https://doi.org/10.17221/137/2025-PSE

An overview and current progress of gibberellic acid-mediated abiotic stress alleviation in plants

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Citation: Mahamud M.A., Imran S., Paul N.C., Rabbi R.H.M., Jahan N., Sarker P., Hoque M.N., Sumi M.J., Asaduzzaman M., Ur Rehman S., Brestic M., Bárek V., Skalicky M., Hossain A., Rhaman M.S. (2025): An overview and current progress of gibberellic acid-mediated abiotic stress alleviation in plants. Plant Soil Environ., 71: 453–479.

Abstract: Abiotic stressors are the main barriers to successful crop production in this era. The balance of redox and metabolic activities in plants is negatively impacted by abiotic stresses, which ultimately limit the plants' capacity to grow and develop. The phytohormones are tiny molecules that control how plants grow and develop, as well as how they react to alterations in their environment. Phytohormone, gibberellic acid (GA) has been proven in a number of

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Supported by the VEGA project No. 047SPU-4/2025, Introduction of practical teaching into the subject Green Infrastructure.

recent research to increase plants' ability to withstand abiotic stress. By regulating numerous physio-biochemical and molecular processes, GA plays a crucial part in reducing the perturbations caused by abiotic stresses in plants. Recent findings have shown that GA controls the activity of antioxidant enzymes, stress-responsive genes, photosynthetic machinery, and reduced oxidative damage. Besides, GA has been involved in cross-talk with other phytohormones to regulate abiotic stress in plants. This review summarises the current research on the application of GA and discusses how GA might support crop growth and production in adverse conditions. The interaction of GA with other phytohormones, potential mechanisms for reducing abiotic stress in plants, the disadvantages of employing GA, and its promise for the future are also covered in this review.

Keywords: plant growth regulator; salinity; drought; climate change; chlorophyll content

The demand for food increases every day with the growth of the global population; consequently, the agriculture sector is under pressure to augment food production and meet the surging requirements (Rhaman et al. 2021). Globally, abiotic stresses are non-living environmental factors that can negatively affect plant growth, development, and productivity. Abiotic stressors like drought, heat, salinity, and low temperatures can severely reduce agricultural yields by disrupting plant water balance, nutrient uptake, and growth, leading to lower crop productivity and compromised plant health (Baghour et al. 2022, Rhaman et al. 2022). To address this challenge, researchers have been developing and implementing strategies that help crops withstand abiotic stress factors.

The application of plant growth regulators (PGRs), for instance, auxins, cytokinins, gibberellins, abscisic acid, ethylene, and salicylic acid to stressed plants is a widely used approach to mitigate stress and increase yield (Wani et al. 2016). PGRs are involved in the physiological, biochemical, and molecular mechanisms plants use to adapt to saline conditions, enhancing growth and yield by mitigating the negative effects of salinity. Gibberellic acid, often known as GA, is a PGR that occurs naturally in plants and is essential for different processes in relation to the growth and development of plants (Wheeldon and Bennett 2021). GA is produced in plants through a complicated biochemical process involving multiple enzymes and precursors. It is a key player in the regulation of plant development. It regulates important processes such as vegetative growth, flowering induction, and seed germination (Castro-Camba et al. 2022).

Currently, abiotic stresses, such as salinity, drought, heavy metals, extreme temperatures, nutrient deficiencies, etc., are a major concern for agricultural production (Gull et al. 2019). Abiotic stressors have a significant impact on plant growth progressions. Numerous studies have shown that GA is a widely used phytohormone to mitigate the negative effects of abiotic stressors and that GA regulates a number of physiological and molecular processes, including photosynthesis, osmolyte accumulation, mineral uptake, reactive oxygen species (ROS) signal transduction, and antioxidant defense, to increase plant tolerance to these stressors (Wang et al. 2019, Hasanuzzaman et al. 2020, Khan et al. 2020a). For instance, GA can improve photosynthetic efficiency by stimulating chlorophyll synthesis and increasing photosynthetic enzyme activity in *Camellia oleifera* Abel (Wen et al. 2018). Salinity stress is a widespread problem in many parts of the world that can significantly affect plant growth and yield (Hoque et al. 2022). Studies have demonstrated that exogenous application of GA increases the uptake of essential nutrients such as K^+ and reduces the uptake of ions such as Na^+ (Shahzad et al. 2021). Similarly, drought stress affects plant growth and survival in a number of ways, including decreased yields, changed plant distribution, stomatal closure, altered root growth, reprogrammed metabolic pathways, and more physiological changes (Farooq et al. 2024). Goldani et al. (2021) reported that GA increases water use efficiency by promoting stomatal closure and reducing transpiration rates in Persian petunia. Moreover, GA also stimulates the synthesis of osmolytes, for instance, soluble sugars, proline, and glycine betaine, which help plants maintain water balance and protect cell membranes from injury brought on by drought stress in several plants (Hadif 2019, Jan et al. 2019, Khan et al. 2020a). It is well-reported that exposure to heavy metals such as Pb and Cd reduced different plants' photosynthesis, plant growth, and yield (Bashir et al. 2019, Hasan et al. 2020). GA can mitigate heavy metal contamination in crops by improving morpho-physiological processes and enzymatic functions

(Uzal and Yasar 2017). Extreme temperatures (high or low) worldwide can lead to reduced photosynthesis, cell survival, and water transport in different plants (Parthasarathi et al. 2022, Devi et al. 2023). GA3 did not significantly enhance thermotolerance but improved test weight and cell expansion gene expression under heat stress. It also helps increase antioxidant enzyme activity and photosynthesis rates (Nagar et al. 2021). For instance, the application of GA increases the heat tolerance of tomato by enhancing the activity of antioxidant enzymes like catalase (CAT) and superoxide dismutase (SOD) (Guo et al. 2022).

The preceding conversation makes it clear that abiotic stress is a grave danger to global food production. The application of GA to crops is a potential remedy that can improve agricultural yields by promoting plant growth and development as well as increasing their tolerance to abiotic stresses. Although GA, a plant growth regulator, has been shown to enhance plant growth and production, its mechanisms for controlling abiotic stress are not entirely understood. Therefore, this review emphasises the biosynthesis of GA in plants and its potential role in mitigating abiotic stress as well as its role in mediating stress in plants. This review also highlights the limitations of applying GAs and future promises for plant production.

A schematic presentation shows the role of gibberellic acid for enhancing plant tolerance to abiotic stress (Figure 1). Abiotic stress conditions negatively impact plant growth and productivity by inducing oxidative stress, disrupting physiological processes, and altering biochemical pathways. These effects include reduced seed germination, plant growth, chlorophyll content, nutrient uptake, and overall crop yield, along with increased reactive oxygen species (ROS) production, membrane leakage, and stress-related injuries. GA application mitigates these adverse effects by modulating a range of morpho-physiological and biochemical responses. Specifically, GA enhances seed germination, seedling vigour, plant height, shoot and root growth, chlorophyll biosynthesis, and reproductive parameters. It also

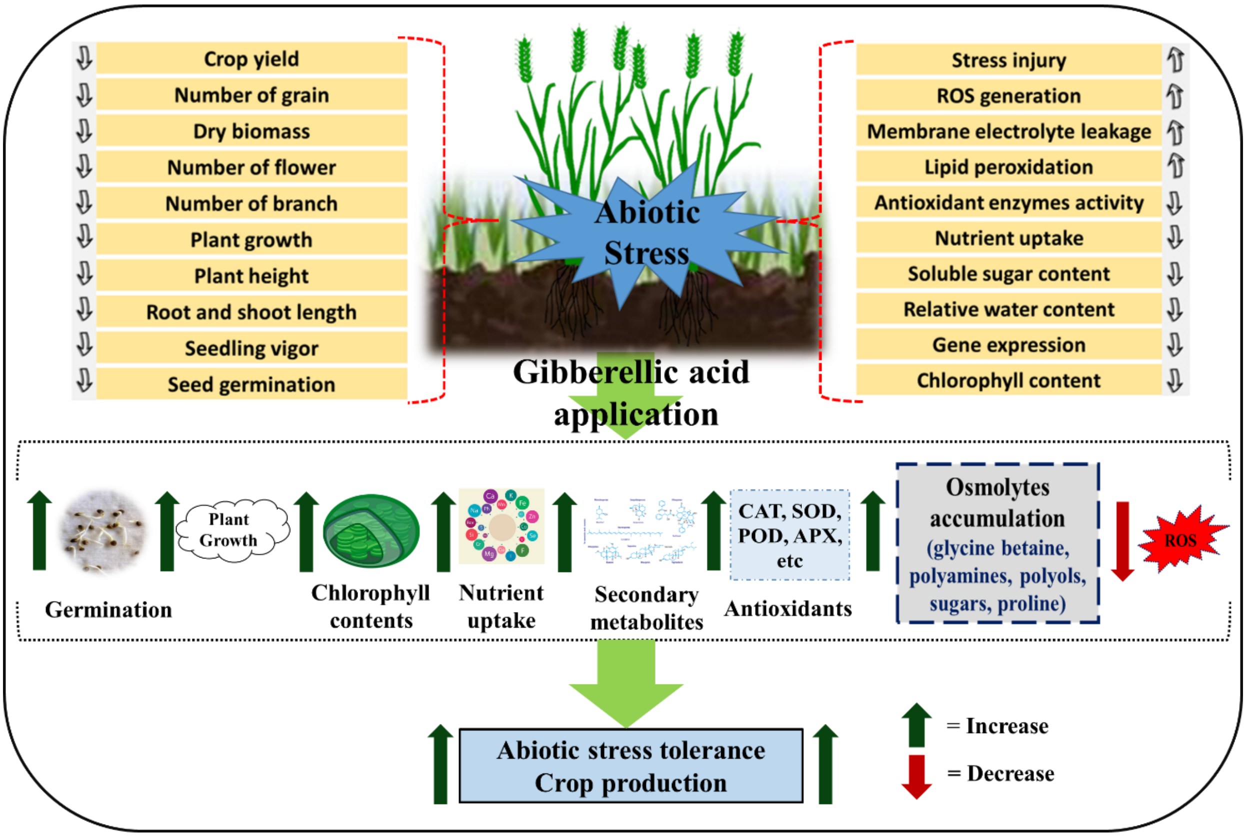

Figure 1. Schematic presentation of the role of gibberellic acid (GA) application in enhancing plant tolerance to abiotic stress. CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; APX – ascorbate peroxidase. Source: Authors' own prepared, unpublished material

improves nutrient uptake, boosts the accumulation of osmolytes (e.g., glycine betaine, proline, polyols), and stimulates antioxidant defence systems (e.g., CAT, SOD, POD, APX) to scavenge ROS. Furthermore, GA upregulates secondary metabolite production and stress-responsive gene expression, improving water retention and reducing lipid peroxidation.

