the most abundant PA found in leaves, while the higher level of Spd is present in other plant organs. Polyamines are implied in response to different abiotic stresses. Generally, transgenic plants overexpressing PA biosynthetic enzymes, such as spermidine synthase, arginine decarboxylase and S-adenosylmethionine synthetase, showed the protective roles of polyamines under abiotic stress conditions. Moreover, exogenous application of PAs showed increased stress tolerance in several plant species" [46].

4. CONCLUSION

Use of phytohormones have emerged as a pivotal technique in modern agricultural practices for managing stress in plants. They play a crucial role in protecting plants from a range of abiotic stresses such as floods, droughts and salinity by enhancing antioxidant enzyme activity, reducing oxidative damage and promoting overall plant development. This application of phytohormones not only ensures the sustainability of crop production but also enhances the resilience of horticultural crops to adverse environmental conditions.

In flood-prone areas, where excessive water can suffocate roots and disrupt normal physiological processes, phytohormones help plants maintain vigour by regulating growth and development. Similarly, in drought-affected regions, phytohormones mitigate the impact of water scarcity by enhancing water use efficiency and supporting root growth, thereby improving drought tolerance.

Saline soils, which restrict water uptake and cause ion toxicity, pose another significant challenge for crop productivity. Phytohormones aid in regulating ion transport and maintaining cellular homeostasis, enabling plants to thrive in saline environments. They also contribute to the harmonization of the germination process, crucial for initiating plant growth cycles under stress conditions. By enhancing seed viability and breaking dormancy, phytohormones ensure a more synchronized and successful germination, which is particularly beneficial in unpredictable climates.

The utilization of phytohormones in agriculture underscores their multifaceted role beyond mere growth regulation. They act as signaling molecules that orchestrate adaptive responses in plants, ensuring survival and productivity under adverse conditions. Through targeted application and research, scientists continue to explore the specific mechanisms by which phytohormones can be optimized for different crops and environmental stresses, aiming to enhance global food security and sustainability.

In conclusion, phytohormones represent a promising avenue for sustainable agriculture, offering practical solutions to mitigate the impact of abiotic stresses and support robust crop production in challenging environments worldwide.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Sairam M, Santosh DT, Gaikwad DJ, Maitra S. Advances in Modern Agricultural Practices; 2024.
2. Francini A, Sebastiani L. Abiotic stress effects on performance of horticultural crops. Horticulturae. 2019;5(4): 67.
3. Raza MA, Van der Werf W, Ahmed M, Yang W. Removing top leaves increases yield and nutrient uptake in maize plants. Nutrient Cycling in Agroecosystems. 2020;118:57-73.
4. Gupta S, Maurya D, Kashyap S. Effective Administration of Plant Growth Regulators in Horticultural Crops: A Review. Int. J. Plant Soil Sci. 2023;35(11):36-4. Available:https://journalijpss.com/index.php/IJPSS/article/view/2943 [Accessed on: 2024 Jul. 9].
5. Prajapati L, Kushwaha SP, Bharose R. Response of foliar applied growth regulators on yield and quality traits of basmati rice (*Oryza sativa* L.). Curr. J. Appl. Sci. Technol. 2020;39(12):16-20. Available:https://journalcjast.com/index.php/CJAST/article/view/2622 [Accessed on: 2024 Jul. 9].
6. Hossain MA, Cho JI, Han M, Ahn CH, Jeon JS, An G, Park PB. The ABRE-binding bZIP transcription factor OsABF2 is a positive regulator of abiotic stress and ABA signalling in rice. Journal of Plant Physiology. 2010;167(17):1512-1520.
7. EL Sabagh A, Islam MS, Hossain A, Iqbal MA, Mubeen M, Waleed M, Abdelhamid MT. Phytohormones as growth regulators during abiotic stress tolerance in plants. Frontiers in Agronomy. 2022;4:765068.
8. Wani SH, Kumar V, Shriram V, Sah SK. Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal. 2016;4(3): 162-176
9. Kohli A, Sreenivasulu N, Lakshmanan P, Kumar PP. The phytohormone crosstalk paradigm takes center stage in understanding how plants respond to abiotic stresses. Plant Cell Reports. 2013; 32:945–957.
10. Verma V, Ravindran P, Kumar PP. Plant hormone-mediated regulation of stress responses. BMC Plant Biology. 2016;16: 86.
11. Saini S, Kaur N, Pati PK. Phytohormones: Key players in the modulation of heavy metal stress tolerance in plants. Ecotoxicology and Environmental Safety. 2021;223:112578.
12. Salvi P, Manna M, Kaur H, Thakur T, Gandass N, Bhatt D, Muthamilarasan M. Phytohormone signalling and crosstalk in regulating drought stress response in plants. Plant Cell Reports. 2021;40:1305-1329
13. Wu J, Shu S, Li C, Sun J, Guo S. Spermidine-mediated hydrogen peroxide signaling enhances the antioxidant capacity of salt stressed cucumber roots. Plant Physiology Biochemistry. 2018; 128:152–162.
14. Sytar, O., Kumari, P., Yadav, S., Brestic, M., and Rastogi, A. 2019. Phytohormone priming: regulator for heavy metal stress in plants. Journal Plant Growth Regulator, 38: 739– 752.
15. Loreti E, Van-Veen H, Perata P. Plant responses to flooding stress. Curr. Opi. Plant Bio. 2016;33: 64-71.
16. Kapazoglou A, Ganopoulos I. Tani E, Tsaftaris A. Epigenetics, epigenomics and crop improvement. Adv. Bot. Res. 2018;86:287-324.
17. Went FW. Experimental plant physiology. Cambridge University Press; 1935.

