International Journal of Advanced Biochemistry Research

ISSN Print: 2617-4693
ISSN Online: 2617-4707
NAAS Rating: 5.29
IJABR 2025; 9(6): 1016-1022
www.biochemjournal.com
Received: 20-03-2025
Accepted: 25-04-2025

Avantika Bisht
Research Scholar, Department of Horticulture, Lovely Professional University, Punjab, India

Niharika Thakur
Research Scholar, Department of Horticulture, Lovely Professional University, Punjab, India

Akash Kumar
Research Scholar, Department of Horticulture, Lovely Professional University, Punjab, India

Sudhanshu Singh
Research Scholar, Department of Horticulture, Lovely Professional University, Punjab, India

Anmol
Assistant Professor, Department of Horticulture, Lovely Professional University, Punjab, India

Shailesh K Singh
Professor, Department of Horticulture, Lovely Professional University, Punjab, India

Manish Bakshi
Associate Professor, Department of Horticulture, Lovely Professional University, Punjab, India

Corresponding Author:
Manish Bakshi
Associate Professor, Department of Horticulture, Lovely Professional University, Punjab, India

Application of brassinosteroid to enhance abiotic stress tolerance in fruit crops: A review

Avantika Bisht, Niharika Thakur, Akash Kumar, Sudhanshu Singh, Anmol, Shailesh K Singh and Manish Bakshi

DOI: https://www.doi.org/10.33545/26174693.2025.v9.i6l.4652

Abstract
Plant growth, development and productivity are significantly impacted by climatic and environmental stresses such as heavy metal, salinity, and drought contamination and temperature extremes. These stresses disrupt essential physiological processes like photosynthesis, nutrient uptake, and hormonal balance, reducing crop yield & quality. Brassinosteroids (BRs), a part of plant steroidal hormones, has resulted to modulate stress response, enhance plant resilience. BRs play a role in mitigating these stresses through antioxidant defense systems, gene expression regulation, and cellular homeostasis maintenance. They are also used in agriculture to improve crop tolerance to these stresses, leading to increased biomass, yield and survival rates. However, challenges remain in understanding the molecular interaction and potential trade-offs associated with BR application under diverse environmental contexts. Future research should focus on optimizing BR-mediated strategies using genomic, transcriptomic, and epigenetic approaches.

Keywords: Brassionosteroids, abiotic stress, drought, salinity, heavy metals

Introduction

Brassinosteroids (BRs) have shown promise in helping fruit crops survive with abiotic stresses (Divi *et al.*, 2009) [16]. Brassinosteroids are immune modulators that promote plant development and growth by regulating enzymatic reactions, protein synthesis, and defense compounds. They also regulate cellular differentiate, pollen development, fruit ripening, and nutrient distribution, promoting better crop yield (Parveena *et al.*, 2020). Brassinosteroids, like 24-epibrssinolide (EBR), regulate metabolism and improve quality by promoting photosynthesis and enzyme activity (Li *et al.*, 2016) [40]. Brassinosteroids protects crops from pesticide toxicity. It also stimulates cypermethrin, chlorothalonil, and carbendazim, indicating its potential as environmentally friendly, natural substances for reducing pesticide exposure risks (Xia *et al.*, 2009) [75]. Brassinosteriods play critical role in various physiological processed in plants (Table 1). Plants use physiological and molecular defense systems, such as hormones, antioxidant enzymes, signalling pathways, defense-related genes, to adapt the salt stress (Anwar *et al.*, 2022) [4]. Fruit crops are important parts of the world's agricultural system, giving populations all over the world access to key nutrients and a source of income (Smith *et al.*, 2020) [59]. But a wide range of substances that are abiotic, such as high temperature, drought or exceptionally low temperature, and salt are frequently threaten their productivity and quality (Mittler, 2006) [45]. These stresses severely impede the yield, growth, and development of fruit crops (Fahad *et al.*, 2017) [17]. It is therefore essential to investigate novel approaches to improve fruit crops' resistance to abiotic stress in the context of these difficulties.

When plants are stressed by drought, brassinosteroids are essential for maintaining water balance and osmotic adjustment, which reduces water deficits and increases plant survival (Nakashita *et al.*, 2003) [47]. There is a great deal of communication between Brassinosteroids and other signaling pathways, including light and hormone. BZR1 regulates signaling elements and co-regulates target genes with transcription factors associated with the movement of light (Sun *et al.*, 2010) [62].

The impact of BR has mostly concentrated on one plant attribute or a group of phenotypes. For instance, it has been observed that overexpression (OE) of DWF4, which encodes a C-22 hydroxylase, in an ectopic and organ-specific manner that catalyses a crucial stage in the biosynthesis of Brassinosteroids, increases the length of inflorescences, size and number of branches, and the quantity of seeds produced from plants (Choe *et al.*, 2001) [10].

