



Gibberellic Acid: A Versatile Regulator of Plant Growth, Development and Stress Responses

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Abstract

The global agricultural system has been badly affected by adverse environmental changes in the past few years. These changes, including the rise of abiotic and biotic stressors negatively altered the growth and physiology of crop plants. Abiotic stresses, such as salinity, temperature extremes, drought, and heavy metals/metalloids, are major environmental constraints limiting crop growth, productivity, and sustainability worldwide. These stresses adversely affect plant metabolic activities and redox homeostasis, eventually leading to a reduction in plant growth and development. Plant growth regulators (PGRs) play a key role in regulating plants developmental processes and defensive responses under adverse environmental conditions. Among PGRs, gibberellic acid (GA₃), an endogenous tetracyclic diterpenoid plant hormone, regulates many growth and developmental aspects of crop plants. GA₃ plays a pivotal role in mitigating abiotic stresses induced-perturbations in plants by modulating various physio-biochemical and molecular processes. Based on recent reports, this review article describes the role of exogenously applied GA₃ in improving seed germination, phenotypic characteristics, metabolic processes, yield and quality components, and post-harvest life of fruits, vegetables, and flowers. In this article, we summarize research concerning GA₃ biosynthesis and signaling and discuss the potential role of GA₃ in mediating tolerance to various abiotic stresses. Moreover, the present article enlightens the current research concerning the signaling pathway in gibberellin and gibberellin-mediated crosstalk with other plant hormones.

Keywords Abiotic stresses · Gibberellic acid · Plant growth regulators · Physio-biochemistry · Redox homeostasis · Signaling

Introduction

Plants face myriad environmental stresses broadly divided into abiotic and biotic stresses. Abiotic stresses like heavy metals, water scarcity, salinity, and varying temperature are the main environmental restraints that adversely hamper phenotypic features, physio-biochemical processes, and production of crop plants (Zhu 2016; Shah et al. 2021, 2022a, b). Plants are equipped with various

inherent physio-biochemical and molecular mechanisms to overcome these perturbations. These mechanisms include alteration in gene expression, synthesis of special proteins, maintaining ionic balance, accumulating osmolytes, and enhancing antioxidant defense machinery (Sharma et al. 2022). Numerous efforts have been practiced to influence the endurance of plants against environmental calamities. Among them, the supplementation of plant growth regulators (PGRs), including auxins, brassinosteroids, abscisic acid, ethylene, cytokinins, gibberellins (GAs), jasmonic acid, nitric oxide, polyamines, salicylic acid and strigolactones play a regulatory role in boosting defensive responses in plants (Islam et al. 2021; Sabagh et al. 2021). The use of PGRs has become a common practice for improving the productivity and quality of horticultural and agricultural crop production and also for the mitigation of abiotic stresses (Shah et al. 2023). PGRs are small chemical messenger molecules that influenced growth, physiological and biochemical features, and plant

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genotypic functions (Rademacher 2015; El Sabagh et al. 2022). Among PGRs, GAs, an important phytohormone/plant growth regulator, modulates several growth and developmental processes in crop plants. Gibberellin comprises several compounds belonging to tetracyclic diterpenoid carboxylic acid groups. Gibberellins, generally recognized as gibberellic acid (GA_3), was first identified by Western scientists in the 1950s. In Asia, rice farmers know about a fungal disease called *bakanae* disease or foolish seedlings that have led to the identification of GAs (Gupta and Chakrabarty 2013; Taiz et al. 2015). Gibberellic acid produced from *Gibberella fujikuroi* can be commercially used for horticultural and agricultural purposes. It improved the growth and productivity of orchards, crops, and ornamental plants. The first GA was identified (GA_1) in runner bean seeds in 1958. However, most plants that produce GA, like GA_1 and GA_4 , have diverse roles in their physiological functions. Gibberellic acid induces growth and development processes in crop plants, including cell expansion, cell division, seed germination, mobilization of endosperm storage reserves, internode elongation, transition to flowering, sex expression, and development of fruits (Schwechheimer 2008; Rodrigues et al. 2012; Othman and Leskovar 2022). It has also been suggested that the treatment of GA_3 extends the post-harvest life of fruits, vegetables, and flowers by delaying senescence, inhibiting chlorophyll degradation, and increasing the antioxidant system (Kuchi et al. 2017).

Gibberellin is actively involved in plant mechanisms associated with imparting tolerance to stress in crop plants by improving ion homeostasis, membrane permeability, antioxidant system, osmolyte accumulation, and expression of stress-mitigation genes (Emamverdian et al. 2020; Nagar et al. 2021). Gibberellin takes part in key tolerance responses of plants against abiotic stresses such as by increasing plant antioxidant activities that scavenge deleterious ROS. Studies by several workers proposed that exogenous applications of GA_3 help plants to nullify the damaging consequences of environmental stresses (Hamayun et al. 2010; Elahi et al. 2022). The exogenous application of GA_3 improves growth, photosynthetic pigments, net photosynthetic rate, enzyme activities, mineral nutrient acquisition, and yield efficiency of several crop plants under adverse environmental conditions (Afroz et al. 2006; Abdel-Hamid and Mohamed 2014; Rady et al. 2021; Shahzad et al. 2021). The developmental processes in the plant life cycle indicate coordinated alterations in molecular mechanisms of plant growth through complex signaling networking and synchronized participation of various hormone signaling components. It has been confirmed that the relations between various phytohormones are necessary in integrating and remodeling plant growth and enhancing their stress resistance mechanism. GA_3 interacts with other PGRs both synergistically as well

as antagonistically to modulate many plants metabolic processes (Weiss and Ori 2007; Shaki et al. 2019; Banerjee and Roychoudhury 2019; Abbas et al. 2022).

Considering the diverse functions of GA_3 in the life cycle of plants in view, the present article aims to timely review the biosynthesis, signaling, and role of GA_3 in the growth and development of crop plants. In this article, we have also focused on GA_3 -mediated abiotic stress tolerance in crop plants. Moreover, an attempt has also been made to discuss molecular insight regarding the crosstalk of GA_3 with other PGRs in plants.

Biosynthesis

Gibberellins are naturally occurring phytohormone produced in many parts of plants, including germinating seeds, developing seeds, young leaves, and internodes. Gibberellins encompass a large group of plant growth substances with different functions during the entire life cycle of higher plants. The rate of GA biosynthesis and catabolism regulates how the GA hormone pool occurs in plants in a tissue and developmentally mediated manner. The GA biosynthetic pathways and catabolism are under strict genetic control (Taiz et al. 2015). The biosynthetic pathway of GA illustrated in (Fig. 1.) starts from geranyl–geranyl diphosphate (GGPP). The GGPP was synthesized from isopentenyl diphosphate (IPP), a 5-carbon central intermediate for many isoprenoid/terpenoid compounds. Two routes generate the IPP: the methyl erythritol phosphate (MEP) pathway in plastids and the mevalonic acid (MVA) pathway in the cytosol (Kasahara et al. 2002; Hedden and Thomas 2012).