BIOSYNTHESIS OF GIBBERELLIN IN PLANTS

Gibberellin is a tetracyclic diterpenoid compound that plays crucial roles in regulating various aspects of growth and development, including seed germination, stem elongation, leaf expansion, flowering, and fruit development. The biosynthesis of gibberellins in plants is a complex, multi-step process involving several key enzymes and occurs primarily in plastids, the endoplasmic reticulum (ER), and the cytosol (Shah et al. 2023). Despite considerable efforts to understand the production and transport of GA, the proper location of bioactive GA in plants or tissues, to exert its effects, remains to be verified. The presence of GA in actively growing tissues such as shoot apex, tender leaves, and buds was discovered using a quantitative analysis and bioassay of dwarf plants (Gupta and Chakrabarty 2013). The biosynthesis of GAs begins with the formation of geranylgeranyl diphosphate (GGPP). This 20-carbon molecule serves as the common precursor for all diterpenoids, including GAs, which is then converted into ent-kaurene (ent-K) *via* two enzymatic steps. Subsequently, a sequence of hydroxylation and oxidation events converts ent-kaurene into bioactive gibberellins. Ent-copalyl diphosphate synthase and GA 20-oxidase are important enzymes in this process (Hedden 2020). GA is usually produced in higher plants from the methylerythritol phosphate (MEP) pathway. Production of the bioavailable GA occurs *via* this pathway from GGDP (Hedden and Thomas 2012). Eight steps of the MEP pathway have been identified namely; (*i*) conversion of GGDP to ent-copalyldiphosphate (ent-CPD) by ent-copalyldiphosphate synthase; (*ii*) formation of ent-kaurene from ent-CDP by ent-kaurene synthase; (*iii*) formation of ent-kaurenol from ent-kaurene by ent-kaurene oxidase (KO); (*iv*) formation of ent-kaurenal by KO from ent-kaurenol; (*v*) formation of ent-kaurenoic acid by KO from ent-kaurenal; (*vi*) ent-kaurene acid oxidase (KAO) then convert ent-kaurenoic acid to ent-7a-hydroxykaurenoic acid; (*vii*) formation GA12-aldehyde from ent-7a-hydroxykaurenoic acid by KAO, and (*viii*) formation of GA12 from GA12-aldehyde by KAO (Hedden 2020). Finally, the biosynthesis continues with the conversion of GA12 into various forms of GAs, including GA9, GA20, and eventually GA1, which is one of the most bioactive forms of gibberellin. These transformations are catalysed by enzymes such as GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox), which are responsible for the production of bioactive GAs like GA1 and GA3 (Achard et al. 2009). On the other hand, the presence of GA in xylem and phloem fluid has been reported, which shows that GA is carried over long distances. Grafting tests have supported the transfer of the active GA and its intermediates (Binenbaum et al. 2018). The inconsistent results of many tests could not accurately determine the location of bioactive GA production. Most bioactive GA is located in the actively growing parts of plants (Hedden and Thomas 2012). Again, in the growing regions of rice, the presence of *OsGA20ox1*, *OsGA20ox2*, *OsGA3ox1*, *OsGA3ox2*, and SLENDER RICE1 (*SLR1*) genes indicates active synthesis of bioactive gibberellins (GAs), with Galpha and *SLR1* involved in GA signaling (Kaneko et al. 2003).

Gibberellin synthesis is mainly seen in immature tissues and developing seeds in plants, where it is essential for growth and development (Sona et al. 2023). This involves the mevalonate (MVA) pathway (to produce GA precursor, ent-kaurenoic acid), where acetyl-CoA is converted to mevalonic acid (Kildegaard et al. 2021). Subsequently, mevalonic acid is transformed into isopentenyl pyrophosphate (IPP), which serves as the essential building block for the synthesis of several isoprenoids, such as sterols, hormones like gibberellins, and other essential terpenoids (Bajguz and Piotrowska-Niczyporuk 2023). The schematic diagram for the biosynthesis of gibberellic acid in plants is presented in Figure 2.

THE GIBBERELLIN-MEDIATED ABIOTIC STRESS TOLERANCE IN PLANTS

Salinity stress

During the different stages of growth, plants experience a variety of environmental factors, one of which is salinity, which interferes with numerous physiological, biochemical, and molecular processes (Raza et al. 2022). Many excellent articles have recently been published on the negative consequences of salt stress by different scientists (Ali et al. 2021, Baghour et al. 2022, Iqbal et al. 2022). Salinity stress

https://doi.org/10.17221/137/2025-PSE

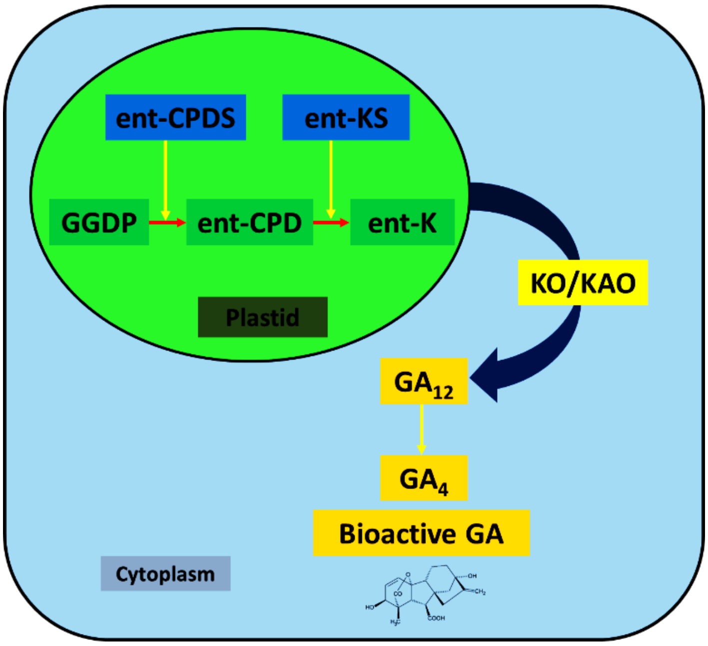

Figure 2. Biosynthesis of gibberellic acid in plants. See text for details and references. GA – gibberellin; GA12 – gibberellin A_{12}; GA4 – gibberellin A_4; ent-CPDS – ent-copalyl diphosphate synthase; ent-KS – ent-kaurene synthase; GGDP – geranyl geranyl diphosphate; ent-CPD – ent-copalyl diphosphate; ent-K – ent-kaurene; KO – ent-kaurene oxidase; KAO – ent-kaurene acid oxidase. Source: Authors' own prepared, unpublished material

limits plant growth and productivity by disrupting physiological processes like photosynthesis (Abou Seeda et al. 2022). It can suppress nucleic acids by causing damage to DNA and RNA, affecting their stability and function (Gumi and Rabi'u Bello 2024).

It is well-reported that GAs applications are good substances for minimising the adverse effects of salinity stress (Table 1). Exogenous GA increased morphological and physiological traits, including root number, plant height, capsule number, seed weight, relative water content (RWC), biomass accumulation, chlorophyll content, and fixed oil percentage under saline conditions (Rashed et al. 2017, Vetrano et al. 2020).

In the case of salinity, morphological characteristics were improved through GA application in papaya (Álvarez-Méndez et al. 2022) and maize (Rauf et al. 2022). Leaf area, number of fruits, levels of bioactive gibberellins, jasmonic acid, abscisic acid, salicylic acid, lycopene content, ascorbic acid, and proline content with proper growth of the plants were obtained from GA-treated tomato (Prajapati et al. 2018) plants under salinity. Gurmani et al. (2022) illustrated that net assimilation rate and antioxidant enzyme activity were improved with reduced Na^+ transportation in GA-treated pea plants. GA suppressed the overproduction of ROS and enhanced glyoxalase I and glyoxalase II enzyme activity under salinity in tomato (Siddiqui et al. 2020). Exogenous GA also promotes anthocyanin osmoprotectants (proline and soluble protein) and glycine betaine with superior growth parameters in wheat and okra treated with salt stress (Wang et al. 2019, Iqbal et al. 2022). GA efficiently protects seedlings from salt damage by boosting morphology, CAT, and POD activities in sorghum (Ali et al. 2021). Pal et al. (2016) observed that GA increased salicylic acid (SA) biosynthesis and played an essential part in plant defence mechanisms by improving plant growth and salt tolerance through increased levels of stress phytohormones under saline conditions. It was indicated that major genes of rice involved in lipid biosynthesis, like monogalactosyldiacylglycerol synthase (*OsMGD*), were significantly upregulated by GA application along with increased chlorophyll content and the expression of the activity of the *LeNHX4* antiporter under saline conditions (Liu et al. 2018, Baghour et al. 2022). Due to the fact that seed priming with a PGR is thought to be significant in the activation of α-amylase, an enzyme required for germination, seed performances like vigour index, protein contents, and seedling growth were enhanced (Krishna and Mahadevaswamy 2019, Islam et al. 2022). Despite its beneficial benefits on plants under salt stress, GA has several drawbacks. Under salt stress, various plant species and even cultivars within a species may react differently to GA priming. Exogenous GA treatment under salinity was observed to increase N, Ca, P, and reduce K, Cu, Mn, Fe, and Zn contents in maize (Dinler et al. 2021).