Functional dynamics of Brassinosteroids

Many model plants have been used to study the biosynthesis and signaling pathways of BRs, which has significantly advanced our knowledge of the ways in which supervise biological processes, particularly those associated to the growth and development of plants (Choe, S, 2004) [9]. Beyond cell elongation and division, BRs control growth promotion, xylem differentiation, cell division, photomorphogensis, plant reproduction in response to abiotic and biotic stressor (Nolan *et al.*, 2019) [48]. BR deficiency or inability in plants leads to dwarfism, senescence and delayed flowering, male sterlity, de-etiolation in the dark, and low seed germination (Clouse, 2015) [14]. Increased crop output and enhanced adaptability to stress and the results of over expressing the genes in charge of BR biosynthesis, which raises endogenous BR levels (Xia *et al.*, 2018) [74]. Brassinosteroids, either independently or through hormonal cross-talks, are believed to activate the ABA pathway and optimize the machinery for stress-responsive transcripts (Ye *et al.*, 2017) [78] or turn on antioxidant defence systems (Lima and Lobato 2017) [41].

Epigenetic regulation: In order to control gene expression patterns linked to abiotic stress responses, brassinosteroid affect epigenetic alterations such DNA methylation and histone modifications. This allows for long-term adaptability to stressful situations (Kim *et al.*, 2006) [32].

Modulation of root architecture: By encouraging the growth of lateral roots, improving the growth of root hair, and modifying the root system's architecture to maximize the efficiency of water and nutrient intake, brassinosteroids affect root growth and architecture under abiotic stress (Bajguz & Hayat, 2009) [7]. BR receptor's increased endosomal localization and improved signaling imply that the plant's endophytic apparatus controls BR signaling. BR modify gene expression prior to alteration in cells or the body, impacting complex metabolic processes that regulate cell division and differentiation. They modulate processes particular to expansion and progress, such as photomorphogenesis, cellular expansion, and skotomorphogensis (Clouse and Feldmann, 1999) [12].

Mechanisms governing Brassinosteroid regulation in plants

The BR signal transduction pathway is essential for the development and growth of plant life. Stress tolerance occurs by BRI1- EMS suppressor and Brassinazole resistant (BZR1) (BES 1) transcription factors, which are sensed by Brassinosteroid Insensitive 1 (BRI 1) receptor kinase (Li *et al.*, 2009) [37]. In order to cause BRI 1 Kinase Inhibitor 1 (BKI 1) to dissociate, exogenously applied BR binds to BRI 1. BAK 1 and BRI 1sequential transphosphorylation activates BRI 1 and increases BRI 1 Suppressor 1 (BSU1) activity. Dephosphorylated BZR1 and BES1 control BR-targeted genes, boosting the production of hormones and antioxidant enzymes (Takeuchi *et al.*, 1996) [64].

BRs and stress tolerance: an interwined mechanism

Brassinosteroids, plant steroidal hormones, are significant for plant physiological functions and stress adaptation (biotic and abiotic) (Li *et al.*, 2013) [37]. They control hormones and defense enzymes during stress responses, and their molecular and physiological mechanisms are discussed (Wei *et al.*, 2015) [71].

BRs role in Plant Drought stress

When plants don't get enough water, they experience drought stress, which slows down plant development and production. Numerous physiological functions, including photosynthesis, food intake, and hormone balancing, are disturbed (Farooq *et al.*, 2012) [19]. Stress cuts down the supplies required by plants for their growth and energy, making it harder for them to reproduce seeds (Todaka *et al.*, 2015) [66]. Abscisic acid accumulation and drought tolerance are related, and exogenous BR control may elevate ABA levels and lessen the adverse impacts of drought on plants (Wang *et al.*, 2019) [69, 70]. Research indicates that Brassinosteroids treatment can mitigate the long-lived effects of drought on the life of plant. For example, *Brassica juncea* plants show that after 60 days of drought stress, decreased growth and photosynthetic rate; 28-homobrassinolide post-drought treatment boosts photosynthetic rate and growth (Fariduddin *et al.*, 2009) [18]. Condition of stress in plants cause drawbacks in the above-ground growth due to interwined positive feedback loops. Stomata closure, a system that prevents water loss and controls CO_2 levels, inhibiting photosynthetic productivity and encouraging reactive oxygen species (ROS) formation. This impairs photosynthetic apparatus and causes lipids and proteins to undergo oxidation (Raza *et al.*, 2023) [54]. However, maintaining sufficient CO2 levels has resulted in the evolutionary decoupling of CO2 uptake and light reactions in CAM plants. Overheating of the leaf tissue, a drop in water mass flow, and a reduction in turgor and nutrient uptake all have an adverse effect on plant growth and photosynthetic activity. Overall, the physiological processes that are altered by drought stress result in low production and growth restrictions (Farooq *et al.*, 2009) [20]. Exogenous substances (BRs) can aid improve plant growth circumstances, such as EBr (24-Epibrassinolide), which has been proven to enhance the rate of survival of young plants during dry spell (Kagale *et al.*, 2007) [30]. Drought stresses can activate genes like superoxide dismutase (SOD), which transforms O_2-into H_2O_2 and triggers a defence response (Liu *et al.*, 2017) [43]. BRs can accelerate the growth of plants by cell wall potential, proline content, increasing photosynthetic efficiency, soluble and activity of SOD and lowering malondialdehyde (MDA) content and leaf electrical permeability (Zhang *et al.*, 2008) [81]. Drought-induced osmotic stress has the ability to also prevent plants from properly absorbing water (Yuan *et al.*, 2010) [79]. Cells influence plant physiological activities (Krishna, 2003) [33]. The combination of sodium nitroprusside and 24-epibrassinolide, a NO donor, and 24-epibrassinolide, effectively mitigated drought stress in potted kiwifruit seedlings, reducing plant biomass, while maintaining normal water metabolism (Xia *et al.*, 2022) [73].