18. Miller CO. Skoog F, Okumura FS, Von Saltza MH, Strong FM. Isolation, structure and synthesis of kinetin, A substance promoting cell division. Journal of the American Chemical Society. 1955;77(11): 1392.
19. Ullah A, Sun H, Yang X, Zhang X. A novel cotton WRKY gene, GhWRKY6- like, improves salt tolerance by activating the ABA signalling pathway and scavenging of reactive oxygen species. *Physiologia plantarum*. 2018;162(4):439-454.
20. Ciura J, Kruk J. Phytohormones as targets for improving plant productivity and stress tolerance. Journal of Plant Physiology. 2018;229:32-40.
21. Zheng Y, Wang X, Cui X, Wang K, Wang Y, He Y. Phytohormones regulate the abiotic stress: An overview of physiological, biochemical, and molecular responses in horticultural crops. Frontiers in Plant Science. 2023;13:1095363.
22. Klingler JP, Batelli G, Zhu JK. ABA receptors: The START of a new paradigm in phytohormone signalling. Journal of Experimental Botany. 2010;61(12):3199-3210.
23. Chavez L, González LM. *Mecanismos moleculares* involucrados en la tolerancia de las plantas a la salinidad. ITEA. 2009;105(4):231-256.
24. Chavez Suárez L, Ramírez Fernández R. Signalling pathway in plants affected by salinity and drought. ITEA. 2010;106(3): 157-169.
25. Schachtman DP, Goodger JQ. Chemical root to shoot signaling under drought. Trends in Plant Science. 2008;13(6):281-287.
26. Li C, Lv J, Zhao X, Ai X, Zhu X, Wang M, Xia G. TaCHP: a wheat zinc finger protein gene down-regulated by abscisic acid and salinity stress plays a positive role in stress tolerance. Plant Physiology. 2010;154(1): 211-221
27. Awan FK, Khurshid MY, Mehmood AJIJIRB. Plant growth regulators and their role in abiotic stress management. Int. J. Innov. Res. Biosci. 2017;1:9-21.
28. Shi Y, Tian S, Hou L, Huang X, Zhang X, Guo H. et al. Ethylene signalling negatively regulates freezing tolerance by repressing expression of CBF and type-A ARR genes in Arabidopsis. Plant Cell. 2012;24:2578–2595.
29. Yang C, Li W, Cao J, Meng F, Yu Y, Huang J, Liu J. Activation of ethylene signaling pathways enhances disease resistance by regulating ROS and phytoalexin production in rice. The Plant Journal. 2017;89(2):338-353.
30. Kendrick MD, Chang C. Ethylene signaling: New levels of complexity and regulation. Current Opinion in Plant Biology. 2008;11(5): 479-485.
31. Maheshwari DK, Dheeman S, Agarwal M. Phytohormone-producing PGPR for sustainable agriculture. Bacterial Metabolites in Sustainable Agroecosystem. 2015;159-182
32. Horváth E, Pál M, Szalai G, Páldi E, Janda T. Exogenous 4- hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants. Biologia Plantarum. 2007;51:480–487.
33. Wasternack C. Action of jasmonates in plant stress responses and development—applied aspects. Biotechnology Advances. 2014;32(1):31-39.
34. Takeuchi K, Gyohda A, Tominaga M, Kawakatsu M, Hatakeyama A, Ishii N. et al. RSOsPR10 expression in response to environmental stresses is regulated antagonistically by jasmonate/ ethylene and salicylic acid signaling pathways in rice roots. Plant Cell Physiol. 2011;52: 1686–1696.
35. Yoshikawa H, Honda C, Kondo S. Effect of low-temperature stress on abscisic acid, jasmonates, and polyamines in apples. Plant Growth Regul. 2007;52:199–206.
36. Nolan T, Vukasinovi N, Liu D, Russinova E, Yina Y. Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. Plant Cell. 2020;32: 295–318.
37. Grove MD, Spencer GF, Rohwedder WK, Mandava N, Worley JF, Warthen Jr JD. et al. Brassinolide, a plant growth-promoting steroid isolated from Brassica napus pollen. Nature. 1979;281(5728):216–217.
38. Chung KY, Rasmussen SG, Liu T, Li S, DeVree BT, Chae PS., et al. Conformational changes in the G protein Gs induced by the β2 adrenergic receptor. Nature. 2011;477(7366):611–615.
39. Divi UK, Rahman T, Krishna P. Gene expression and functional analyses in brassinosteroid-mediated stress tolerance. Plant Biotechnology Journal. 2016;14(1): 419– 432.
40. Kaur H, Sirhindi G, Bhardwaj R, Alyemeni MN, Siddique KHM, Ahmad P.