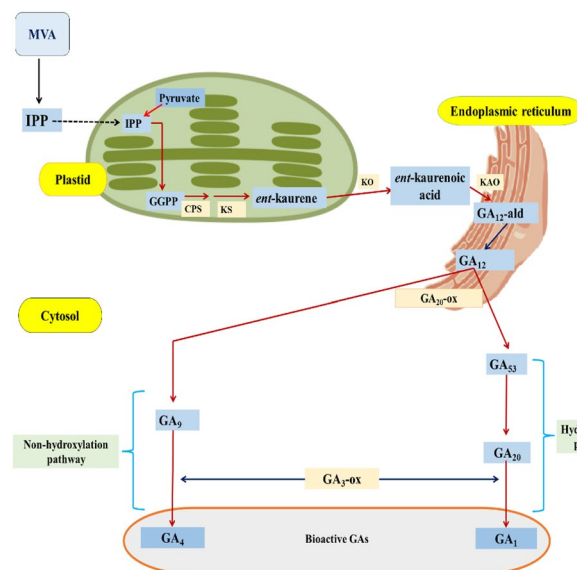


Fig. 1 An overview of gibberellins biosynthesis in plants

The GA biosynthetic pathway can be categorized into three phases (Hedden 2020). The first phase occurred in plastids where GGPP was changed into *ent*-kaurene catalyzed by two enzymes: the *ent*-copy-diphosphate synthase (CPS) and the *ent*-kaurene synthase (KS) (Van Schie et al. 2007; Taiz et al. 2015). In *Arabidopsis thaliana* L., enzymes CPS and KS are transcribed by single locus GA1 and GA2, respectively (Yamaguchi et al. 1998), while *Oryza sativa* L. by OsCPS1 and OsKS1 respectively (Sakamoto et al. 2004). The second phase takes place in the endoplasmic reticulum (ER); *ent*-kaurene is oxidized to GA₁₂-aldehyde catalyzed by cytochrome P450 monooxygenases including *ent*-kaurene oxidase (KO) and *ent*-kaurenoic acid oxidase (KAO). The GA₁₂-aldehyde is transformed into GA₁₂ (Hedden et al. 2002; Davidson et al. 2006). In *A. thaliana* L., KO is located at the chloroplast membrane and KAO at ER, facilitating *ent*-kaurene exit from plastid and oxidizing it when entered ER. The KAO enzyme is encoded by two genes, KAO1 and KAO2 (Regnault et al. 2014), and the KO enzyme is encoded by OsKO1, OsKO2, and OsKO5 genes in *A. thaliana* L. and *Oryza sativa* L., respectively (Zhang et al. 2020). GA₁₂ undergoes hydroxylation to form GA₅₃. The third phase occurred in the cytosol in which GA₁₂ and GA₅₃ served as precursors for the non-13-hydroxylation pathway and 13-hydroxylation pathway to form GA₉ and GA₂₀, respectively catalyzed by GA20-oxidase (GA20ox). The last stage of biosynthesis is the 3 β-hydroxylation of GA₉ and GA₂₀ mediated by GA3-oxidase (GA3ox) to form GA₄ and GA₁, respectively, bioactive GAs in plants (Salazar-Cerezo et al. 2018; Hedden 2020). Moreover, the bioactive GA₄ and GA₁ are inactivated by GA2-oxidase (GA2ox). The GA2-oxidase enzyme is encoded by seven genes, viz., GA2ox1, GA2ox2, GA2ox3, GA2ox4, GA2ox6, GA2ox7, and GA2ox8. The GA2-oxidase is a key enzyme in controlling GAs concentration during plant growth and development and responding to adverse environmental conditions (Li et al. 2019).

Signaling

Gibberellins regulate many features of plant physiology by modulating transcriptional and post-transcriptional changes at the cellular level (Schwechheimer 2008). There are many components that are involved in signaling responses regulated by GAs. The signaling of GA in plants involves a homeostatic balance between the gene expression involved in the GA biosynthesis, GA receptor, and enzyme concentration that inactivates bioactive GA (Sun and Gubler 2004; Daviere and Achard 2013). The crucial part in GA signaling is the GA receptor, i.e., GID1 (gibberellin insensitive dwarf 1) identified from *Oryza sativa* L. GID1 is a soluble protein located in the cytosol and nucleus, has a C-terminal domain for GA binding

and a flexible N-terminal domain (Griffiths et al. 2006; Ueguchi-Tanaka et al. 2007). The DELLA proteins (consisting of an N-terminal DELLA/TVHYNP motif and a C-terminal GRAS domain) are negative regulators of GA signaling in many crop plants and restrain the growth of plants (Yoshida et al. 2014). Moreover, DELLA prevents the binding of phytochrome interacting factors (PIFs) to their promoter sites and thereby interferes with their transcriptional activity. Gibberellin binds to its receptor GID1, and the GID1 undergoes conformational changes and allows the binding of the DELLA repressor protein, forming the GID1-GA-DELLA complex. The GID1-GA-DELLA complex is recognized by SCF^{GID2/SLY1} (skp1-cullin F-box), an E3 ubiquitin ligase that triggers polyubiquitylation and degrades DELLA repressor protein through 26S proteasome. The GID2 and SLY1 (SLEEPY1) are a subunit of F-box protein and deactivate repressors (such as SPY1, GAI, and RGA) of the GA signaling pathway in the presence of GA in the cell. After the degradation of the DELLA repressor resulted in the activation of transcription factors PIFs such as PIF3 and PIF4 and bHLH (basic helix-loop-helix), these transcription factors thus activated GA-regulated genes to cause a rapid change in gene expression and regulate biological response (Hartweck 2008; Hirano et al. 2008; Taiz et al. 2015). Additionally, two GATA family transcription factors GNC (GLUCOSE NITROGEN CARBON) and CGA1/GNL (CYTOKININ-INDUCED GATA FACTOR1/GNC-LIKE) were considered redundant regulators of plant growth. The GNC and GNL expression is repressed by PIFs mediated by GAs and requires the GID1-GA complex and degradation of DELLA. GA modulates many characteristics of plant physiology, including embryo, seed and root development, seed germination, leaf expansion, elongation of the stem, pollen maturation, and floral development (Richter et al. 2010; Schwechheimer 2012). Ramesh and Kumar (2006), Hamayun et al. (2010), and Saleem et al. (2020) suggested that supplementation of GA₃ significantly promoted seed vigor, plant height, plant biomass, antioxidant system, and photosynthesis of plants under changing environmental conditions. A diagrammatic illustration of mode of action of GA in plant cell is given in Fig. 2.

Growth and Development

Gibberellin plays a vital role in improving diverse facets of growth and development such as seed germination, morphological attributes, physiological and biochemical responses, yield, and quality traits of various crop plants (Fig. 3). Findings of several workers suggested that supplementation of

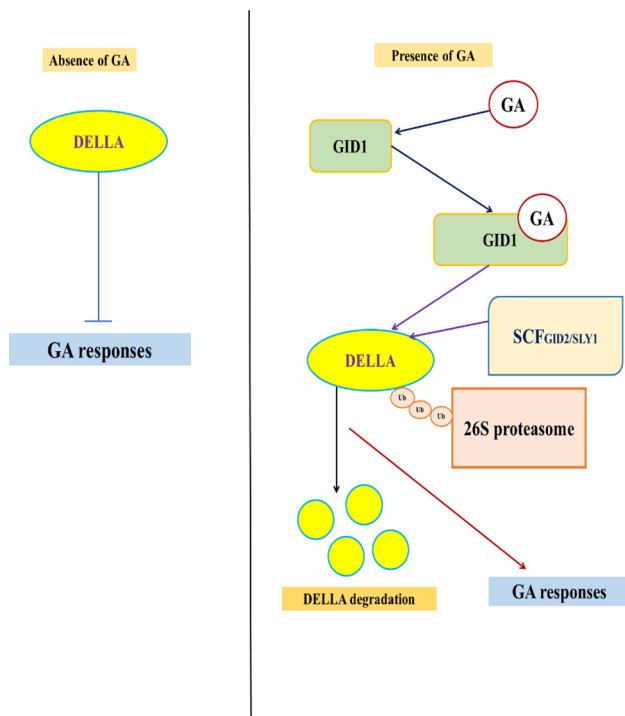


Fig. 2 Mechanism of action of gibberellin in plant cell

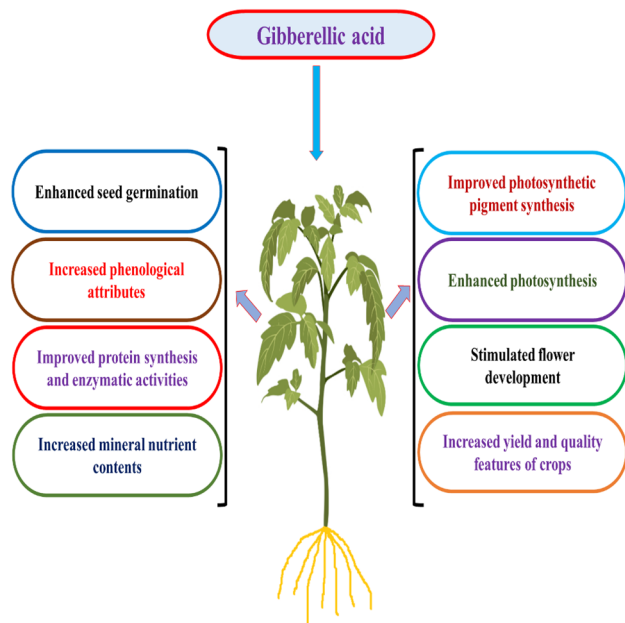


Fig. 3 A representation of gibberellin role in growth and development of plants

GA₃ influences every phase during the life cycle of plants. These studies have been summarized in below sections.