Involvement of BRs on Salt stress

The usage of BRs hormones has been considered helpful in relieving salt pressure. BRs have a various type of protective and enhancing impacts on the number and size of plants (Khripach *et al.*, 2002). Reduced yield and progress happen by high salt reduced growth and yields are caused by the soil's high salt material, which also impacts plants ion balance and water uptake. It prevents photosynthesis and messes with the way cell work (Munns *et al.*, 2008) [46]. Plant growing on saline substrates faces three interrelated stresses: osmotic, salt-specific, and oxidative, which increase the degree of damage caused by salt (Figure1). These stresses include elevated pH of the root zone; unbalance nutrition, reduced root respiration in sodic soils, structural issues, and low oxygen content (Garcia *et al.*, 2009). Both annual and perennial plants become similarly affected by salinity, first by disturbing the balance of osmosis and then by producing the effects specific to salt. Annual crops may experience the amounts of salt in leaves can grow extremely dangerous in just a matter of days or weeks, while perennials typically show up months or year after being exposed to salt (Melgar *et al.*, 2008) [44]. Plants can either exhibit high susceptibility to both osmotic or salt specific stresses, or they can tolerate both equally, depending on the species. Plant's vegetative and sexually active stages are impacted by salinity; certain species show acceptance to salt during germination while other show an intolerance to it in their growth stages (Yamaguchi and Blumwald, 2005) [76]. BRs can be used as seed treatments, root treatments, or foliar sprays (Feng *et al.*, 2014) [21]. Proline, a necessary compatible solute, helps maintain balance of REDOX; ROS detoxifies, and protects structure of protein (Han *et al.*, 2014) [24]. BRs have been shown the activity of antoxidant enzymes increases and assemblage of proline (Hayat *et al.*, 2010) [26]. The significance of BR in stress tolerance, plants that had been silenced with SIBRI1, SIBAK and SIDWARF were subjected to salt stress. Plants struggling in salty soil given a special pre-treatment with BRs grew much better and healthier than plants just given plain water (Zhu *et al.*, 2016) [82]. Salt suppression germination of seed and seedling growth can be lessened by presoaking seeds in NaCl and BRs (Anuradha, 2001) [3].

Utilizing BRs could considerably minimize damage to chloroplast and nuclei brought on by salt through the rooting media. BRs have a crucial role in regulating the tolerance of salt in plants, but not always. EBL can enhance putrescine the process to tetraamine spermine (Spm) and triamine spermidine (Spd), considerably increasing salt stress generally reduces rate of seed germination, even some species experience a germination boost at low salt concentration when it falls below 150mM, the need as BRs diminish, the same EBL concentration may no longer be sufficient to trigger the desired plant growth response, resulting in hormonal stress intensity dependent biphasic effects (SLDB) (Liu *et al.*, 2020) [42].

Involvement of Brassinosteroids in temperature stress management

Temperature is the integral environmental part that influences the growth of plants, with low temperatures producing physiological dysfunction and alteration in the cell structure, physiological state, and biochemical metabolism of plants (Xi *et al.*, 2013) [72]. Exogenous epibrassinolide (EBR) application has been found to adjust their physiological, morphological, and biochemical traits to increase their resistance to low-temperature stress (Li *et al.*, 2016) [36]. They alter cellular metabolism, protein stability, and membrane fluidity, especially in both low and high temperatures, negatively impact the capacity of plants to grow and develop (Wahid *et al.*, 2007) [67]. Chilling and frost-induced freezing stress, along with other abiotic stresses, can significantly impact the normal metabolism of plants, particularly fruits that are tropical or subtropical (Table 2). These fruits have a low temperature sensitivity and easy spoil, affecting their quality (Fariduddin *et al.*, 2014). BR alleviates chilling stress and low temperatures by boosting chlorophyll levels preserving photosynthetic activity, triggering gene expression, elevating plant hormones, and turning on signal transduction pathways (Li *et al.*, 2015) [35]. When treated with BR seedling also increased tolerance to chilling stress, thereby genes which are responsible for cold stress are activate through signal transduction pathways, and defense system (Shu *et al.*, 2016) [57]. Low-temperature stress typically affects the cell structure, biochemical metabolism, physiology, and morphology of plants (Krishna *et al.*, 2017) [34]. Low temperature stress can reduce development of plants and inhibit photosynthesis (Sui, 2015). High temperature negatively impact plant metabolism, growth and development (Sun *et al.*, 2019) [91].