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Table 1. Salinity stress management in crops through exogenous gibberellin (GA) application

Plant species	Stress level (NaCl)	Treatments and methods of application	Effects and outcomes	Reference
Rice (*Oryza sativa* L.)	5.84 g/L	exogenous application of GA: 3.46 mg/L	Increased chlorophyll content; upregulated monogalactosyldiacylglycerol synthase (*OsMGD*); improved the harmful effects of salinity.	Liu et al. (2018)
	0.1 and 0.2 g/L	Soaking of seed in GA: 0.1. 0.2. and 0.3 g/L	Increased GP and vigour index; increased chlorophyll *a*, *b* and protein contents; improved salt tolerance.	Krishna and Mahadevaswamy (2019)
Sweet leaf (*Stevia rebaudiana* Bertoni)	4.68 g/L	foliar spray of G1: 0.05 and 0.1 g/L	Enhanced aerial growth; improved root mass; increased enzyme activities (CAT, SOD, POD); decreased lipid peroxidation; reduced membrane damage; lowered hydrogen peroxide levels.	Janah et al. (2024)
Lettuce (*Lactuca sativa* L.) and Rocket (*Eruca sativa* L.)	0.58 and 1.17 g/L	exogenous GA: 0.35 mg/L	Enhanced biomass accumulation, leaf expansion, leaf number, stomatal conductance, water use efficiency and nitrogen use efficiency.	Vetrano et al. (2020)
Black cumin (*Nigella sativa* L.)	0.99, 1.98, 2.97, and 3.96 g/L	GA spraying: 0.1 g/L	Increased plant height, dry weight, number of capsules, roots per plant, root weights, seeds per plant, 1 000 seeds weight, chlorophyll content, fixed oil percentage and RWC.	Rashed et al. (2017)
Tomato (*Lycopersicon esculentum* L.)	2.99, 5.84, 8.84, and 11.69 g/L	GA: 0.1 g/L	Increased chlorophyll concentration, lycopene, ascorbic acid, proline, shoot length, leaf area, fresh weight, dry weight, and number of fruits.	Prajapati et al. (2018)
	7.31 g/L	exogenous GA3: 10 mg/L	Increased the expression or the activity of *LeNHX4* antiporter; improved salinity tolerance, and increased fruit yield and quality.	Baghour et al. (2022)
	5.84 g/L	exogenous application on seedlings with GA: 0.49 mg/L	Enhanced activity of glyoxalase I and glyoxalase II enzymes and redox homeostasis, chlorophyll, proline and glycine betaine. Reduced ROS and methylglyoxal (MG).	Siddiqui et al. (2020)
Maize (*Zea mays* L.), pea (*Pisum sativum* L.) and grass pea (*Lathyrus sativus* L.)	2.34, 3.51, 4.68, and 7.01 g/L	priming seeds with GA: 0.2 g/L	Improved GP, shoot and root length; reduced MGT; ameliorated salinity stress.	Tsegay and Andargie (2018)

Continuous Table 1. Salinity stress management in crops through exogenous gibberellin (GA) application

Plant species	Stress level (NaCl)	Treatments and methods of application	Effects and outcomes	Reference
Sweet sorghum (*Sorghum bicolor* L.)	5.84, 8.77, 11.69, and 14.61 g/L	GA in nutrient solution: 5.9 mg/L	Increased total chlorophyll contents, carotenoids, water soluble carbohydrates, fresh weight, dry weight, stem length, root length, and water content; reduce the effect of salinity.	Forghani et al. (2018)
	5.84 and 11.69 g/L	GA application: 50, 100, and 150 mg/L	Increased morphology, RWC, chlorophyll content, soluble proteins, CAT, POD; GA efficiently protect seedlings from salt damage.	Ali et al. (2021)
Okra (*Abelmoschus esculentus* L.)	5.84 g/L	Foliar application of GA: 35 mg/L	Increased antioxidant activities, chlorophyll, carotenoids, K, Ca, Mg and Fe in leaves and roots, as well as levels of osmo-protectants (proline and soluble protein); decreased EL, H_2O_2 and lipid peroxidation; alleviate salinity stress.	Wang et al. (2019)
Papaya (*Carica papaya* L.)	5.84 g/L	exogenous application of GA: 35 mg/L	Increased stem height, thickness, biomass; reduced stomatal opening, increased papaya seedlings‘ adaptation against salt stress.	Álvarez-Méndez et al. (2022)
Pea (*Pisum sativum* L.)	2.92 g/L	exogenous application of GA: 35 mg/L	Enhanced chlorophyll content, antioxidant enzyme activity, plant biomass, soluble protein content and reduced Na^+ transport ameliorate the effect of salinity.	Gurmani et al. (2022)
Maize (*Zea mays* L.)	0.88 g/L	GA seed priming: 0.35, 0.7, 1.05, 1.4, and 1.75 g/L	Increased growth, chlorophyll content, root-shoot biomass, and alleviated salt stress.	Rauf et al. (2022)
	0.36 g/L	foliar applications of GA3: 0.05 and 0.1 g/L combined with Mepiquat chloride	Enhanced growth, biochemical parameters, nutritional content, boosted yield, K^+ ion concentration, oil percentage, chlorophyll content, soluble protein and proline levels; reduced oxidative stress and sodium ion accumulation.	Sona et al. (2023)
	3.51 and 7.01 g/L	hydro-priming and foliar spray of GA3: 0.1 g/L	Enhanced root and shoot length; increased fresh and dry weights, chlorophyll content, antioxidant enzyme activities, total soluble protein, and potassium ion concentration; reduced oxidative stress, hydrogen peroxide content, and sodium ion concentration.	Shahzad et al. (2021)

https://doi.org/10.17221/137/2025-PSE

Continuous Table 1. Salinity stress management in crops through exogenous gibberellin (GA) application

Plant species	Stress level (NaCl)	Treatments and methods of application	Effects and outcomes	Reference
Wheat (*Triticum aestivum* L.)	8.77 g/L	exogenous GA: 0.1 and 0.15 g/L	Increased anthocyanin and glycine betaine, various growth parameters; reduce the effect of salinity.	Iqbal et al. (2022)
	0, 2.92, 4.67, and 7.01 g/L	seed priming and exogenous application of GA: 35 mg/L	Increased GP of seed and seedling growth parameters; mitigates the effect of salinity.	Islam et al. (2022)
Summer squash (*Cucurbita pepo* L.)	2.92 g/L	seed priming with GA: 1.5 mmol and JA: 1.7 mg/L	Reduced Na^+ and Cl^- concentrations; reduced TBARS and chlorophyll *a*/*b* ratio; increased SOD, CAT, and APX activities; increased K^+ and Mg^{2+} quantities; increased K^+/Na^+ ratio; increased RNA and DNA quantities; increased chlorophyll *b;* increased carotenoid concentration; enhanced growth of salinised plants.	Al-harthi et al. (2021)

DNA – deoxyribonucleic acid; RNA – ribonucleic acid; GA – gibberellic acid; GP – germination percentage; RWC – relative water content; ROS – reactive oxygen species; GA1 – gibberellin A1; GA4 – gibberellin A4; JA – jasmonic acid; ABA – abscisic acid; SA – salicylic acid; H_2O_2 – hydrogen peroxide; MGT – mean germination time; CAT – catalase; POD – peroxidase; SOD – superoxide dismutase; EL – electrolyte leakage; TBARS – thiobarbituric acid reactive substances

DROUGHT STRESS

Drought is a detrimental stressor that inhibits plant growth and development. Drought stress occurs when the ability of a plant to get water to the roots is compromised or when transpiration rates increase significantly (Ahluwalia et al. 2021). Drought stress significantly impacts plant biomass, quality, and energy, arising from temperature variations, light intensity, and low rainfall. It adversely affects plant morphology, physiology, biochemistry, and photosynthesis. Plants adopt complex adaptations such as altering transpiration, leaf rolling, and osmotic regulation to cope with water scarcity. Strategies for alleviating drought stress include breeding, omics technologies, seed priming, and the use of growth hormones and protective compounds (Seleiman et al. 2021). The phytohormone GA has been reported (Table 2) to control uptake of nutrients, water balance, stomatal control, photosynthesis and the formation of ROS under stress conditions, and several reports found that GA can confer stress caused by drought in plants (Jan et al. 2019, Goldani et al. 2021, Miri et al. 2021).

Miri et al. (2021) found increased RWC, chlorophyll content, reduced ionic leakage, and improved yield from GA-treated cowpea plants under drought stress. Exogenous application of GA enhances osmoprotectant activity, antioxidants, GA level, indole-3-acetic acid and cytokinins content with decreased malondialdehyde (MDA) and abscisic acid levels in faba bean under drought stress (Rady et al. 2021). Similarly, GA supplementation increased chlorophyll content, assimilate deposition in grain, and reduced panicle sterility of rice under drought stress conditions (Khan et al. 2016). Exogenous application of GA in maize also increased leaf area index (LAI), leaf area duration (LAD), crop growth rate (CGR), net assimilation rate (NAR) and total dry matter (TDM) under drought conditions, resulting in better crop yield (Sarwar et al. 2017). Similarly, Jan et al. (2019) found that supplementation of GA in sunflower increased SOD, CAT and ascorbate peroxidase (APX) activities under drought stress. Similarly, increased antioxidant enzymatic activities such as ascorbate, APX, CAT, reduced/oxidised glutathione (GSH/GSSG) ratio, reduced monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase

Table 2. Drought stress management in crops through exogenous gibberellin (GA) application