Seed Germination

Seed germination is an essential step in the lifespan of seed plants. It is controlled by many environmental aspects (light, moisture, and temperature, etc.) and by endogenous phytohormones (Abscisic acid and GA₃). The period of seed dormancy and the optimum moment to induce germination is critical for improving plant lifecycle and preventing potential threats in the first phases of seedling development. It is well known that GA is the main hormone intricated in seed dormancy breakdown, and the ABA/GA balance is the main regulator of seed dormancy and germination. Gibberellic acid positively regulates seed germination, whereas ABA maintains seed dormancy (Kim and Park 2008; Ravindran and Kumar 2019). Gibberellin promotes seed germination by increasing proteasome degradation of RGL2 (a DELLA repressor that stops germination), whereas ABA-induced AB15 (a leucine zipper transcription factor) that repressed seed germination (Piskurewicz et al. 2008). Endogenous GA acts as a positive regulator in this process to trigger the expression of the hydrolytic enzyme (especially α-amylase) in the aleurone layer of cereal grains, which substantially degrades the endospermic starch reserve (Damaris et al. 2019). Studies have revealed that both endogenous GA and the exogenous application of GA promote seed germination in crop plants, including *Oryza sativa* L. and *Capparis ovata* L. (Vieira et al. 2002; Soyler and Khawar 2007). Balaguera-Lopez et al. (2008) described that pre-sowing of *Solanum lycopersicum* L. seeds in 900 mg/L GA₃ led to a higher proportion of seed germination over the control. Roychowdhury et al. (2012) also investigated the effect of pre-sowing seed treatment of GA₃ on seed dormancy. They observed that *Dianthus caryophyllus* L. seeds soaked in 20 ppm GA₃ suppressed the effect of seed dormancy by significantly increasing seed germination percentage over the control. Exogenously applied GA₃ at 150 μM promotes seed germination in *Triticum aestivum* L. by significantly improving the α-amylase activity, rate of germination, and seedling height compared with the control (Wang et al. 2016). Further, Cornea-Cipcigan et al. (2020) suggested that seeds of *Cyclamen* species soaked in 50 mg/L GA₃ significantly increased their germination percentage, germination time, and seedling vigor index. It can be summarized from the above studies that GA₃ acts as a natural regulator in the processes intricate in seed germination by stimulating the hydrolytic enzyme that plays a key role in breaking seed dormancy.

Growth

Gibberellic acid improved plant growth by triggering cell division and elongation process, transitions from meristem to shoot growth, juvenile to adult leaf stage, vegetative to flowering and determining sex expression. Several

observations revealed that GA₃ plays a vital role in controlling various plant growth characteristics. For example, it improves vegetative growth, root, and stem elongation, plant biomass, and leaf area enlargement of many crop plants. The supply of 10⁻⁵ M GA₃ on *Brassica juncea* L. seedlings enhanced dry plant mass, leaf area per plant, and relative growth rate compared with water spray control (Khan et al. 2002). The supplementation of 10⁻⁸ M GA₃ on the foliage of *Lycopersicon esculentum* L. and 400 ppm GA₃ on *Ixora coccinea* L. enhanced their plant height, branch and leaf fresh and dry weight (Khan et al. 2006; Gad et al. 2016). The seedlings of *Papaver somniferum* L. treated with 10⁻⁶ M significantly promoted plant height and dry weight (Khan et al. 2007). The leaf applied 300 ppm GA₃ on *Araucaria heterophylla* L., and 10 μM GA₃ on *Mentha arvensis* L. seedlings significantly increased its plant height, branch length, stem thickness and root length (Gul et al. 2006; Bose et al. 2013). The seed priming of *Solanum lycopersicum* L. with 900 mg/L GA₃ and *Cicer arietinum* L. with 10⁻⁶ M improved plant height, leaf and root fresh weight and total dry mass of the plant (Balaguera-Lopez et al. 2008; Mazid 2014). The pre-treated bulb of *Polianthes tuberosa* L. with 150 pm GA₃ significantly enhanced its plant height, leaves per plant, length, and width (Rani and Singh 2013). The supplementation of 400 mg/L enhanced plant height, tillers per plant, secondary branches and total dry weight of *Linum usitatissimum* L. (Rastogi et al. 2013). Zang et al. (2016) evaluated that spray of 500 mg/L GA₃ enhanced leaf area, leaf fresh and dry weight of *Vaccinium virgatum* L. Similarly, leaf applied 1.2 ml/L GA₃ increased total plant height and internode length of *Hibiscus cannabinus* L. (Muniandi et al. 2018). Leilah and Khan (2021) foliar application of 240 mg/L GA₃ on *Beta vulgaris* L. improved root length, diameter and fresh weight and foliage fresh weight. Further, the spray of 10⁻⁵ M GA₃ increased plant height, fresh weight and dry weight of nodules per plant of *Cicer arietinum* L. (Rafique et al. 2021). The reviewed literature suggested that appropriate concentration of GA₃ application significantly enhanced the growth characteristics of plants by inducing a transition from meristem to shoot growth, plant biomass, leaf expansion, internode elongation, juvenile to the adult phase, vegetative to the flowering stage, defined sex expression and improved overall developmental phase of a plant.

Physio-Biochemistry

Gibberellins are reported to alleviate the harmful effects of salinity by increasing the nutrient-use efficiency, enzymatic activity, chlorophyll content, and absorption of mineral nutrients leading to improved plant physiological functions. The researchers suggested that the exogenous supplementation of GA₃ improved the physio-biochemistry of plants by enhancing the physio-biochemical attributes of many crop

plants. The supplementation of 10⁻⁸ M GA₃ enhanced chlorophyll content, photosynthetic rate (P_N), and CA activity of treated plants over the control plant (Hayat et al. 2001). The seed treatment of *Nigella sativa* L. with 10⁻⁵ M GA₃ enhanced chlorophyll content, CA activity, stomatal conductance (g_s), P_N , protein content, and nitrate reductase (NR) activity (Shah 2007). The *Brassica juncea* L. seedlings treated with 10⁻⁵ M GA₃ improved chlorophyll content, P_N , g_s , NR and CA activity (Siddiqui et al. 2008). Khan et al. (2009) indicated that seed treatment and foliage spray with 10⁻⁶ M GA₃ enhanced chlorophyll content, P_N , CA activity and mineral nutrient content in *Linum usitatissimum* L. The supply of 75 mg/L GA₃ increased P_N , internal CO₂ concentration (C_i), and total chlorophyll content in *Artemisia annua* L. (Aftab et al. 2011). The supplementation of 0.7 mM GA₃ improved chlorophyll, carotenoid, and total soluble sugar content in *Gladiolus communis* L. (Sajjad et al. 2014). The spray of GA₃ at 10⁻⁵ M on *Oryza sativa* L. augmented its chlorophyll, proline and leaf-soluble protein content (Khan et al. 2016). Rai et al. (2017) demonstrated that foliar application of 5 mL/plant GA₃ improved the net assimilation rate, NR activity and sucrose content in *Saccharum officinarum* L. The seedlings of *Vigna radiata* L. treated with 50 ppm GA₃ increased contents of amino acids, chlorophyll, glucose and protein and activity of NR (Baliah et al. 2018). Wang et al. (2019) found that a foliar spray of 0.1 mM GA₃ enhanced chlorophyll and nutrient acquisition in *Abelmoschus esculentus* L. The foliar feeding of 200 mg dm⁻³ GA₃ improved CO₂ assimilation intensity, transpiration rate (E), photosynthetic water-use efficiency, P_N , g_s and C_i in *Amarine tubergenii* L. (Salachna et al. 2020). Further, Rafique et al. (2021) observed treatment of 10⁻⁵ M GA₃ enhanced leghaemoglobin and chlorophyll content in *Cicer arietinum* L. The exogenous application of 10 μM GA₃ kg⁻¹ soil improved P_N , photosynthetic sulfur use efficiency and glutathione content in *Vigna radiata* L. (Hasan et al. 2020). Rady et al. (2021) investigated that treatment of GA₃ on *Vicia faba* L. seedlings increased relative water content (RWC), total chlorophyll and carotenoid contents, soluble sugar, protein, ascorbate, glutathione and total phenolic content and nutrient acquisition. Shahzad et al. (2021) determined that foliar application of 100 ppm GA₃ augmented chlorophyll content, soluble protein and total phenolic contents in *Oryza sativa* L. In summary, GA₃ enhanced crop plants' physiological and metabolic processes by increasing photosynthetic pigment synthesis, enzymatic activities, protein and sugar content, mineral nutrient uptake, non-enzymatic antioxidant content and photosynthetic efficiency.