Plants have evolved extensive and multifaceted regulatory systems to safeguard themselves against biotic and abiotic dangers (Rehman *et al.*, 2016) [55]. Phytohormones (BR, ABA, SA, and GA) fundamentally influence signal transduction pathways, which also activate defence mechanisms. (Acharya *et al.*, 2009) [1]. BR has been shown to control the growth of plant and physiological responses to natural stressors like the stress of high temperatures; resulted in increased antioxidant enzyme activity and reduced glutathione, ascorbate and oxidized glutathione contents (Jin *et al.*, 2015) [29].

Brassinosteriod and heavy metal stress tolerance

Natural elements of the earth's crust that are heavy metals are absorbed and accumulated by plants (Bajguz, 2010) [6]. High concentrations of heavy metals can have harmful effects on the metabolic pathways of plants, inhibit vital molecules, obstruct the plant's nutrient and ion transport system, push essential ions out of cellular sites, and eliminate or upset the balance of antioxidant enzymes (Sharma *et al.*, 2014) [56]. Heavy metal-contaminated soils negatively impact crop yield and quality, and consumption of these products can lead to food chain contamination (Hasan *et al.*, 2019) [25]. High levels of dangerous metals in such soil can increase the risks associated with consuming these contaminated foods (Wang *et al.*, 2019) [69, 70].

Cadmium (Cd) is an example of a heavy metal which negatively impact plant's CO_2 ability for absorption and photosynthetic system (Rajewska *et al.*, 2016) [53]. Under Cd stress, application of Epibrassinolide (0.1µM) improves Fv/Fm, photosynthetic pigments content, and CO_2 assimilation ability, resulting in considerable increase in biomass accumulation (Ahammed *et al.*, 2013) [2]. The amount of Cd that is taken up by roots and transferrered to the leaves has decreased by exogenous EBR, while HBL treatment alleviates the decrease in PDII seedling development, photochemistry, and photochemistry caused by Cd (Singh and Prasad, 2017) [58]. In *Brassica juncea* heavy metals like nickel promotes the production of several BRs, including typhasterol, dolicholide, castasterone and epibrassinolide (Kanwar *et al.*, 2012) [31]. It has been established that Brassinosteroid protect plants against stress caused by heavy metals, improving tolerance to Cd stress, photosynthesis, and antioxidant activity. However, regarding metal stress, it is yet unknown if exogenous BR affects endogenous BR levels (Choudhary *et al.*, 2012) [11].

Table 1: Brassinosteroid application at different stages of plant growth and its effect on plants

Crop	Brassinosteroid concentration	Stage of application	Effects	Citation
Tomato	0.5mg/L	Pre-flowering	Enhanced fruit quality and yield, increases fruit set	Zhang *et al.,* (2014) [18] Yang *et al.*, (2011) [77]
Strawberry	0.3mg/L	Flowering	Improved fruit size and color, enhanced stress resistance	Ayub *et al.*, (2018) [5]
Mango	1mg	Pre-flowering	Increases total no. of flower per inflorescence, pollen viability, fruit set level.	Tepkaew *et al.*, (2022) [65]
Grape	0.4mg/L	Post-harvest	Reduced fruit decay, extended storage period	Symons *et al.*, (2006) [63]
Citrus	0.6mg/L	Pre-bloom	Enhanced flowering, increased fruit set	Rahim *et al.*, (2015) [52]

Table 2: Different types of Brassinosteroid effects on stress tolerance in fruit crops

S. No.	Brassinosteroid used	Fruit Crops	Type of Abiotic stress	Observed Effects	Citations
1.	28-Homobrassinolide	Grape	High Temperature	Enhanced heat stress tolerance	Parada *et al.*, 2022 [49]
2.		Mango	High salinity	Better water retention, increased leaf area	Patel *et al.*, 2024 [50]
3.	24-Epibrassinolide	Pomegranate	Chilling stress	High antioxidant enzymes activities along with maintained quality	Islam *et al.*,2022 [28]
4.		Banana	Chilling tolerance	Influence the accumulation pattern of protein	Li *et al.*, 2018 [39]

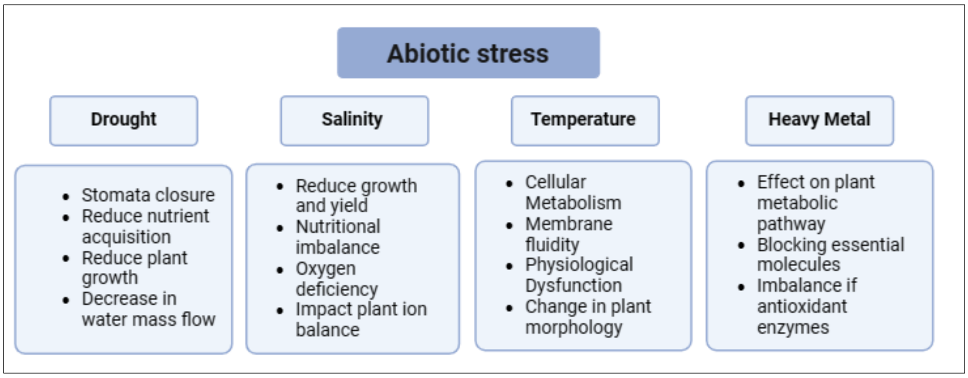

Fig 1: Different effects of abiotic stress on plant

Conclusion

In conclusion, a review of salinity, drought, heavy, and temperature stresses in plants demonstrates considerable negative effects on physiological systems and overall plant health. These stresses affect important systems like photosynthesis, water and nutrient intake, and hormonal balance, resulting in lower growth and output. However, current evidence suggests that brassinosteroids (BRs) plays a promising role in moderating theses consequences via a variety of pathways, including hormonal cross-talk, antioxidant defense enhancement, and epigenetic gene expression modification.