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Persian petunia (*Petunia* sp.)	irrigation with 50% and 25% of the field capacity	GA was sprayed: 0.1 and 0.2 g/L	Enhanced stomatal conductance, RWC and number of flower; adverse effects of water deficit was alleviated.	Goldani et al. (2021)
Sunflower (*Helianthus annuus* L.)	aqueous solutions of polyethylene glycol (PEG 6000): 10, 30 and 60 g/L	foliar sprays of GA: 0.05 g/L	Increased proline, RWC, total phenolic content and maximise SOD, CAT, APX contents; improve water stress tolerance.	Jan et al. (2019)
Rapeseed (*Brassica napus* L.)	drought stress by 35–40% of field capacity	seed priming GA: 0.5 g/L	Enhanced antioxidant enzymes activity, proline, seed yield, reduced ROS; alleviate drought stress.	Khan et al. (2020a)
Cowpea (*Vigna unguiculata* L.)	plots were irrigated at 75, 60, and 45% of field capacity	GA: 0, 0.06 and 0.12 g/L	Increased RWC, carotenoids, total chlorophyll contents and yield; decrease ionic leakage; drought stress tolerance was increased.	Miri et al. (2021)
Faba bean (*Vicia faba* L.)	drought stress: 60% field capacity	foliar application of GA: 20 mg/L	Increased osmoprotectants, antioxidant capacity, IAA, and cytokinins; decreased MDA and ABA; improved drought tolerance.	Rady et al. (2021)
Sesame (*Sesamum indicum* L.)	drought periods of 24, 48, 72 and 96 h after wilting point	seed priming with GA: 0.05, 0.1, 0.15, 0.2, and 0.25 g/L	Increased chlorophyll content, root-leaves ratio, glucose content, 1 000-grin weight, biological yield and total production; alleviate drought stress.	Hadif (2019)
Wheat (*Triticum aestivum* L.)	drought stress levels of –0.35, –0.70, and –1.40 MPa using (PEG 6000)	seed priming with GA: 0.1 and 0.2 g/L	Increased germination rate, MGT, GI, seedling vigour, radicle and plumule growth; mitigate drought stress.	Salih and Tuncturk (2020)
	drought stress: 60% and 40% field capacity	spraying of GA3: 0.1 and 0.2 g/L	Improved growth, crop growth rate; increased RWC; reduced MDA, H_2O_2 content; enhanced CAT, SOD, and APX activity; increased proline content; improved yield.	Lamlom et al. (2025)
	drought stress by using 120 g/L polyethylene glycol (PEG)	seedling spray with 5 mL of GA (0.1 g/L)	Enhanced CAT and APX activities; decreased MDA, H_2O_2, free proline (Pro), MG, GSH/GSSG, MDHAR and DHAR activities; improved drought tolerance.	Moumita et al. (2019)

Continuous Table 2. Drought stress management in crops through exogenous gibberellin (GA) application

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Maize (*Zea mays* L.)	no irrigation at critical growth stages	GA: 0.15 g/L	Increased LAI, LAD, CGR, NAR, total dry matter, crop yield; alleviated drought stress.	Sarwar et al. (2017)
	drought levels of 0, 0.15, 0.50, 1.05, and 1.75 MPa by using NaCl solution	seeds were soaked in GA (0, 0.2 g/L)	Increased GP, MGT, GI, RWC, SVI, root length, and shoot length.	Gnawali and Subedi (2021)
Potato (*Solanum tuberosum* L.)	irrigation: 80, 65, 50 and 35% of the field capacity	GA sprayed on leaves: 0.2 g/L	Increased LAI, water saturation deficit, transpiration rate and number of tubers; reduced the effect of water stress.	Pourasadollahi et al. (2019)
Rice (*Oryza sativa* L.)	water stress up to temporary wilting	50 mL of GA: 3.5 mg/L	Increased chlorophyll content, greater grain assimilate deposition, growth and yield attributes; reduced panicle sterility.	Khan et al. (2016)
Chia (*Salvia hispanica* L.)	seed germination at 0.1, –0.2, –0.3 and –0.4 MPa osmotic potential, using PEG 6000	pre-soaking the seeds with GA: 0.14 g/L	Increased GP, germination speed index, shoot and root lengths, total dry mass, proline, soluble sugars, free amino acids; ameliorate osmotic stress.	Costa et al. (2021)

RWC – relative water content; SOD – superoxide dismutase; CAT – catalase; APX – ascorbate peroxidase; ROS – reactive oxygen species; IAA – indole-3-acetic acid; MDA – malondialdehyde; ABA – abscisic acid; MGT – mean germination time; GI – germination index; MG – methylglyoxal; MDHAR – monodehydroascorbate reductase; DHAR – dehydroascorbate reductase; LAI – leaf area index; LAD – leaf area duration; CGR – crop growth rate; NAR – net assimilation rate; GP – germination percentage; SVI – seedling vigour index; H_2O_2 – hydrogen peroxide; GSH – reduced glutathione; GSSG – glutathione disulfide

(DHAR) were found by the application of GA under PEG-induced drought in wheat (Moumita et al. 2019). For instance, Costa et al. (2021) reported that Chia seed primed with GA improved shoot length and root length, total dry matter content, proline contents, total soluble sugars, and total free amino acids under drought stress. GA Primed seeds also showed increased germination rate, germination index (GI), seedling vigour, radicle and plumule growth, fresh weight and dry weight of wheat under drought stress conditions (Salih and Tuncturk 2020). Seed priming with GA in rapeseed (Khan et al. 2020a) or sesame (Hadif 2019) successfully alleviated drought stress by scavenging ROS and accumulation of proline contents. Different plant species successfully reduce drought stress when GA is used exogenously and through seed priming. However, there are a few limitations when applying GA while there is water scarcity. Coelho et al. (2018) observed that there was no variation in plant height and node count in two *Kalanchoë* species under different GA concentrations applied externally. Once more, in *Lisianthus* cultivars, exogenous gibberellic acid administration decreases the antioxidant capacity of leaves and increases Tip-burn (calcium deficiency disorder) effects (Kuronuma et al. 2024).

TEMPERATURE STRESS

Temperature is a crucial factor in plant growth, succession and metabolism. However, it becomes detrimental when it goes above or below the threshold level, which is a stress factor for the plants. High temperature stress can create a water deficit condition in plant tissues, which ultimately leads to membrane disruption, reduction in transpiration rate, failure of protein synthesis, decrease in enzymes, ion uptake and ion transport, which in turn hinders plant development (Yang et al. 2021). Extended exposure can cause irreversible tissue damage, serious agricultural output decreases, and in extreme situations, plant death. Moreover, efforts to improve crops are hampered by cold stress (Bhat et al. 2022). Numerous reports showed that the application of GA can reduce temperature stress in plants (Table 3). In a study by Zhu et al. (2016), it was observed that, in storage conditions, GA solution significantly reduced chilling injury and preserved the quality of tomato.

Some studies also reported that the application of GAs can have both positive and negative impacts on plants, particularly in relation to high and low temperature stress. GAs promotes accelerated growth of plant which therefore, can lead to weak and more vulnerable overstimulation of plants, impaired protective mechanisms, reduced antioxidants, destabilisation of cellular membranes, lower photosynthetic efficiency etc. under both low and high temperature conditions (Aftab and Hakeem 2021). Also, some imbalanced interactions between GAs and stress hormones were observed. GAs has antagonistic effects on abscisic acid (ABA), meaning that GA application may reduce the plant's ability to synthesise ABA during temperature stress. Moreover, during high-temperature conditions crops that are in flowering or fruiting stages, application of GA can cause damage to reproductive organs (Shu et al. 2018).

HEAVY METAL STRESS

Extended mining operations have resulted in heavy metal pollution, which poses a recurring risk to agricultural land across the globe which ultimately threatening food safety and crop productivity (Allevato et al. 2019, Vardhan et al. 2019, Saleem et al. 2020). It is well-known that GA is a diterpenoid compound, which plays key roles in reducing the effects of heavy metal contamination of various crops by facilitating proper physiology, morphology, and enzymatic activities (Table 4) (Ji et al. 2015, Uzal and Yasar 2017).

It has been found that the application of GA decreased the harmful impact of heavy metals in many crops like rice (Wang et al. 2017), jute (Saleem et al. 2020), and mungbean (Hasan et al. 2020b). Hasan et al. (2020a) observed that supplementation of GA increased leaf area, dry mass, photosynthesis and GSH contents of Cd-stressed mungbean. Additionally, Chen et al. (2021) noted that spraying of GA to lettuce increased the root length, total root tip number and surface area, ultimately resulting in an increased biomass under Cd stress. They also found that GA reduced root-to-shoot translocation of Cd by downregulating the expression of iron transport protein (IRT1), natural-resistance-associated-macrophage protein1 (Nramp1), heavy metal/Cd transporting ATPase (HMA2 and HMA4), which eventually alleviated the toxic impact of Cd-exposed soil. Bashir et al. (2019) conducted a study on Cd-stressed soybeans. They observed that the foliar application of GA reduces the toxicity of Cd by controlling the expression of many stress genes related to Cd transport, including *NRAMP* and *IRT*. Another study by Javed et al. (2021) showed that foliar spray of GA on old pea under Cu stress enhanced above-ground biomass accumulation, chlorophyll content, photosynthetic rate, and transpiration rate. They also found that GA decreased MDA, H_2O_2 contents and EL. Similarly, Cu stress in spinach was alleviated by the supplementation of GA. GA alleviated the toxic effect of Cu by reducing oxidative damage, antioxidant enzyme activities and the proline concentration (Gong et al. 2021). The Cu-induced toxicity and oxidative damage in jute (*Corchorus capsularis* L.) were relieved by GA application (Saleem et al. 2020). They reported that GA reduced oxidative damage and toxicity by increasing photosynthetic pigments, protein, and monosaccharide contents. It has been documented that GA adversely regulates the flow of Fe from roots to shoots, hence modulating Fe homeostasis in rice plants (Wang et al. 2017). Besides these roles of GA in heavy metal stress mitigation, GA has been shown to enhance the phytoextraction of heavy metals like Cu (Javed et al. 2021) by promoting plant growth and increasing biomass, which allows for greater uptake and accumulation of these metals in different plant species.