Yield and Quality

GA₃ not only improves phenotypic traits and metabolic facets but also augments crop plant yield and quality characteristics.

Zang et al. (2016) evaluated that spray of 500 mg/L GA₃ enhanced the number of inflorescences/plants, flower number/inflorescence, fertile seed number and fruit weight of *Vaccinium virgatum* L. than the control plant. Further, the supplementation of 75 ppm GA₃ influenced the flowers/plant, total fruit/plant, fruit set and total fruit yield in *Fragaria ananassa* L. (Sharma and Singh 2009). The seed treatment and foliar spray of 10⁻⁶ M GA₃ improved capsules/plant, seeds/capsule, 1000-seed weight and seed yield/plant in *Linum usitatissimum* L. (Khan et al. 2010b, a). The foliar treatment of 50 mg/L GA₃ improved the number of buds, fruit set, average fruit weight and yield in *Syzygium samarangense* L. (Moneruzzaman et al. 2011). Nkansah et al. (2012) proposed that spray of 25 ppm GA₃ increased fruit set, number of fruits per cluster, fruit weight and yield in *Mangifera indica* L. The foliar spray of 400 mg/L GA₃ increased capsule per plant, seeds per capsule and seed yield in *Linum usitatissimum* L. (Rastogi et al. 2013). Abd El-Razek et al. (2013) reported that foliar application of 100 mg/L increased fruit length and diameter, seed weight, oil content, fruit weight, and yield in *Olea europaea* L. Pan et al. (2013) noticed that supply of 20 mg/L GA₃ enhanced panicle number, number of spikelets/panicles, grain filling percentage and 1000-grain weight of *Oryza sativa* L. The foliar spray of 50 ppm GA₃ improved the number of pods/plants, pod length and pod fresh and dry weight of *Abelmoschus esculentus* L. (Shahid et al. 2013). The seed treatment of *Cicer arietinum* L. with 10⁻⁶ M GA₃ enhanced pod number, seed yield/plant, and seed protein content (Mazid 2014). Akand et al. (2016) suggested that foliar application of 60 ppm influenced the number of the flower cluster and fruit per plant, dry matter of fruits, and yield of *Lycopersicon esculentum* Mill. The foliar treatment of 5 ppm GA₃ improved fruit weight, fruit width, and fruit length in *Rubus sp.* (Colak 2018). Rahman et al. (2019) indicated that supplementation of 75 ppm GA₃ increased flower and fruit clusters per plant, fruit number and weight per plant, and fruit yield t/ha in *Solanum lycopersicum* L. Abbas et al. (2020) reported that foliar spray of 1.0 and 1.2 g/L GA₃ increased the number of fruits, fruit weight and yield in *Momordica charantia* L. Talat et al. (2020) found that spray of 25 and 45 ppm GA₃ improved fruit weight and juice weight in *Citrus reticulata* L. The foliar application of 240 mg/L GA₃ on *Beta vulgaris* L. enhanced foliage yield, sucrose content, and sugar yield t/ha (Leilah and Khan 2021). Rafique et al. (2021) also described that a spray of 10⁻⁵ M GA₃ increased the number of pods/plants, 50 seeds weight, seed protein, and carbohydrate content, and grain yield in *Cicer arietinum* L. The above studies indicated that GA₃ significantly improved yield and quality components, including pollen maturation, development of flowers, fruits and seeds, and seed and oil yield of crop plants.

Post-Harvest Life of Fruits, Vegetables and Flowers

Fruits and vegetables are essential for human nutrition and are immensely suggested for a healthy diet. They are a rich source of energy, minerals, vitamins, antioxidants, dietary fibers, and other phytochemicals. On the other hand, flowers facilitate the reproduction of flowering plants, produce seeds, and pass genetic information to the next generation. However, improper post-harvest handling, like poor storage and transportation facilities and the premature senescence of flowers because of adverse climatic conditions, resulted in a worldwide economic loss (Yahia and Carrillo-Lopez 2018). To overcome this problem, it is desirable to maintain both the quality and quantity of consumable commodities through various healthy and eco-friendly post-harvest quality safeguarding strategies. The exogenous supply of GA₃ is an efficacious approach that enables a longer shelf-life for fruits and vegetables (Kuchi et al. 2017). The soaking of *Toona sinensis* with 100 mg/L GA₃ remarkably reduced its browning and decaying and alleviated the chilling stress-induced injuries by maintaining a higher level of reducing sugar, proline and increasing enzymatic and non-enzymatic antioxidants activity over the water treatment (Hu et al. 2018a, b). The addition of GA₃ 10⁻⁶ M to mineral nutrient solutions in a floating hydroponic system at the preharvest stage showed positive effects by retarding senescence and increasing the shelf life of *Lactuca sativa* L. and *Eruca sativa* Mill. After harvest (Miceli et al. 2019). The comparative transcriptome analysis of harvested leaves tissue of *Brassica rapa* L. showed that the activity of several differentially expressed genes like chlorophyll catabolic genes BrPPH and BrRCCR, bioactive GA degradation gene BrGA20×1 and NAC transcription factor BrNACo87 which are involved in chlorophyll and GA degradation, respectively during leaf senescence were significantly inhibited by the foliar treatment of 100 μM GA₃ (Fan et al. 2021). The fruits of *Capsicum annum* L. dipped in 2 ppm GA₃ for 30 s and then stored at 1 °C resulting in a delay in the change of skin color, total ascorbate and phenolic content and an increase in antioxidant activities and provided a longer shelf life to its green fruits (Panigrahi et al. 2017; Maurya et al. 2020). The browning of *Lactuca sativa* L. leaves was significantly inhibited during cold storage by the treatment of 0.1 mg/L GA₃, and it further enhanced the content of soluble protein and sugar, decreasing the activity of polyphenol oxidase and peroxidase (Tian et al. 2014). The fruits of *Abelmoschus esculentus* L. immersed in 0.1 g/L GA₃ solution could postpone its senescence and maintain fruit quality and chlorophyll content. GA₃ downregulate the expression of genes such as AeNOL, AeNYC, AeSGR, AeCLH, AePAO, AePPH, AeRCCR, and AeHCAR involved in chlorophyll degradation

(Xiao et al. 2022). The treatment of GA₃ at 0.1 mmol dm⁻³ delayed leaf yellowing and increased flower longevity of *Lilium longiflorum* (Rabiza-Swider et al. 2015). The cut flowers of *Anthurium andraeanum* L. sprayed with 144 μM GA₃ extended the vase life of flowers, delayed senescence and increased the phenol content and activity of polyphenol oxidase, peroxidase, and superoxide dismutase (do Nascimento et al. 2018). The spray of 150 ppm GA₃ significantly enhanced the freshness of flowers and delayed aging in *Chrysanthemum morifolium* L. (Singh and Bala 2018).

Amelioration of Abiotic Stresses

Abiotic stresses (such as salinity, drought, heavy metals, and varying temperature) cause severe effects on the growth, physiological and biochemical processes, and productivity of crop plants. Gibberellic acid is an important chemical

messenger that modulates various cellular processes to induce plant tolerance against abiotic stresses. Studies suggested that the exogenous application of GA₃ alleviates the negative effects of abiotic stresses by improving the physio-biochemical processes of plants (Fig. 4). In this section, findings regarding GA₃-mediated responses to various abiotic stresses in several crop plants are discussed below.