Homobrassinolide regulates antioxidant enzyme activities and gene expression in response to salt and temperature-induced oxidative stress in *Brassica juncea*. Scientific Reports. 2018;8(1) :8735.

41. Ogweno JO, Song XS, Shi K, Hu WH, Mao WH, Zhou YH, Nogués S. Brassinosteroids alleviate heat-induced inhibition of photosynthesis by increasing carboxylation efficiency and enhancing antioxidant systems in Lycopersicon esculentum. Journal of Plant Growth Regulation. 2008; 27:49-57.
42. Chen D, Shao Q, Yin L, Younis A, Zheng B. Polyamine function in plants: development, and roles in abiotic stress responses. Front. Plant Sci. 2019;9:1945.
43. Childs C, Holdsworth RE, Christopher AL, Jackson, Manzocchi T, Walsh JJ, Yielding G. Introduction to the geometry and growth of normal faults. Geological Society, London, Special Publications. 2017; 439(1):1-9.
44. Gholami M, Fakhari AR, Ghanati F. (Selective regulation of nicotine and polyamines biosynthesis in tobacco cells by enantiomers of ornithine. Chirality. 2013;25, 22–27.
45. Sariyev A, Barutcular C, Acar, M, Hossain A, EL, Sabagh, A. Sub-surface drip irrigation in associated with H2O2 improved the productivity of maize under clay-rich soil of Adana, Turkey. Phyton International Journal of Experimental Bot. 2020;89(3):519–528.
46. Minocha R, Majumdar R, Minocha SC. Polyamines and abiotic stress in plants: A complex relationship. Frontiers in Plant Science. 2014;5: 175.

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