OTHER STRESSES

In addition to the above-discussed stresses, plants also faced several others stress like excessive waterlogging, toxicity of boron (B) and fluoride (F), and toxicity of nanoparticles (NPs), which are increasing day by day and significantly affecting plant growth progressions and yield. Several earlier observations reported that GA application successfully mitigated

https://doi.org/10.17221/137/2025-PSE

Table 3. Role of gibberellin (GA) in temperature stress mitigation in crops

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Persian Cyclamen (*Cyclamen persicum* L.)	temperatures between 23 °C and 36 °C and 60% relative humidity	GA3 solutions: 0, 30, 75, and 90 mg/L	Increased germination rate, reduced mean germination time, improved plant height, and enhanced heat stress tolerance.	Cornea-Cipcigan et al. (2022)
Tomato (*Solanum lycopersicum* L.)	storage at 4 ± 1 °C for 14, 21, and 28 days plus 3 days at 20 ± 1 °C	dipping the fruit into a 0.17 g/L GA solution	Upregulate *GA2ox1*, SA; downregulate *GA20ox1* and *GAox1* genes, chilling injury index during long-term cold storage; induce fruit tolerance to chilling stress.	Zhu et al. (2016)
	grown at 25 °C (day)/20 °C (night), then gradually increased to 45 °C/35 °C	foliar application of GA3: 25, 50, 75, and 100 mg/L	Increased biomass, photosynthetic performance, nutrient content, antioxidant activity, reduced oxidative stress and mitigation of heat stress.	Guo et al. (2022)
Wheat (*Triticum aestivum* L.)	15 days at 40 °C for 6 h each day	foliar spray of GA3: 5 mg/L mmol + sodium nitroprusside: 100 µmol for 10 DAS	Improved plant height, fresh and dry weight, photosynthetic rate, stomatal conductance, and Rubisco activity under heat stress.	Zhang et al. (2023)
Toon sprout (*Toona sinensis* Juss.)	freezing at 4 ± 1 °C with relative humidity 80% to 90% for 5 days	soaking in GA: 0.1 g/L solution for 20 min	Prevented anthocyanin breakdown; increased total flavonoid, Vit C, CAT, SOD; maintained reducing sugar, soluble sugar and proline; reduced MDA, H_2O_2, POD, browning and decay index; mitigated the effect of temperature shock.	Hu et al. (2018)

HSTI – heat stress tolerance index; SA – salicylic acid; EL – electrolyte leakage; MDA – malondialdehyde; CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; H_2O_2 – hydrogen peroxide; Vit C – vitamin C

waterlogging, toxicity of B, F, and NPs (Table 5). It has been reported that GA application mitigated ZnO and CeO_2-NPs toxicity in wheat and increased plant growth, chlorophyll contents, nutrients, and antioxidant activities, which finally increased grain yield (Iftikhar et al. 2019, 2020). Moreover, GA seed treatment of rice improved the fluoride tolerance by increasing plant growth, RWC, IAA, photosynthetic pigments and decreasing EL, H_2O_2, and MDA (Banerjee and Roychoudhury 2020). In contrast, foliar application of GA increased tomato plant growth, chlorophyll contents, antioxidant activities and reduced B toxicity (Kaya et al. 2020). It has been reported that GA application under waterlogging conditions in mung bean plants increased growth, chlorophyll content and grain yield (Islam et al. 2021).

https://doi.org/10.17221/137/2025-PSE

Table 4. Role of gibberellin (GA) in heavy metal stress mitigation

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Pea (*Pisum sativum* L.)	Cu: 2 000 mg/kg of soil	exogenous application GA: 0, 10, 50, and 100 mg/L	Increased biomass accumulation, chlorophyll content, photosynthetic rate, transpiration rate, CO_2 concentration, Cu content and SOD activity; decreased MDA, H_2O_2 contents and EL; boosted phytoextraction of Cu.	Javed et al. (2021)
Wheat (*Triticum aestivum* L.)	Cd: 6 mg/kg with drought stress	exogenous application of GA3-BC: 0%, 0.6% (GA3-BC), 0.9% (GA3-BC)	Improved shoot length, root length, seedling length, and shoot fresh weight; enhanced chlorophyll *a*, chlorophyll *b*, and total chlorophyll; decreased electrolyte leakage; regulation of antioxidants (lipid peroxidation, SOD, CAT, APX, GR, GPX, GST, and DPPH).	Anwar et al. (2023)
	Cr: 0, 300, and 600 mg/kg of soil	spraying of GA3: 5 mg/L	Improved growth; enhanced chlorophyll *a*, *b*, and total chlorophyll; decreased prolein content; reduced SOD, CAT, and APX; increased N, P, K uptake; decreased Cr content in leaves and roots.	Sarwar et al. (2025)
Maize (*Zea mays* L.)	Cd: 0, 6, and 12 mg/kg of soil; Pb: 0 and 400 mg/kg of soil; and drought stress	10 mg/L GA3 + 0.75% BC and rhizobacteria (RB); 10 mg/L GA3 + 0.5% BC and RB	Enhanced germination rates, shoot and root lengths, shoot and root protein levels, phenolic content in shoots and roots, and chlorophyll content in shoots and roots.	Anwar et al. (2024a)
	Cd: 8 and 16 mg/kg of soil	soil treatment with GA3: 10 mg/L mmol + 0.75% biochar	Enhanced germination, increased root and shoot length, improved leaf, root, and shoot protein levels, higher leaf, root, and shoot phenolics, elevated chlorophyll content and improved tolerance to cadmium stress.	Anwar et al. (2024b)
Tomato (*Solanum lycopersicum* L.)	seedlings treatment with 100% acid mine water: 400 mL	seedlings were sprayed with 1 mL of 70 mg/L GA3 solution	Taller tomato plants significantly reduced the accumulation of heavy metals (Cd, Cr, Cu, Ni, and Zn) in the seedlings' roots, stems, and leaves.	Ogugua et al. (2022)
Spinach (*Spinacia oleracea* L.)	Cu: 3–5 mg/kg of soil	exogenous application of GA: 0, 3, 5, 10, 20, 40, 60, and 80 mg/L	Increased photosynthetic parameters and biomass; reduced oxidative damage, antioxidant enzyme activities and the proline concentration; increased Cu tolerance.	Gong et al. (2021)

https://doi.org/10.17221/137/2025-PSE

Continuous Table 4. Role of gibberellin (GA) in heavy metal stress mitigation

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Mungbean (*Vigna radiata* L.)	Cd: 200 mg/kg of soil	Application of GA: 3.5 mg/L	Improved LAI, plant dry mass, photosynthesis, p-SUE, GSH, dry mass, ATP-S activity, SAT activity, Cys content; mitigate Cd toxicity.	Hasan et al. (2020b)
Jute (*Corchorus capsularis* L.)	Cu: 2 221 mg/kg of soil	soil application of GA: 10, 50, and 100 mg/L	Increased plant growth, biomass, photosynthetic pigments, gaseous exchange attributes, and ROS alleviated Cu toxicity.	Saleem et al. (2020)
Rice (*Oryza sativa* L.)	Fe: 100 mmol	exogenous application GA: 0.035 mg/L	Increased shoot length, chlorophyll concentration, Fe-deficiency-induced leaf chlorosis, reduced Fe transport from roots to shoots, and translocation within the shoot.	Wang et al. (2017)
	seedling treatment with Cd: 50 µmol	exogenous application of GA: 0.35 mg/L and kinetin: 2 µmol	Decrease in Na^+ accumulation; increase K^+ accumulation in both root and shoot; improve NO_3^- and PO_4^{3-} accumulation; reduce Cd accumulation in root and shoot; improve relative water content in shoots.	Akter and Samad (2024)
	UV-B stress	spraying of GA: 17.5 and 35 mg/L	Increased chlorophyll *a*, *b*, total chlorophyll, and carotenoid content; increased proline, phenolic, and total flavonoid content; reduced momilactone A and B; increased superoxide radical scavenging (DPPH) activity.	Rayee et al. (2025)
Lettuce (*Lactuca sativa* L.)	Cd: 20 µmol	spraying of GA: 0, 0.35, 1.75, and 3.5 mg/L	Increased the biomass, down-regulated expression of *IRT1*, *Nramp1*, *HMA2* and *HMA4*; reduced Cd root-to-shoot translocation, which alleviated the toxic effects of Cd.	Chen et al. (2021)
Soybean (*Glycine max* L.)	Cd: 1.784 and 4.46 µmol	exogenous application of GA	Regulating the expression of stress genes, such as NRAMP and IRT, which are related to Cd^{2+} transport, mitigated Cd^{2+} toxicity.	Bashir et al. (2019)
Fenugreek (*Trigonella corniculata*)	Pb: 0 and 500 mg/kg of soil	GA3: 0.25 and 0.5 mg/L combined with quantum dot biochar	Improved growth; enhanced chlorophyll *a*, *b*, and total chlorophyll; decreased MDA and EL; reduced SOD, POD and increased CAT, APX; boosted anthocyanin content.	Shahzad et al. (2024)
Barley (*Hordeum vulgare* L.)	Pb: 30, 60, and 90 mmol	foliar spray of GA3	Improved growth; increased chlorophyll *a*, *b*, total chlorophyll, and carotenoids; increased RWC; reduced MDA, H_2O_2; enhanced CAT, APX activity; increased ascorbic acid and prolein content; reduced Pb uptake and translocation.	Ullah et al. (2025)