GA₃ and Salt Stress

Soil salinity is a major environmental threat that impairs the growth and development of crop plants by causing osmotic, ionic, and oxidative stress, metabolic disorder, and nutrient deficiency (Isayenkov and Maathuis 2019; Islam et al. 2021). The potential of GA₃ in imparting tolerance to salt stress has been studied in various crop plants, and there is ample evidence that GA₃ protect plant species from salinity-induced damages by maintaining membrane stability,

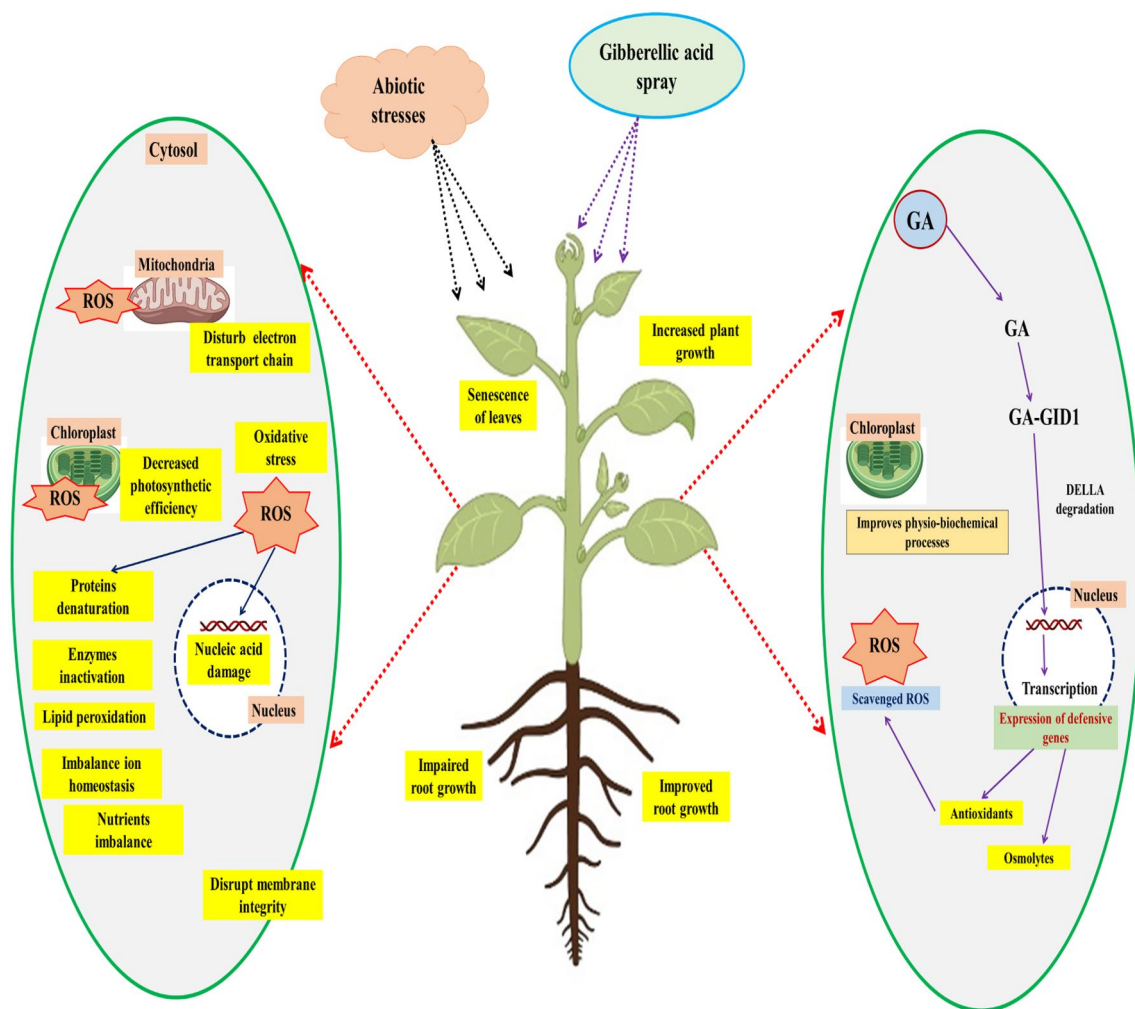


Fig. 4 Harmful effects of abiotic stress on plants and role of exogenously applied GA₃ in alleviating the negative effects of abiotic stresses by improving physio-biochemical processes and defense system of plants

ion homeostasis, upregulating antioxidant enzyme activities, maintaining compatible solute concentration, protecting photosystems and also inducing expression of stress genes. For example, Hamayun et al. (2010) reported that 5 μM GA₃ spray attenuated the salt stress-induced effect on growth and photosynthesis by significantly increasing endogenous phytohormones level, leaf chlorophyll content, daidzein and genistein content in *Glycine max* L. Further, Khan et al. (2010a, b) observed that 10⁻⁶ M GA₃ application overcomes salt toxicity by improving growth, antioxidant system, OP accumulation, and mineral nutrient contents in *Linum usitatissimum* L. Ali et al. (2012) found that treatment of 10⁻⁶ M GA₃ reversed salt stress-induced effect on growth performance of *Hibiscus sabdariffa* L. by improving its biomass and CA activity. Iqbal and Ashraf (2013) and Younesi and Moradi (2014) demonstrated that pre-treatment of *Triticum aestivum* L. and *Medicago sativa* L. seeds with GA₃ alleviated salt stress-induced inhibitory effect on their performance by improving significantly seed germination, plant biomass, photosynthetic efficiency, ion homeostasis, antioxidant defense system, endogenous hormonal homeostasis while decreasing lipid peroxidation. Further, Shaddad et al. (2013) reported that 100 ppm GA₃ spray treatment confers salt stress tolerance in *Triticum aestivum* L. by improving the contents of photosynthetic pigments, carbohydrates, amino acids, proteins and proline. Similarly, the foliar application of 100 mg/L GA₃ mitigated the negative effects of salt stress by increasing plant biomass, water status, chlorophyll content, OP content, antioxidant enzyme activities and mineral nutrient acquisition in *Rosa damascina* L. (Ali et al. 2014). Besides, Tsegay and Andargie (2018) studied the effect of pre-treatment of 0.2 g/L GA₃ on seed germination and growth performance of three crops viz., *Zea mays* L., *Pisum sativum* L. and *Lathyrus sativus* L., with salinity stress. They observed that GA₃ pre-treatment reversed the salt-induced effect by significantly enhancing germination percentage, shoot and root length, root fresh and dry weight and reduced mean germination time. Moreover, Wang et al. (2019) revealed that a spray of GA₃ at 0.1 mM mitigated the harmful effects of salt stress in *Abelmoschus esculentus* L. by improving antioxidant enzyme activities, proline content and by decreasing electrolyte leakage and lipid peroxidation. Chauhan et al. (2019) and Zhu et al. (2019) found that pre-treatment of *Avena sativa* L. and *Sorghum bicolor* L. seeds with GA₃ relieved salt stress-induced effect on seed germination and crop growth by enhancing water uptake, seed germination percentage, length of the radical and plant biomass. Further, Moula et al. (2020) reported that foliar feeding of GA₃ improved the performance of *Olea europaea* L. growth under salt stress by significantly enhancing leaf chlorophyll content, photosynthetic assimilation and mannitol content. Furthermore, the foliage of *Solanum lycopersicum* L. treated with GA₃ (1.4 μM) ameliorated salt-induced osmotic and

oxidative stress damages by increasing glycine betaine and proline content, glutathione and ascorbate content and enzymatic antioxidants (Siddiqui et al. 2020). Moreover, Ghani et al. (2021a, b) investigated the foliar application of GA₃ (100 mg/L) nullified salinity effect on the growth of *Allium cepa* L. by significantly enhancing growth parameters and total soluble protein content. Based on the above-appraised literature, it may be summarized that GA₃ plays a pivotal role in imparting salt tolerance in crop plants by enhancing membrane permeability, OP accumulation, nutrient acquisition, ion homeostasis, and activities of antioxidants while limiting lipid peroxidation and ROS generation.