Future research should dig deep into how BRs help plants handle stresses and how they work with other plant hormone. Also, it's key to find the best ways to use BRs for the most gain and least cost, as different plants and places might need different plans. It's a good idea to study how different plants can use BRs to make farming stronger. And if we keep studying how BRs and plant deal with tough times, we could make crops that have lots of these good hormones in them. This could help crops grow better when the world gets harsher due to weather. In the end, using this BRs info in farming will need lots of teamwork. Plant experts, farm experts, and farmers will need to work as one to have farms that last and stay strong in the years to come.

Acknowledgment

We would like to express our gratitude towards Dr.Manish Bakshi, Dr. Shailesh Kumar Singh and host institute for their guidance and support.

Conflict of Interest

The author declares that there is no conflict of interest among the authors

References

1. Acharya BR, Assmann SM. Hormone interactions in stomatal function. Plant molecular biology. 2009;69:451-462.
2. Ahammed GJ, Choudhary SP, Chen S, Xia X, Shi K, Zhou Y, *et al.* Role of brassinosteroids in alleviation of phenanthrene–cadmium co-contamination-induced photosynthetic inhibition and oxidative stress in tomato. Journal of experimental botany. 2013;64(1):199-213.
3. Anuradha S, Seeta Ram Rao S. Effect of brassinosteroids on salinity stress induced inhibition of seed germination and seedling growth of rice (*Oryza sativa* L.). Plant Growth Regulation. 2001;33:151-153.