CO_2 – carbon dioxide; H_2O_2 – hydrogen peroxide; SOD – superoxide dismutase; MDA – malondialdehyde; EL – electrolyte leakage; CAT – catalase; APX – ascorbate peroxidase; GR – glutathione reductase; GPX – glutathione peroxidase; GST – glutathione S-transferase; DPPH – 2,2-diphenyl-1-picrylhydrazyl; LAI – leaf area index; p-SUE – photosynthetic S-use efficiency; GSH – reduced glutathione; SAT – serine acetyl transferase; ATP-S – ATP-sulfurylase; ROS – reactive oxygen species; POD – peroxidase; RWC – relative water content

https://doi.org/10.17221/137/2025-PSE

Table 5. Role of gibberellin (GA) in other stress mitigation

Plant species	Stress level	Treatments and methods of application	Effects and outcomes	Reference
Wheat (*Triticum aestivum* L.)	nanoparticle (ZnO-NPs): 0, 300, 600, 900, 1 200 mg/kg of soil	foliar spray of GA: 0, 0.1, and 0.2 g/L	Increased plant height, spike length, root and grain dry biomass; chlorophyll *a*, *b*, carotenoid, P, K, Fe and Mn content; SOD, POD, CAT, APX activities; reduced and MDA EL, H_2O_2; mitigated ZnO-NPs induced toxicity.	Iftikhar et al. (2019)
	nanoparticle (CeO_2-NPs): 100, 200, 300, 400, and 600 mg/kg of soil	foliar spray of GA: 0, 0.1, and 0.2 g/L	Increased plant height, spike length, root and grain dry biomass; chlorophyll *a*, chlorophyll *b*, carotenoid, P, K, Fe and Mn content; SOD, POD, CAT, APX activities; reduced and MDA EL, H_2O_2; alleviates CeO_2-NPs induced toxicity.	Iftikhar et al. (2020)
Weeds		spraying of GA3: 0, 0.1, and 0.2 g/L	Improved growth; reduced weeds‘ dry weight; improved competition against weeds; improved N, K, and protein content of wheat grain; improved yield.	Hamoda et al. (2025)
Indica rice (*Oryza sativa* cv. IR-64)	fluoride (NaF): 25 mg/L	seeds soaked in 0.15 g/L of GA	Increased shoot length, root length, fresh weight, dry weight, RWC; decreased EL, H_2O_2, MDA content concentration; increased IAA, chlorophyll, xanthophyll, anthocyanin, flavonoid, total phenolic content (TPC); 2,2-diphenyl-1-picrylhydrazyl (DPPH), CAT, APX and guaiacol peroxidase (GPOX); improved fluoride tolerance.	Banerjee and Roychoudhury (2020)
Tomato (*Solanum lycopersicum* L.)	boron toxicity: 0.12 g/L	foliar spray of GA: 0.1 g/L	Increased total dry weight, shoot and root dry weight; increased chlorophyll *a* and chlorophyll *b*, and photosystem II efficiency (F_v/F_m); (RWC, leaf water potential (ΨI) and proline content, SOD, POD, CAT; reduced EL, H_2O_2, and MDA concentration; induced tolerance to B toxicity.	Kaya et al. (2020)
Mung bean (*Vigna radiata* L. Wilczek)	waterlogging	foliar spray of GA: 0.1 and 0.15 g/L	Increased plant height, number of leaves, leaf chlorophyll index, shoot growth, total dry matter, number of pods, grain yield, straw yield and harvest index; alleviated the detrimental effects of waterlogging in mung bean plants.	Islam et al. (2021)

H_2O_2 – hydrogen peroxide; SOD – superoxide dismutase; MDA – malondialdehyde; EL – electrolyte leakage; CAT – catalase; APX – ascorbate peroxidase; ROS – reactive oxygen species; POD – peroxidase; RWC – relative water content; IAA – indol 3-acitic acid

MECHANISMS REGULATING GA-INDUCED ABIOTIC STRESS TOLERANCE

Plants are subjected to a wide range of abiotic stressors, including salinity, drought, high and low temperatures, heavy metals, etc., during their developmental stages of life (Jogawat 2019). GAs are plant growth hormones that trigger different physiological responses in plants under stress conditions and increase the rate of source-sink metabolism *via* influencing photosynthesis. According to Vetrano et al. (2020) and Guo et al. (2022), applying GA considerably enhanced stomatal conductance as well as the rate of photosynthesis in comparison to salt stress alone.

Exogenous application of GA has been demonstrated to stimulate osmolyte production in sunflower (Jan et al. 2019), okra (Wang et al. 2019), rapeseed (Khan et al. 2020a), Persian petunia (Goldani et al. 2021) and fava bean (Rady et al. 2021) plants under stress conditions. When sunflower plants are subjected to water stress, they accumulate more proline when treated with GA, as a fundamental technique for improving cell osmotic potential and greater water use efficiency (Jan et al. 2019). On the other hand, Khan et al. (2020a) observed that priming with GA increased the activity of hydrolytic enzymes and proline content in the cells, ultimately resulting in increased relative water content and water uptake in rapeseed under drought conditions. Similarly, increased concentration of osmoprotectants due to exogenous GA application contributes to the maintenance of cell turgor by means of osmotic adjustment (Rady et al. 2021). Meanwhile, under NaCl-stressed conditions, the concentration of osmo-protectants such as proline and soluble protein increased when okra seedlings were treated with GA (Wang et al. 2019).

However, GA has been reported to effectively scavenge ROS generation, including H_2O_2, that has the ability to damage biomolecules such as DNA, protein, and lipids, and reduce MDA concentration in wheat plants under nanoparticle stress (Iftikhar et al. 2020). Similarly, foliar spraying of GA enhanced the enzymatic activities of antioxidant enzymes such as SOD, POD, CAT, and APX, and reduced the ROS production and MDA content under abiotic stress (Iftikhar et al. 2019, Javed et al. 2021). While seed priming with GA reduced accumulation of H_2O_2 and the stress marker MDA, which experienced lowered oxidative stress in rice seedlings under fluoride stress (Banerjee and Roychoudhury 2020). Consequently, the addition of GA raised the endogenous H_2S content, which enhanced the efficiency of photosystem II (F_v/F_m) and chlorophyll synthesis by reducing H_2O_2 accumulation and increasing antioxidant activity in the tomato plants under boron toxicity (Kaya et al. 2020).

GAs play a vital role in mitigating abiotic stresses by modulating various molecular and physiological pathways in plants. The primary mechanism involves the GA-mediated regulation of DELLA proteins, which act as growth repressors. Under abiotic stress conditions, the biosynthesis of GA is typically reduced, leading to the accumulation of DELLA proteins that limit growth and help plants conserve energy. However, exogenous GA application can mitigate these effects by promoting the degradation of DELLA proteins *via* the ubiquitin-proteasome pathway, thereby restoring growth (Hedden and Thomas 2012). GA antagonises ABA, a hormone that typically promotes stress tolerance by inducing stomatal closure to conserve water during drought (Shu et al. 2018). This interplay ensures that plants can maintain a balance between growth and survival under adverse conditions. Moreover, GA has been shown to upregulate the expression of aquaporins, which improve water uptake and transport, thus alleviating drought stress (Patel and Mishra 2021). GA also modulates ion homeostasis by enhancing the activity of Na^+/H^+ antiporters in the plasma membrane and tonoplast, which helps plants cope with salinity stress by reducing sodium ion toxicity (Ahmad et al. 2021). Furthermore, GA influences the expression of heat shock proteins (HSPs) that protect cellular proteins from denaturation under high-temperature stress (Khan et al. 2020b). Additionally, GA-induced modulation of photosynthetic machinery helps maintain carbon fixation efficiency during stress conditions, thereby sustaining energy production (Gururani et al. 2015). In summary, the multifaceted role of GA in stress mitigation involves a combination of hormonal crosstalk, antioxidant defence, ion homeostasis, protein protection, and water regulation, all of which contribute to enhancing plant resilience under abiotic stress conditions. However, environmental factors and stress could also influence GA to act differently; for that matter, there is a scope to explore all the aforesaid effects of GA in the future.

CROSSTALK OF GA AND OTHER PHYTOHORMONES IN ABIOTIC STRESS TOLERANCE

Agricultural lands have trouble with multiple abiotic stressors that negatively affect plants' growth, devel-

https://doi.org/10.17221/137/2025-PSE

opment, and survival. Several articles described that phytohormones such as GA, ethylene (ET), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), auxins, cytokinin's etc. could be a key metabolic engineering target for creating crop plants resistant to abiotic stress. In this section, crosstalk between GA and other phytohormones has been summarised (Figure 3).

Ethylene

Ethylene (ET) is engaged in a variety of physiological processes, including seed germination, growth and development of plants, flower senescence (particularly ripening of fruit), leaf and petal abscission, and acts as a crucial stress response regulator (Khan et al. 2024). As ET manages plants' growth and development process, ET promotes the production of apical hooks while inhibiting root elongation by obstructing the DELLA repressor protein (Achard et al. 2003). Moreover, ET can lower the GA level and improve the accumulation of the DELLA repressor protein. On occasion, it was slowed down in *Arabidopsis thaliana* L. plants for flowering by repressing floral meristem-identity genes, *viz*., LEAFY (*LFY*) and SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS 1 (*SOC1*) (Achard et al. 2007). The expression of the C-repeat/