GA₃ and Water Stress

Water (drought) stress is an acute environmental cue that affects various plant processes, leading to reduced crop productivity worldwide (Kaur and Asthir 2017; Seleiman et al. 2021). It causes several interrelated physio-biochemical disorders that are detrimental to plants by disrupting cellular metabolism and causing cell damage through ionic and oxidative stress. The most severe repercussions of water stress are the gradual/rapid water loss through stomata, leading to cell dehydration and cell/tissue death. Evidence suggests that GA₃ plays a pivotal role in improving the performance of plants under drought/water stress. Studies have shown that exogenous GA₃ mitigates the water stress-generated effects, as seen in *Brassica napus* L., *Zea mays* L., and many other crop plants (Li et al. 2010; Al-Shaheen and Soh 2016; Khan et al. 2016). Pre-treatment of *Zea mays* L. seeds with GA₃ (500 mg/L) attenuated drought-induced effect on growth by improving germination rate, dry seedling weight, germination and vigor index, antioxidant enzyme activities and chlorophyll and OP content (Yuan et al. 2014). Further, Al-Shaheen and Soh (2016) demonstrated that foliar spray of 100 and 300 ppm GA₃ improved *Zea mays* L. growth performance under drought stress by improving photosynthetic pigment and OP concentration and seed protein content. In another study, Khan et al. (2020a, b, c) also observed that GA₃ minimized the severity of drought stress in *Brassica napus* L. by enhancing antioxidant enzymes and OP concentration activities. They also reported GA₃ mediated increase in protein contents, glucosinolate, unsaturated fatty acids (erucic, oleic, linoleic, and linolenic acid), and saturated fatty acid (palmitic acid). Further, Miri et al. (2021) reported that 120 ppm GA₃ spray treatment attenuated the reduction in yield of *Vigna unguiculata* L., under drought stress by improving LRWC, photosynthetic pigments, 100-seed weight, and seed yield. Moreover, Rady et al. (2021) studied the effect of foliar application of 20 mg/L GA₃ on drought stressed *Vicia faba* L. plants. They observed that foliar application of GA₃ nullified drought stress-induced

perturbations by increasing growth, water use efficiency, photosynthetic pigments, LRWC, soluble sugars, membrane stability index, OP content, and antioxidant enzyme activities in *Vicia faba* L. From the above observations, it can be inferred that GA₃ minimized water stress-induced effects in crop plants by enhancing soluble sugar content, membrane permeability, fatty acids content, OP accumulation, and antioxidant enzyme activities.

GA₃ and Heavy Metal Stress

Soil contaminated with hazardous heavy metals (HMs) has become a subject of concern for sustainable agriculture. HMs stress causes serious threats to crop plant productivity by altering growth and developmental processes, leading to the death of plants. Soil can receive HMs from industrial effluents, urban run-off, burning liquid/toxic fuel, sewage waste disposal, domestic garbage dump, etc. Plants ameliorate the toxic effects of HMs through various mechanisms, including chelation (mediated by phytochelatins) and sub-cellular compartmentalization (Ghori et al. 2019). There is ample literature available on the significance of GA₃ in reducing HMs stressed-induced impact in plant species. For instance, exogenously applied GA₃ was reported to ameliorate the harmful effects of cadmium and lead in *Lupinus albus* L. by significantly improving leaf chlorophyll, soluble protein, carbohydrate, and proteases, amylases, and catalases activity (Sharaf et al. 2009). Further, exogenously applied 10⁻⁸ M GA₃ mediated increased proline accumulation and activities of antioxidant enzymes were reported to ameliorate the nickel stress-induced damages in *Triticum aestivum* L. (Siddiqui et al. 2011). Increased antioxidant enzyme activities and OP accumulation in copper-stressed *Spinacia oleracea* L., were also reported (Gong et al. 2021). In another study, Zhu et al. (2012) reported that leaf applied improved cadmium stress tolerance by decreasing lipid peroxidation and expression of cadmium uptake-related gene *IRT1* in *Arabidopsis thaliana* L. Amri et al. (2016) studied the ameliorative effect of pre-treatment of *Hordeum vulgare* L. seeds with 0.5 μM GA₃ for 96 h in the presence of cadmium toxicity. They observed that exogenous application of GA₃ improved tolerance to cadmium stress by increasing hydrolytic enzymes, sugar and amino acid content of the endosperm and mobilization of starch and protein from endosperm to seedling roots. Kaya et al. (2020) demonstrated that GA₃ mediated enhanced contents of endogenous hydrogen sulfide, leaf calcium and potassium, and proline ameliorated the severity of boron toxicity in *Solanum lycopersicum* L. Moreover, GA₃ (50 ppm) improved tolerance to lead toxicity by significantly increasing biomass, photosynthetic pigment, phenolic content, and antioxidant enzyme components in *Daucus carota* L. (Ghani et al. 2021a, b). Additionally, exogenously applied GA₃ was evidenced to

alleviate the oxidative stress damages by enhancing the antioxidant defense system, OP accumulation, photosynthetic efficiency, and growth in copper-exposed *Corchorus capsularis* L. and *Pisum sativum* L. plants (Saleem et al. 2020; Javed et al. 2021) and cadmium exposed *Vigna radiata* L. and *Pisum sativum* L. (Hasan et al. 2020; Sun et al. 2020). In conclusion, GA₃ alleviated HMs toxicity in crop plants by improving endogenous hormones level, OP accumulation, and antioxidant enzyme activities.

GA₃ and Temperature Stress

Global warming leads to variations in temperature. High and low temperatures have become a potential environmental cue that negatively affects many physio-biochemical and metabolic processes in plants, including germination of seeds, seedling growth, photosynthesis, protein structure, enzymes activities, membrane stability, and cell/tissue death (Mathur et al. 2014; Szymanska et al. 2017). Various studies have shown that supplementation of GA₃ differentially benefits crop plants exposed to extreme temperatures by enhancing their inherent defense system (Haroun et al. 2018; Hu et al. 2018a, b; Aziz and Peksen 2020). In *Raphanus sativus* L., seed priming with GA₃ (900 μM) improves seed germination, coleoptile, and radicle length, and fresh weight of seedlings, thus improving high-temperature stress tolerance (Cavusoglu and Kabar 2007). Similarly, Li et al. (2013) reported that pre-sowing seed treatment with GA₃ (5 μmol/L) alleviated chilling stress toxicity by improving seed germination rate, germination index, lengths, and weights of radical and coleoptiles and starch degradation in *Triticum aestivum* L. Furthermore, GA₃ treatment maintained redox homeostasis in *Gladiolus hortulanus* L. under variable temperatures by increasing membrane stability, antioxidant enzyme activities, and decreasing membrane leakage (Saeed et al. 2014). In *Solanum lycopersicum* L., GA₃ (0.5 mM) treatment alleviates the toxic effects of cold stress in *Solanum lycopersicum* L. fruits by modulating the accumulation of endogenous hormones (Ding et al. 2015 and Zhu et al. 2016). In another study, Xie et al. (2018) reported that GA₃-mediated low-temperature tolerance was associated with the upregulated expressions of UDP-glucose pyrophosphorylase, granule-bound starch synthase, β-amylase, ADP-glucose pyrophosphorylase, and invertase inhibitor genes in *Solanum tuberosum* L. In addition, the heat stress-induced inhibitory effect on *Phoenix dactylifera* L. performance was reversed by GA₃ treatment, which regulates endogenous salicylic acid, abscisic acid accumulation, and activities of antioxidant enzymes (Khan et al. 2020a, b, c). From the above-cited literature, it may be summarized that GA₃ mitigated the effects of varying temperatures in crop plants by regulating endogenous hormone levels, OP

accumulation, ion homeostasis, and antioxidant defense system.