4. Anwar A, Zhang S, Lilong HE, Jianwei GAO. Understanding the physiological and molecular mechanism of salinity stress tolerance in plants. Notulae Botanicae Horti Agrobotanici Cluj-Napoca. 2022;50(4):12959-12959.
5. Ayub RA, Reis L, Lopes PZ, Bosetto L. Ethylene and brassinosteroid effect on strawberry ripening after field spray. Revista Brasileira de Fruticultura. 2018;40:e-544.
6. Bajguz A. An enhancing effect of exogenous brassinolide on the growth and antioxidant activity in *Chlorella vulgaris* cultures under heavy metals stress. Environmental and Experimental Botany. 2010;68(2):175-179.
7. Bajguz A, Hayat S. Effects of brassinosteroids on the plant responses to environmental stresses. Plant physiology and biochemistry. 2009;47(1):1-8.
8. Belkhadir Y, Chory J. Brassinosteroid signaling: a paradigm for steroid hormone signaling from the cell surface. Science. 2006;314(5804):1410-1411.
9. Choe S. Brassinosteroid biosynthesis and metabolism. In: Plant hormones: biosynthesis, signal transduction, action! Dordrecht: Springer Netherlands. 2004. p. 156-178.
10. Choe S, Fujioka S, Noguchi T, Takatsuto S, Yoshida S, Feldmann KA. Overexpression of DWARF4 in the brassinosteroid biosynthetic pathway results in increased vegetative growth and seed yield in *Arabidopsis*. The Plant Journal. 2001;26(6):573-582.
11. Choudhary SP, Yu JQ, Yamaguchi-Shinozaki K, Shinozaki K, Tran LSP. Benefits of brassinosteroid crosstalk. Trends in plant science. 2012;17(10):594-605.
12. Clouse SD. Molecular genetics of brassinosteroid action. Brassinosteroids: Steroidal plant hormones. 1999;163-190.
13. Clouse SD. Brassinosteroid signal transduction: from receptor kinase activation to transcriptional networks regulating plant development. The Plant Cell. 2011;23(4):1219-1230.
14. Clouse SD. A history of brassinosteroid research from 1970 through 2005: thirty-five years of phytochemistry, physiology, genes, and mutants. Journal of Plant Growth Regulation. 2015;34:828-844.
15. Cui J, Zeng G, Gao F, Jiang Y, Wang Y, Li D, Xi Z. Cloning, characterization and expression analysis of a brassinosteroids biosynthetic gene VvDET2 in Cabernet Sauvignon (*Vitis vinifera* L.). Plant Cell, Tissue and Organ Culture (PCTOC). 2023;154(1):43-54.
16. Divi UK, Krishna P. Brassinosteroid: a biotechnological target for enhancing crop yield and stress tolerance. New biotechnology. 2009;26(3-4):131-136.
17. Fahad S, Bajwa AA, Nazir U, Anjum SA, Sadia S, Nasim W, Ihsan MZ. Crop production under drought and heat stress: plant responses and management options. Frontiers in plant science. 2017;8:265598.
18. Fariduddin Q, Khanam S, Hasan SA, Ali B, Hayat S, Ahmad A. Effect of 28-homobrassinolide on the drought stress-induced changes in photosynthesis and antioxidant system of *Brassica juncea* L. Acta Physiologiae Plantarum. 2009;31:889-897.
19. Farooq M, Hussain M, Wahid A, Siddique KHM. Drought stress in plants: an overview. Plant responses to drought stress: From morphological to molecular features. 2012;1-33.
20. Farooq M, Wahid A, Lee DJ. Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. Acta Physiologiae Plantarum. 2009;31:937-945.
21. Feng ZT, Deng YQ, Fan H, Sun QJ, Sui N, Wang BS. Effects of NaCl stress on the growth and photosynthetic characteristics of *Ulmus pumila* L. seedlings in sand culture. Photosynthetica. 2014;52(2):313-320.
22. Fridman Y, Savaldi-Goldstein S. Brassinosteroids in growth control: how, when and where. Plant Science. 2013;209:24-31.
23. García-Sánchez F, Syvertsen JP. Substrate type and salinity affect growth allocation, tissue ion concentrations, and physiological responses of Carrizo citrange seedlings. HortScience. 2009;44(5):1432-1437.
24. Han G, Wang M, Yuan F, Sui N, Song J, Wang B. The CCCH zinc finger protein gene AtZFP1 improves salt resistance in *Arabidopsis thaliana*. Plant molecular biology. 2014;86:237-253.
25. Hasan MK, Ahammed GJ, Sun S, Li M, Yin H, Zhou J. Melatonin inhibits cadmium translocation and enhances plant tolerance by regulating sulfur uptake and assimilation in *Solanum lycopersicum* L. Journal of Agricultural and Food Chemistry. 2019;67(38):10563-10576.
26. Hayat S, Hasan SA, Yusuf M, Hayat Q, Ahmad A. Effect of 28-homobrassinolide on photosynthesis, fluorescence and antioxidant system in the presence or absence of salinity and temperature in *Vigna radiata*. Environmental and Experimental Botany. 2010;69(2):105-112.
27. Hussain A, Mun BG, Imran QM, Lee SU, Adamu TA, Shahid M, Yun BW. Nitric oxide mediated transcriptome profiling reveals activation of multiple regulatory pathways in *Arabidopsis thaliana*. Frontiers in plant science. 2016;7:198158.
28. Islam M, Ali S, Nawaz A, Naz S, Ejaz S, Shah AA, Razzaq K. Postharvest 24-epibrassinolide treatment alleviates pomegranate fruit chilling injury by regulating proline metabolism and antioxidant activities. Postharvest Biology and Technology. 2022;188:111906.
29. Jin SH, Li XQ, Wang GG, Zhu XT. Brassinosteroids alleviate high-temperature injury in *Ficus concinna* seedlings via maintaining higher antioxidant defence and glyoxalase systems. AoB plants. 2015;7:plv009.
30. Kagale S, Divi UK, Krochko JE, Keller WA, Krishna P. Brassinosteroid confers tolerance in *Arabidopsis thaliana* and *Brassica napus* to a range of abiotic stresses. Planta. 2007;225:353-364.
31. Kanwar MK, Bhardwaj R, Arora P, Chowdhary SP, Sharma P, Kumar S. Plant steroid hormones produced under Ni stress are involved in the regulation of metal uptake and oxidative stress in *Brassica juncea* L. Chemosphere. 2012;86(1):41-49.
32. Kim HJ, Ryu H, Hong SH, Woo HR, Lim PO, Lee IC, Hwang I. Cytokinin-mediated control of leaf longevity by AHK3 through phosphorylation of ARR2 in *Arabidopsis*. Proceedings of the National Academy of Sciences. 2006;103(3):814-819.
33. Krishna P. Brassinosteroid-mediated stress responses. Journal of Plant Growth Regulation. 2003;22:289-297.