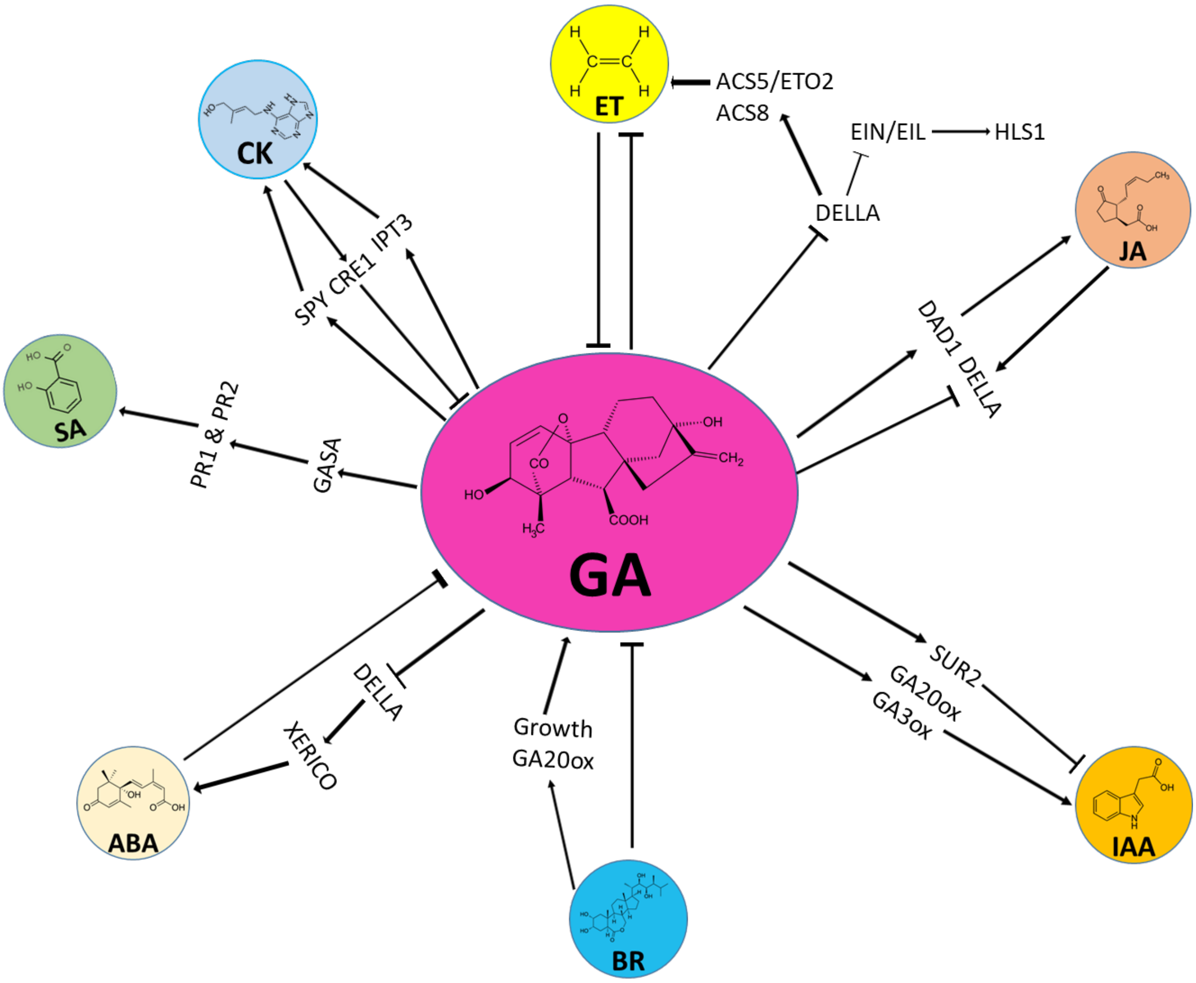

Figure 3. Crosstalk of gibberellic acid (GA) and other phytohormones in abiotic stress tolerance. Arrows indicate activation, and blunt-end lines indicate repression or inhibition. See text for details and references. ABA – abscisic acid; BR – brassinosteroids; CK – cytokinin; ET – ethylene; IAA – indole-acetic acid; JA – jasmonic acid; SA – salicylic acid; ACS5/ETO2 – ACC synthase 5/ETO2; ACS8 – ACC synthase 8; CRE1 – cytokinin response 1; EIN/EIL – ethylene insensitive 3/EIN3-like 1; HLS1 – Hookless 1; DAD1 – defective anther dehiscence 1; DELLA – Della proteins; SUR2 – superroot 2; GA3ox – GA3-oxidase; GA20ox – GA20-oxidase; IPT3 – Isopentenyl transferase 3; SPY – spindly; GASA – gibberellic acid-stimulated *Arabidopsis*; PR1 and PR2 – pathogenesis-related protein 1 and 2; XERICO – XERICO gene. Source: Authors' own prepared, unpublished material

drought-responsive element binding factor (*CBF1*/*DREB1b*) gene (a member of APETALA2/ETHYLENE RESPONSE FACTOR family transcription factor) progress tolerance to low temperatures, but it also inhibits growth by allowing DELLA to build up (Achard et al. 2008a). In *Oryza sativa* L., ET response factors such as SNORKEL1 and SNORKEL2 are allowed for adaptation in deep water. The output of these genes initiates internode expansion by GA signaling (Hattori et al. 2009). Interaction between DELLA protein and DNA-binding domain of the ETHYLENE INSENSITIVE 3/EIN3-LIKE 1 (EIN3/EIL1) and impedes the expression of the HOOKLESS 1 (*HLS1*) gene. GA collaborated with ET by expressing the *HLS1* gene in *Arabidopsis thaliana* L. to induce the development of the apical hook (An et al. 2012).

Abscisic acid

Abscisic acid (ABA) regulates gene expression to maintain root growth, which maximises water intake and modulates long-term growth responses (Xie et al. 2021). GA and ABA often showed an antagonistic behaviour in the regulation method. Furthermore, the balance of antagonistic interaction between these two hormones controls the seed germination process (Gayatri et al. 2021). When seeds are germinated, the aleurone cells receive GAs released by the embryo, which induce some transcription genes that encode some enzymes. To provide nutrients for the embryo's growth, the endosperm releases an enzyme that is digested along with certain carbohydrates and proteins. The alpha amylase enzyme was suppressed by ABA; thus, ABA identified a GA- induced Myb-like protein (GAMyb) that binds to the GA response element box of the a-amylase promoter. As a result of salt stress, ROS production increases, activating the ABA signaling, and ultimately increasing the ABA levels (Achard et al. 2008b). Another article reported that a DELLA mutant gene allowed the growth inhibition brought on by ABA, suggesting the significance of DELLA protein in ABA-related stress responses that take place in the environment (Lorrai et al. 2018). In addition to ABA, GA has an antagonistic relationship with melatonin. *MdGA2ox7* alleviated cold and salt stress damage in *Arabidopsis* and apple in concert with melatonin (Yan et al. 2024).

Auxins

Auxins, particularly indole acetic acid (IAA), regulate a variety of plant growth and development processes from the embryonic stage to senescence. According to studies conducted on *Arabidopsis*, rice, and pea, IAA increases GA production by triggering *GA3ox* and *GA20ox*, and deactivating *GA2ox* (Yin et al. 2007, O'Neill et al. 2010). Auxin-related genes are modulated by GAs, but the outcomes of these reactions rely on a specific set of auxin response factors (ARFs) generated by GA. While ARF6 and ARF8 promote the elongation of hypocotyl (Oh et al. 2014), GA3 negatively regulates ARF10/16/17 during grape parthenocarpy *via* the action of the microRNAs miR160a/b/c (Zhang et al. 2019). As GA therapy restores the wild-type phenotype, and signaling-deficient mutants in *Arabidopsis* exhibit decreased activity of PIN-FORMED (PIN) protein auxin transporters, demonstrating that GAs are required for the correct function of PIN proteins (Willige et al. 2011). This GA-dependent management has biological consequences, such as modifying gravitropism in the roots of *Arabidopsis* through PIN2 stabilisation (Willige et al. 2011) or promoting xylogenesis in *Populus* through the upregulation of PIN1 (Yuan et al. 2019). The auxin homeostasis gene SUPERROOT2 (*SUR2*) is upregulated in *Eucalyptus* roots by GAs (Liu et al. 2018), whereas in *Arabidopsis*, GA3 enhances root responses to IAA by modulating auxin transporters (AUX1 and PIN1, PIN2, and PIN3) (Li et al. 2015).

Salicylic acid

Salicylic acid (SA) is crucial for controlling the growth and development of plants, fruit ripening, as well as the reaction to abiotic stress conditions. Two genes PR1 and PR2 related to pathogenesis are produced by drought stress those are recognised as SA-inducible genes (Miura et al. 2013). SA communicate thermotolerance in many plants (Sangwan et al. 2022). SA enhanced antioxidant quantity so that it reduces the extent of lipid peroxidation in oxidative stress conditions (Liu et al. 2022). Evidence showed that, in GASA genes, the GA family participated in abiotic stress responses and demonstrated that during seed germination, *FsGASA4* transgenic lines of *Arabidopsis* are more resilient to heat, oxidative, and salt stressors. GAs play a potential role in biosynthesis and overall action of SA, which enhances the expression of ics1 and npr1, indicating that the inhibitory effects of abiotic stresses are reversed by the overexpression of *GASA* in *Arabidopsis* seedlings (Alonso-Ramírez et al. 2009).

Jasmonic acid

A crucial signaling molecule, jasmonic acid (JA), is triggered by a variety of environmental stresses, including salt, drought, and other biotic and abiotic difficulties (Wang et al. 2021). JA has a great possibility of ameliorating the threatening impact of environmental stresses (Dar et al. 2015). JA is obtained from α-linolenic acid of chloroplast membranes, and it has a level enlargement during salt and drought stresses by inducing JA biosynthesis genes (Tani et al. 2008). For example, rice plants have orthologues of JA biosynthesis genes like OsDAD1, which showed elevated regulation in response to water deficit stress and genes with alleged functions in signaling of JA, such as OsbHLH148 and OsCOI1a, showed differential regulation in stressed conditions (Du et al. 2013). DELLA protein is necessary to increase JA-mediated responses, and those significant results propose that DELLAs function as an interface between GA and the JA signaling process. DELLAs may synergistically affect JA and GA signaling processes (Lyons et al. 2013).

Brassinosteroids

The physiological effects of brassinosteroids (BRs) and GAs, as well as the control of GA biosynthesis, seem to be interdependent. After DELLA degradation, GAs trigger the TF BRASSINAZOLE RESISTANT 1 (*BZR1*), which regulates BR responses in plants. Similarly, BRs influence the transcriptional activity of PHYTOCHROME INTERACTING FACTORS (*PIF*) TFs to contribute to plant responses to light (Oh et al. 2014). Increases in GA levels and the expression of *BZR1*, *BRI1* and EMS SUPPRESSOR 1 (*BES1*) (Unterholzner et al. 2015) are caused by over-expression of the BRs biosynthesis genes DWARF 4 (*DWF4*) and *GA20ox* (Stewart Lilley et al. 2013). BRs and GAs work together at functional levels to encourage cell elongation; however, in rice, excessive BR levels limit GA production (Tong et al. 2014). Additionally, certain oomycetes use the inhibitory impact of high BR levels on GA production as a tactic to reduce immunological responses in rice (Vleesschauwer et al. 2012). As a result, it appears that BRs and GAs impose mutual control over one another's activity through a molecular mechanism.