Gibberellin Crosstalk with Other Plant Growth Regulators

PGRs are structurally different compounds, but their signaling network interacts with each other both

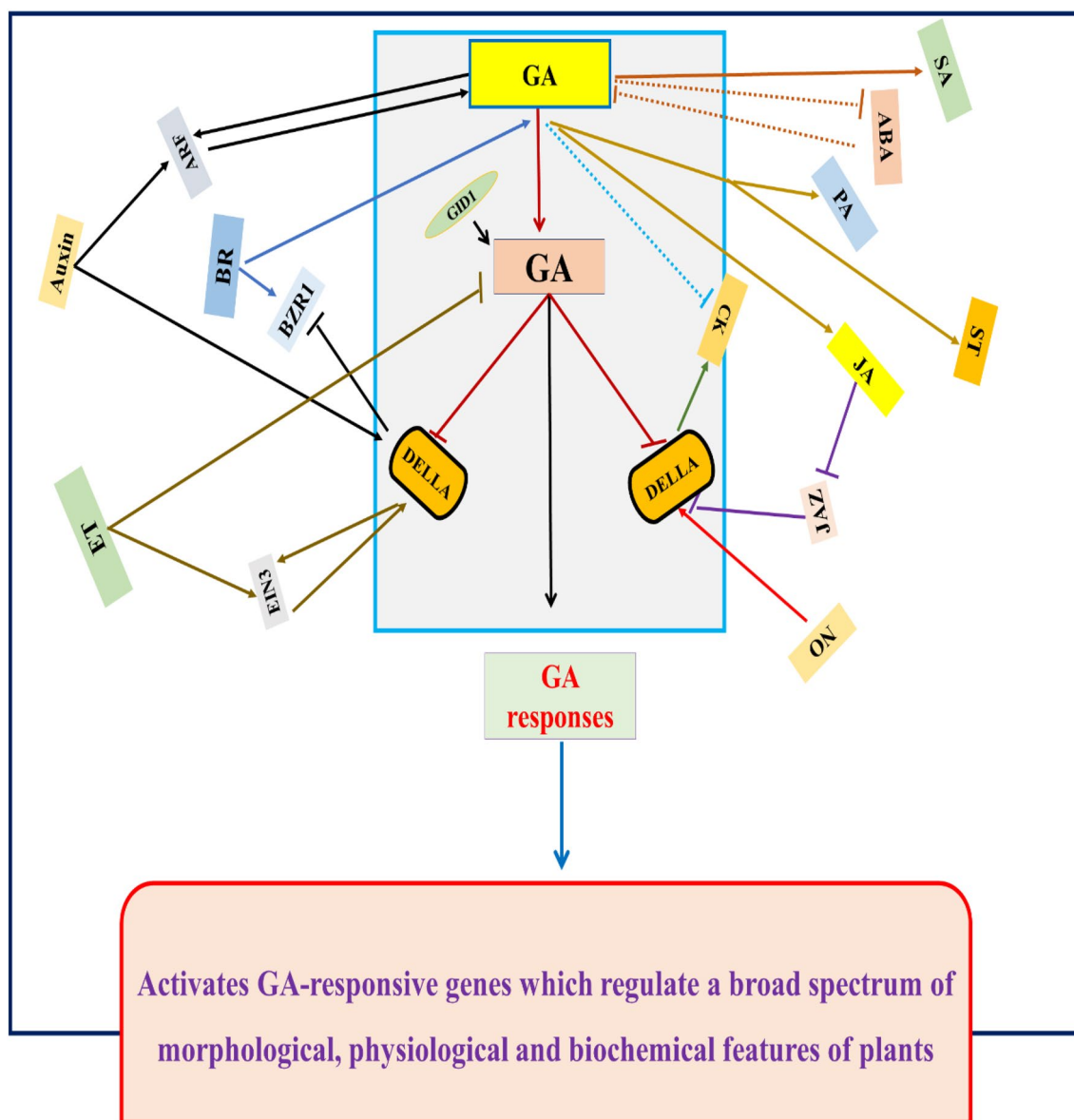


Fig. 5 A schematic model of gibberellin crosstalk with other phytohormones in regulating physiological and molecular responses of crop plants. GA and ABA showed an antagonistic behavior during seed germination. The Aux/IAA and ARF proteins up regulate the gene expression involved in GA metabolism. The BRASSINAZOLE RESISTANT1 (BZR1) is a transcription factor that modulates gene expression in response to brassinosteroid. The DELLA protein GAI inhibits the activity of BZR1. GA inhibits the effects of cytokinin. Ethylene reduced the level of GA and enhanced the DELLA repressor protein accumulation. The JASMONATE ZIM-domain (JAZ) inter-

acts and inhibits DELLA protein and activates bHLH factor PHYTOCHROME INTERACTING FACTOR 3 (PIF3) in the GA signaling pathway. Nitric oxide enhanced the accumulation of DELLA protein and negatively affecting the GID1 receptor of GA. GA (gibberellin), SA (salicylic acid), PA (polyamines), CK (cytokinin), JA (jasmonates), ST (strigolactones), BR (brassinosteroids), NO (nitric oxide), ABA (abscisic acid), GID1 (GIBBERELLIN INSENSITIVE DWARF 1), ARF (auxin response factor) and EIN3 (ETHYLENE INSENSITIVE 3). Sharp arrows indicate positive regulation and blunt arrows show negative regulation

antagonistically or synergistically to control numerous phenotypic and developmental features in plants under both stressful and stressed free environments (Kohli et al. 2013). The interaction among PGRs (Fig. 5) showed that they could co-coordinately moderate genetic machinery and defense system to improve plants endurance against adverse environmental conditions (Khan et al. 2020a, b, c). The interaction between GAs and other PGRs such as abscisic acid (Weiss and Ori 2007), auxin (Hu et al. 2018a, b), brassinosteroids (Tong et al. 2014), cytokinin (Subbaraj et al. 2010), ethylene (Achard et al. 2007), jasmonic acid (Peng et al. 2009), nitric oxide (Bethke et al. 2007), polyamines (Verdolin et al. 2021), salicylic acid (Xie et al. 2007) and strigolactones (Ito et al. 2017) has been established under both stressed free and stressed conditions.

Abscisic Acid

Abscisic acid (ABA) is a sesquiterpene plant hormone that regulates plant growth and developmental phases, including seed development and maturation and synthesis of protein and compatible solutes to tolerate adversities of the environment (Kumar et al. 2022). GA and ABA interaction help in sustaining the balance between germination and seed dormancy which plays an essential role in stress resistance. GA and ABA exhibited antagonistic behavior during seed germination. GA promotes seed germination, whereas ABA retards germination (Golldack et al. 2013). In *Oryza sativa* L., two WRKY genes (OsWRKY51 and OsWRKY71) are inducible for ABA and repressible for GA in embryo and aleurone cells. The WRKY genes established signaling crosstalk between ABA and GA (Xie et al. 2006). GA enhanced net carbon fixation and transport, but ABA only improved sugar transport in roots and berries of *Vitis vinifera* L. (Moreno et al. 2011). ABSCISIC ACID INSENSITIVE 4 (ABI4) gene regulates the primary seed dormancy by moderating the balance between ABA and GA biogenesis in *A. thaliana* L. (Shu et al. 2013). The GIBBERELLIN INSENSITIVE DWARF 1 (GID1), a receptor of GA, modulates stomatal development and patterning in *Oryza sativa* L. GID1 mutant exhibited a decrease in biosynthesis of endogenous ABA. GID1 improved submergence tolerance by regulating the consumption of carbohydrates and its function dependent on ABA and GA signaling (Du et al. 2015). The exogenous application of ABA on *Cucumis melo* L. induced low-temperature tolerance by improving growth characteristics and endogenous GA and SA levels (Kim et al. 2016). Yue et al. (2018) found that exogenous application of ABA and GA on *Camellia sinensis* L. enhanced the expression of CsKS, CsKAO, CsKO, CsGA20ox-2, and CsNECD2 and repressed CsGID1b, CsSDR, CsPYL8, and CsCYP707A2 genes. These genes expression showed that GA and ABA

controlled bud dormancy. Guo et al. (2018) revealed that a *Triticum aestivum* L. specific microRNA 9678 (miR9678) expressed in the scutellum of germinating seeds reduced the GA levels, but ABA enhanced the activity of miR9678. Its overexpression delayed the germination of seeds. Xu et al. (2021a) indicated that exogenous application of ABA and GA regulates bulblet development in *Lycoris radiata* L. GA inhibits bulblet development by down-regulating the expression of carbohydrate metabolism enzymes encoding genes such as LrSUS1, LrSUS2, and AGPase whereas ABA promoted bulblet development by increasing endogenous auxin content and activities of starch synthesis enzymes including SSS and GBSS.