34. Krishna P, Prasad BD, Rahman T. Brassinosteroid action in plant abiotic stress tolerance. Brassinosteroids: Methods and protocols. 2017;193-202.
35. Li J, Yang P, Gan Y, Yu J, Xie J. Brassinosteroid alleviates chilling-induced oxidative stress in pepper by enhancing antioxidation systems and maintenance of photosystem II. Acta Physiologiae Plantarum. 2015;37:1-11.
36. Li J, Yang P, Kang J, Gan Y, Yu J, Calderón-Urrea A, Xie J. Transcriptome analysis of pepper (*Capsicum annuum*) revealed a role of 24-epibrassinolide in response to chilling. Frontiers in plant science. 2016;7:1281.
37. Li L, Yu X, Thompson A, Guo M, Yoshida S, Asami T, Yin Y. *Arabidopsis* MYB30 is a direct target of BES1 and cooperates with BES1 to regulate brassinosteroid-induced gene expression. The Plant Journal. 2009;58(2):275-286.
38. Li P, Chen L, Zhou Y, Xia X, Shi K, Chen Z, *et al*. Brassinosteroids-induced systemic stress tolerance was associated with increased transcripts of several defence-related genes in the phloem in *Cucumis sativus*. PLoS One. 2013;8(6):e66582.
39. Li T, Yun Z, Wu Q, Zhang Z, Liu S, Shi X, Jiang Y. Proteomic profiling of 24-epibrassinolide-induced chilling tolerance in harvested banana fruit. Journal of proteomics. 2018;187:1-12.
40. Li X, Ahammed GJ, Li ZX. Brassinosteroids improve quality of summer tea (*Camellia sinensis* L.) by balancing biosynthesis of polyphenols and amino acids. Frontiers in Plant Science. 2016;7:215512.
41. Lima JV, Lobato AKS. Brassinosteroids improve photosystem II efficiency, gas exchange, antioxidant enzymes and growth of cowpea plants exposed to water deficit. Physiology and Molecular Biology of Plants. 2017;23:59-72.
42. Liu J, Yang R, Jian N, Wei L, Ye L, Wang R, Zheng Q. Putrescine metabolism modulates the biphasic effects of brassinosteroids on canola and *Arabidopsis* salt tolerance. Plant, Cell & Environment. 2020;43(6):1348-1359.
43. Liu S, Wang W, Li M, Wan S, Sui N. Antioxidants and unsaturated fatty acids are involved in salt tolerance in peanut. Acta Physiologiae Plantarum. 2017;39:1-10.
44. Melgar JC, Syvertsen JP, Martínez V, García-Sánchez F. Leaf gas exchange, water relations, nutrient content and growth in citrus and olive seedlings under salinity. Biologia Plantarum. 2008;52:385-390.
45. Mittler R. Abiotic stress, the field environment and stress combination. Trends in plant science. 2006;11(1):15-19.
46. Munns R, Tester M. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 2008;59:651-681.
47. Nakashita H, Yasuda M, Nitta T, Asami T, Fujioka S, Arai Y, Yoshida S. Brassinosteroid functions in a broad range of disease resistance in tobacco and rice. The Plant Journal. 2003;33(5):887-898.
48. Nolan TM, Vukašinović N, Liu D, Russinova E, Yin Y. Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. The Plant Cell. 2020;32(2):295-318.
49. Parada F, Oklestkova J, Arce-Johnson P. Characterization of endogenous levels of brassinosteroids and related genes in grapevines. International Journal of Molecular Sciences. 2022;23(3):1827.
50. Patel AM, Patel CR, Patel JJ. Enhancing Leaf Nutrient Levels in Polyembryonic Mango (*Mangifera indica* L.) Seedlings: The Impact of Saline Water Irrigation and 28-Homobrassinolide Spray. International Journal of Plant & Soil Science. 2024;36(5):281-292.
51. Praveena J, Dash S, Behera L, Rout GR. Brassinosteroids: A multifunctional phytohormone of plant development and stress responses. Curr. J. Appl. Sci. Technol. 2020;39:174-196.
52. Rahim OH, Abbas AJ. Foliar spraying effect of humic acid & Brassinosteroid on floral and vegetative growth of orange *Citrus sinensis* L. Mahli trees. 2015.
53. Rajewska I, Talarek M, Bajguz A. Brassinosteroids and response of plants to heavy metals action. Frontiers in plant science. 2016;7:197845.
54. Raza A, Mubarik MS, Sharif R, Habib M, Jabeen W, Zhang C, Varshney RK. Developing drought-smart, ready-to-grow future crops. The Plant Genome. 2023;16(1):e20279.
55. Rehman SU, Bilal M, Rana RM, Tahir MN, Shah MKN, Ayalew H, Yan G. Cell membrane stability and chlorophyll content variation in wheat (*Triticum aestivum*) genotypes under conditions of heat and drought. Crop and Pasture Science. 2016;67(7):712-718.
56. Sharma N, Hundal GS, Sharma I, Bhardwaj R. 28-Homobrassinolide alters protein content and activities of glutathione-s-transferase and polyphenol oxidase in *Raphanus sativus* L. plants under heavy metal stress. Toxicology international. 2014;21(1):44.
57. Shu S, Tang Y, Yuan Y, Sun J, Zhong M, Guo S. The role of 24-epibrassinolide in the regulation of photosynthetic characteristics and nitrogen metabolism of tomato seedlings under a combined low temperature and weak light stress. Plant physiology and biochemistry. 2016;107:344-353.
58. Singh S, Prasad SM. Effects of 28-homobrassinoloid on key physiological attributes of *Solanum lycopersicum* seedlings under cadmium stress: photosynthesis and nitrogen metabolism. Plant Growth Regulation. 2017;82:161-173.
59. Smith B, Shayanfar S, Walzem R, Alvarado CZ, Pillai SD. Preserving fresh fruit quality by low-dose electron beam processing for vending distribution channels. Radiation Physics and Chemistry. 2020;168:108540.
60. Sui N. Photoinhibition of *Suaeda salsa* to chilling stress is related to energy dissipation and water-water cycle. Photosynthetica. 2015;53(2):207-212.
61. Sun X, Lin L, Sui N. Regulation mechanism of microRNA in plant response to abiotic stress and breeding. Molecular Biology Reports. 2019;46:1447-1457.
62. Sun Y, Fan XY, Cao DM, Tang W, He K, Zhu JY, Wang ZY. Integration of brassinosteroid signal transduction with the transcription network for plant growth regulation in *Arabidopsis*. Developmental cell. 2010;19(5):765-777.
63. Symons GM, Davies C, Shavrukov Y, Dry IB, Reid JB, Thomas MR. Grapes on steroids. Brassinosteroids are involved in grape berry ripening. Plant physiology. 2006;140(1):150-158.
64. Takeuchi T, Ogasawara M, Konnai M, Takematsu T, Kamuro Y. Promotive effectiveness of brassinosteroid