Cytokinins

Due to limited and imprecise data, the nature of the interactions between cytokinins (CKs) and GAs remain poorly defined. GAs influence cytokinin metabolism differently across plant species. However, in *M. truncatula,* CKs activate their receptor CRE1 (CYTOKININ RESPONSE 1), which lowers the GA levels (Fonouni-Farde et al. 2018). Additionally, GAs enhance the expression of ITP3 (ISOPENTENYL TRANSFERASE 3), a key enzyme involved in cytokinin biosynthesis in *Eucalyptus* (Liu et al. 2018). In mungbean under waterlogging conditions, CK and GA regulate the photosynthesis, antioxidant levels, osmolyte accumulation, and water-use efficiency, while reducing oxidative damage and boosting growth and yield (Islam et al. 2022). It has also been reported that both CKs and GAs work together in *Polygonum cuspidatum* to regulate growth and physiological responses, particularly under varying nitrogen conditions. Under high nitrogen availability, the levels of endogenous cytokinins and GAs both increase, suggesting a coordinated role in managing biomass distribution and integrating environmental cues such as light (Sugiura et al. 2015). In barrel medic and tall fescue, GAs enhance the expression of different cytokinins-degrading genes, which inhibit the tillering of the plant (Fonouni-Farde et al. 2017, Zhuang et al. 2019).

LIMITATIONS OF GA USE

GA in plants has the ability to alleviate the abiotic stresses, and it seems that GA at low concentration increased the abiotic stress tolerance of plants with the aid of maintaining better plant growth, development and ultimate crop yield (Islam et al. 2021). It was observed that the function of the GA is dose-dependent, and results demonstrated that in addition to the dose-dependent response in stressed conditions, plant species, application technique, and growth microenvironment are crucial factors in ensuring the GA functions properly (Iftikhar et al. 2020). On the contrary, the GA has a vital role in many morphological, physiological and biochemical courses of plants (Hadif 2019, Vetrano et al. 2020), but under Cr stress, a higher dose of GA (100 mmol) had a detrimental effect on pea growth, nitrogen absorption, and enzyme activity (Gangwar et al. 2011). Again, it has been documented that the concentration of GA applied to the okra plant under NaCl stress affected the activity of the enzymes. The higher concentration (300 μmol) of GA adversely affected the antioxidant enzyme activity and growth-related parameters compared to the lower concentration

(150 µmol) (Zhu et al. 2019). Thus, due to the application of GA in plants, the appropriate concentration of GA is very important and further research is necessary to optimise the concentration for future use. While in some cases, this clearly shows that GA needs H_2S to increase the chlorophyll content and photosystem II efficiency (F_v/F_m) in tomato (*Solanum lycopersicum* L.) plant under boron toxicity (Kaya et al. 2020). Besides, it has been seen that those different methods of GA application, for instance, foliar spraying, seed priming, and application with irrigation water, have been used to increase the production of different crops under stressed conditions throughout the world (Prajapati et al. 2018, Iftikhar et al. 2019, Banerjee and Roychoudhury 2020). However, the utility of the various methods of GA application varies notably. It depends on factors such as the GA concentration, plant species, application time, and different growth stages of the plant. Therefore, it will be an important task to identify the suitable method of GA application for crop growth and productivity.

GAs in real-world agricultural settings present several practical challenges. One of the primary issues is cost, as GA formulations can be expensive, making widespread application economically unfeasible for some farmers. The cost factor is exacerbated when considering the need for repeated applications to achieve desired effects, especially in large-scale farming operations. Furthermore, the potential side effects of GA application include unintended growth responses or disruptions in plant developmental processes. For instance, excessive GA can cause abnormal plant growth, such as excessive stretching or poor root development, potentially compromising plant health and productivity. Environmental factors, such as temperature and soil conditions, influence GA efficacy and complicate application strategies. Moreover, there is a risk of developing resistance or adaptation in plants over time, which could reduce the effectiveness of GA applications. Addressing these challenges requires a careful balance of cost, precise dosage, and monitoring to ensure that GA applications are both effective and sustainable in enhancing agricultural productivity.

The GA plays a crucial role in promoting plant growth and development, yet its effectiveness varies significantly among different plant species, which limits its broader agricultural use. One limitation is the species-specific response to GA, where certain plants may exhibit enhanced growth while others show little to no benefit. This variability is influenced by intrinsic factors like genetic makeup and hormonal regulation, as well as environmental conditions. For instance, some crops may develop excessive elongation or reduced reproductive performance under GA treatment, which can hinder yield quality and productivity. Furthermore, the application rate and timing must be carefully optimised for each species to avoid adverse effects like lodging in cereals or excessive vegetative growth in fruiting plants. Despite its proven potential, the inconsistent responses across species, coupled with a lack of detailed understanding of its interaction with other plant hormones, limit the use of GA in commercial agriculture. Thus, more research is needed to explore the specific mechanisms governing GA sensitivity in diverse species and tailor its application to optimal agricultural benefits (Hedden 2020).

The large-scale use of GA in agriculture can have several environmental impacts. It may disrupt soil microbial communities, reducing soil fertility and altering nutrient cycling. GA runoff can contaminate water sources, harming aquatic ecosystems and biodiversity. Additionally, non-target plants may absorb GA, causing unintended growth changes and disrupting local ecosystems. Over-reliance on GA can lead to reduced plant resilience, making crops dependent on external growth regulators. GA use should be carefully managed to minimise these effects, promoting sustainable agricultural practices that balance growth enhancement with environmental protection.

However, it is accessible to farmers in various formulations, such as powder, liquid, and granules, through agrochemical suppliers, cooperatives, and online platforms. It is often sold under brand names or combined with other plant growth regulators. Farmers generally access GA from agricultural retailers, but in many countries, its use is regulated, requiring adherence to guidelines to prevent misuse that could harm crops or the environment. In some regions, access may be limited to those with proper licenses or certifications. Additionally, knowledge about GA's benefits and proper use influences its accessibility. Extension services, workshops, and educational programs play a crucial role in informing farmers and enhancing their technical know-how. Cost can also be a factor, with small-scale farmers in developing countries potentially facing higher barriers. Government support and subsidies may help make GA more affordable, improving overall access and use in agricultural practices.

CONCLUSION AND FUTURE PROSPECTS

In summary, GA has been shown to be a key plant growth regulator with remarkable potential to combat the detrimental effects of abiotic stress on agricultural systems. Its many roles include promoting growth, increasing stress tolerance, and promoting sustainable habits. GA increases elongation and cell division in plants, counteracts stress-induced growth limitations, and enhances root development, stomatal conductance, and photosynthesis. This results in healthier, more productive plants that are better able to withstand adverse situations. The role of GA in maintaining osmotic balance through the accumulation of osmolytes such as proline is to provide efficient water uptake while mitigating the effects of water scarcity and salinity. In addition, through its control over the synthesis of antioxidant enzymes, GA protects plants from oxidative stress and promotes cellular health and overall integrity.

Several targeted future research initiatives are essential to enhance the application of GA in agricultural systems. Conducting dose-response studies will help determine the optimal GA concentration for various crops, such as wheat, rice, and soybeans, under abiotic stress conditions. Controlled experiments can reveal the most effective application timings to maximise stress resilience, specifically at the seedling, vegetative, or flowering stages. Additionally, exploring GA interactions with other plant hormones, such as ABA and ethylene, will provide insights into their combined effects on growth and stress tolerance. Field trials targeting specific food and cash crops can assess the impact of GAs on yield and stress resistance in diverse stress environments. Moreover, testing GA in combination with biostimulants, such as amino acids and seaweed extracts, could enhance stress tolerance more effectively than GA alone. Investigating GA-based seed priming techniques may improve germination rates and early growth, particularly in drought-prone areas. New avenues of research should leverage omics technologies to uncover the molecular mechanisms by which GA influences genes and metabolic pathways. Additionally, exploring nanocarriers for GA delivery could improve its efficacy and reduce required dosages. Longitudinal studies are necessary to assess the long-term ecological impacts of GA application, including its effects on soil health and microbial communities. Addressing socioeconomic concerns, research into the cost-benefit analysis of GA application for small-scale farmers is crucial for ensuring accessibility. Finally, developing GA-responsive transgenic plants that can modulate internal GA production in response to environmental stress could provide a dynamic solution for enhancing crop resilience and productivity.

Additionally, integrating GA signaling with the plant's circadian rhythm may offer novel insights, as the circadian clock is known to influence abiotic stress responses. Another key area is the exploration of GA's involvement in regulating epigenetic modifications under stress conditions. Research could investigate how GA influences histone modification, DNA methylation, and small RNA pathways to activate or repress stress-responsive genes. This epigenetic regulation could help plants "remember" stress events, allowing them to better cope with future stresses. Advancements in genomics, transcriptomics, and proteomics offer further avenues for investigating GA's role in abiotic stress. For instance, transcriptome-wide studies could reveal GA-regulated genes that are involved in tolerance mechanisms, while proteomics could identify GA-associated stress proteins. Moreover, exploring GA's interaction with reactive oxygen species signaling and antioxidant pathways could provide insights into how GA regulates oxidative stress under abiotic conditions. Finally, combining GA with emerging technologies such as CRISPR-Cas9 for targeted gene editing could enable the precise modification of GA biosynthesis and signaling pathways in crops to enhance stress resilience without compromising growth. These research areas will be crucial for improving crop productivity and sustainability in the face of global climate change and increasing environmental stressors. Collaboration among researchers, agricultural practitioners, and policymakers will be critical as we seek to harness the potential of GA to develop climate-resilient agricultural systems. A thorough understanding of plant physiology, along with iterative testing and adaptive management tactics, will help improve GA application approaches. GA's multidimensional effect of growth, stress tolerance, and overall plant health makes it a game changer for increasing agricultural production and quality. As global food demand increases in the face of mounting environmental challenges, judicious use of GA has the potential to transform the agricultural landscape into a more resilient and productive one.

Acknowledgements. The authors extend their appreciation to the projects of the the VEGA pro-

https://doi.org/10.17221/137/2025-PSE

ject No. 047SPU-4/2025, Introduction of practical teaching into the subject Green Infrastructure for supporting the study.

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Received: March 31, 2025
Accepted: June 25, 2025