(TS303) and jasmonoid (PDJ) on emergence and establishment of rice seedlings. Proc Jpn Soc Chem Regul Plants. 1996;31:100-101.
65. Tepkaew T, Khamsuk O, Chumpookam J, Sonjaroon W, Jutamanee K. Exogenous brassinosteroids regulate mango fruit set through inflorescence development and pollen fertility. Horticultural Science and Technology. 2022;40(5):481-495.
66. Todaka D, Shinozaki K, Yamaguchi-Shinozaki K. Recent advances in the dissection of drought-stress regulatory networks and strategies for development of drought-tolerant transgenic rice plants. Frontiers in plant science. 2015;6:121920.
67. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environmental and Experimental Botany. 2007;61(3):199-223.
68. Wang H, Wang H, Shao H, Tang X. Recent advances in utilizing transcription factors to improve plant abiotic stress tolerance by transgenic technology. Frontiers in plant science. 2016;7:178807.
69. Wang J, Zhu H, Zhang C, Wang H, Yang Z, Liu Z. Puerarin protects rat liver and kidney against cadmium-induced oxidative stress. The Indian Journal of Animal Sciences. 2019;89(9):927-931.
70. Wang YT, Chen ZY, Jiang Y, Duan BB, Xi ZM. Involvement of ABA and antioxidant system in brassinosteroid-induced water stress tolerance of grapevine (*Vitis vinifera* L.). Scientia horticulturae. 2019;256:108596.
71. Wei LJ, Deng XG, Zhu T, Zheng T, Li PX, Wu JQ, Lin HH. Ethylene is involved in brassinosteroids induced alternative respiratory pathway in cucumber (*Cucumis sativus* L.) seedlings response to abiotic stress. Frontiers in plant science. 2015;6:982.
72. Xi Z, Wang Z, Fang Y, Hu Z, Hu Y, Deng M, Zhang Z. Effects of 24-epibrassinolide on antioxidation defense and osmoregulation systems of young grapevines (*V. vinifera* L.) under chilling stress. Plant Growth Regulation. 2013;71:57-65.
73. Xia H, Liu X, Wang Y, Lin Z, Deng H, Wang J, Liang D. 24-Epibrassinolide and nitric oxide combined to improve the drought tolerance in kiwifruit seedlings by proline pathway and nitrogen metabolism. Scientia Horticulturae. 2022;297:110929.
74. Xia XJ, Fang PP, Guo X, Qian XJ, Zhou J, Shi K, Yu JQ. Brassinosteroid-mediated apoplastic H2O2-glutaredoxin 12/14 cascade regulates antioxidant capacity in response to chilling in tomato. Plant, Cell & Environment. 2018;41(5):1052-1064.
75. Xia XJ, Zhang Y, Wu JX, Wang JT, Zhou YH, Shi K, Yu JQ. Brassinosteroids promote metabolism of pesticides in cucumber. Journal of Agricultural and Food Chemistry. 2009;57(18):8406-8413.
76. Yamaguchi T, Blumwald E. Developing salt-tolerant crop plants: challenges and opportunities. Trends in Plant Science. 2005;10(12):615-620.
77. Yang CJ, Zhang C, Lu YN, Jin JQ, Wang XL. The mechanisms of brassinosteroids' action: from signal transduction to plant development. Molecular plant. 2011;4(4):588-600.
78. Ye H, Liu S, Tang B, Chen J, Xie Z, Nolan TM, Yin Y. RD26 mediates crosstalk between drought and brassinosteroid signalling pathways. Nature Communications. 2017;8(1):14573.
79. Yuan GF, Jia CG, Li Z, Sun B, Zhang LP, Liu N, Wang QM. Effect of brassinosteroids on drought resistance and abscisic acid concentration in tomato under water stress. Scientia Horticulturae. 2010;126(2):103-108.
80. Zhang C, Bai MY, Chong K. Brassinosteroid-mediated regulation of agronomic traits in rice. Plant cell reports. 2014;33:683-696.
81. Zhang M, Zhai Z, Tian X, Duan L, Li Z. Brassinolide alleviated the adverse effect of water deficits on photosynthesis and the antioxidant of soybean (*Glycine max* L.). Plant growth regulation. 2008;56:257-264.
82. Zhu T, Deng X, Zhou X, Zhu L, Zou L, Li P, *et al*. Ethylene and hydrogen peroxide are involved in brassinosteroid-induced salt tolerance in tomato. Scientific reports. 2016;6(1):35392.