Auxins

Auxins are a group of essential phytohormones involved in numerous plant growth and developmental events (Zhao et al. 2010). GA and auxin interactively regulate growth and physio-biochemical processes in plants. For instance, GA and auxin promoted fruit initiation in *Solanum lycopersicum* L. High levels of auxin or GA induce parthenocarp in plants. The repressor of GA signaling, like SIDELLA, and auxin signaling components, such as SIIAA9 and SIARF7, mediate the interaction between them to control fruit initiation (Jong et al. 2011; Hu et al. 2018a, b). The Aux/IAA (indole acetic acid) and ARF proteins upregulate the gene expression involved in GA metabolism, particularly AtGA20ox and AtGA2ox genes in *A. thaliana* L. (Frigerio et al. 2006). GA improved auxin concentration in the stem of *Populus tremula* L. by promoting polar auxin transport. The IAA and GA induced cell and organ growth (Bjorklund et al. 2007). Willige et al. (2011) observed that GA controls the PIN protein level in *A. thaliana* L., which is required to transport auxin in plants. Richter et al. (2013) indicated that GA biosynthetic deficient *A. thaliana* L. showed delayed flowering because GA promotes the synthesis of ARF2 protein. The ARF controls the auxin responses at the cellular level to control plant developmental phases. Shuai et al. (2017) investigated that pre-sowing seed treatment with 10 μ M IAA inhibits seed germination of *Glycine max* L. by increasing the biosynthesis of ABA and impairing GA biosynthesis. The qPCR assay showed that genes involved in ABA biosynthesis were upregulated, whereas GA biosynthetic genes were downregulated. Further, the AFR gene (SIARF5) plays an essential role in modulating the signaling pathways of both auxin and GA in *Solanum lycopersicum* L. during development and fruit set (Liu et al. 2018). Yoneda et al. (2018) suggested that GA and auxin improve steviol glycoside concentration in *Stevia rebaudiana* L. In *Glycine max* L., the combined application of 100 μ M GA and IAA induced hypocotyl elongation and promoted

their endogenous level (Jiang et al. 2020). Kou et al. (2021) observed that exogenous application of 20 mg/L IAA induced stalk elongation and expansion of cell walls by regulating the expression of genes encoding expansin protein and increasing endogenous IAA and GA contents in *Brassica rapa* L. The auxin response factor (ARF6 and ARF8) interacts with DELLA and promotes the senescence of cambium (Ben-Targem et al. 2021). Liang et al. (2021) revealed that the co-application of 50 μ M IAA and GA₃ minimized cadmium toxicity in *Sedum alfredii* L. by increasing plant biomass, chlorophyll content, potassium content, and decreasing malondialdehyde.

Brassinosteroids

Brassinosteroids (BRs), steroidal plant hormones, play an essential role in regulating plant growth and physio-biochemical processes (Fariduddin et al. 2014). GA and BRs exhibited signaling pathways crosstalk to control plant growth and developmental processes. The BRASSINAZOLE RESISTANT1 (BZR1) is a transcription factor that modulates gene expression in response to BRs. The DELLA protein GAI inhibits the activity of BZR1 and regulates the hypocotyl elongation in *A. thaliana* L. (Gallego-Bartolome et al. 2012). The OsGSR1, a member of GAST gene family (GA-stimulated transcript), expression is inhibited by BRs and stimulated by GA. Transgenic *Oryza sativa* L. plant containing OsGSR1 RNAi transcript shows low endogenous BRs. However, OsGSR1 is a positive regulator for BRs and GA signaling (Wang et al. 2009). BRs modulate cell elongation in *Oryza sativa* L. by regulating GA metabolism. Especially, BRs induced the expression of the GA biosynthetic gene, D18/GA3ox-2, and improved cell elongation (Tong et al. 2014). Both GA and BRs regulate seed traits like mesocotyl length in *Zea mays* L. (Hu et al. 2017). The miRNA (OsmiR396d) is involved in the interaction of GA and BRs signaling pathways. The overexpression of OsmiR396d enhanced BRs signaling and impeded the biosynthesis and signaling of GA. Interestingly BZR1 improved the accumulation of OsmiR396d in *Oryza sativa* L. (Tang et al. 2018). Further, the OsmiR159d-OsGAMYBL2 coordinates the functions of GA and BRs in the growth and development of plants by modulating the expression of genes that participated in GA and BRs biosynthesis and signaling (Gao et al. 2018). Que et al. (2018) investigated that exogenous application of 0.5 mg/L 24-epibrassinolide on *Daucus carota* L. promoted cell elongation, GA level and cellulose deposition in its petiole. Zheng et al. (2019) observed that foliar application of 3 mg/L 28-HBR on *Malus pumila* L. seedlings upregulated the expression of genes involved in the biosynthesis of auxin and GA and enhanced plant growth. In *Solanum lycopersicum* L., BRs modulate ovule number by

affecting GA biosynthesis and stabilizing DELLA protein that stimulates ovule primordial initiation (Barro-Trastoy et al. 2020). The late embryogenesis abundant (LEA) protein plays an essential role in dehydration tolerance during seed development. Mutation in the LEA33 gene affects grain size and seed germination in *Oryza sativa* L. LEA proteins may form a molecular regulatory network between GA and BRs signaling pathways to regulate seed germination (Li et al. 2020). Jiang et al. (2020) proposed that GA regulates hypocotyl elongation in *Glycine max* L. by promoting auxin and BRs function. Xiong et al. (2021) revealed that GA and BRs controlled seed germination and embryo growth and promoted glutelin protein mobilization in *Oryza sativa* L.

Cytokinins

Cytokinins (CK) are an important chemical messenger that plays a key role in the modulation of the plant cell cycle and various developmental processes (Cortleven et al. 2019). A negative regulation has been established between these two hormone response pathways. However, their exclusive signaling interaction to regulate developmental processes is poorly understood. GA inhibits the effects of CK. SPINDLY (SPY) is a negative regulator of GA signaling that enhances CK responses in *A. thaliana* L. SPY behaves as a repressor for GA signaling and regulator for cytokinin response (Greenboim-Wainberg et al. 2005). CK and GA alleviate bud dormancy and promote flowering and branching in *Zantedeschia* sp. (Subbaraj et al. 2010). A dominant-active DELLA1 protein controlled the GA signaling and improved cytokinin response1 (CRE1) dependent CK pathway to regulate nodulation in *Medicago truncatula* (Fonouni-Farde et al. 2017).

Ethylene

Ethylene (ET) is a gaseous signaling molecule that regulates many growth and physiological processes in plants (Matilla-Vazquez and Matilla 2014). ET inhibits root growth while promoting apical hook formation in *A. thaliana* L. by hampered degradation of DELLA repressor protein (Achard et al. 2003). ET reduced the level of GA and enhanced the DELLA repressor protein accumulation. It also delays flowering in *A. thaliana* L. by repressing floral meristem-identity genes viz., LEAFY (LFY) and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) (Achard et al. 2007). The expression of the C-repeat/drought-responsive element binding factor (CBF1/DREB1b) gene (a member of APETALA2/ETHYLENE RESPONSE FACTOR family transcription factor) improves tolerance against low

temperature but also restrains growth by permitting the accumulation of DELLA (Achard et al. 2008). The SNORKEL1 and SNORKEL2 are ethylene response factors that permitted *Oryza sativa* L. to adapt in deep water. The product of these genes induced internode elongation through GA signaling (Hattori et al. 2009). DELLA protein interacts with the DNA-binding domain of the ETHYLENE INSENSITIVE 3/EIN3-LIKE 1 (EIN3/EIL1) and inhibits the expression of the HOOKLESS 1 (HLS1) gene. GA stimulates apical hook formation in association with ET by promoting the expression of HLS1 in *A. thaliana* L. (An et al. 2012).

Jasmonic Acid

Jasmonic acid (JA) is a crucial growth-regulating substance that modulates diverse developmental processes of plants (Ruan et al. 2019). GA and JA showed both antagonistic and synergistic interactions to regulate plant growth and development. The JASMONATE ZIM-domain (JAZ) interacts and inhibits DELLA protein and activates bHLH factor PHYTOCHROME INTERACTING FACTOR 3 (PIF3) in the GA signaling pathway, while JA promoted JAZ degradation and free DELLA protein that restrains PIF3 and inhibit GA induced hypocotyl elongation (Yang et al. 2012). Exogenous treatment of JA improved endogenous GA content under salt stress in *Oryza sativa* L. (Seo et al. 2005). GA and JA modulate trichome initiation and stamen development in *A. thaliana* L. (Qi et al. 2014; Song et al. 2014). Further, GA regulates the expression of JA biosynthetic genes such as DAD1 and LOX1 to enhance the synthesis of JA, and a high level of JA stimulates the expression of MYB21, MYB24, and MYB54 to induce stamen filament development (Peng et al. 2009). GA promotes the biosynthesis of JA by regulating the expression of MYB21, MYB24, and MYB57 genes, which are contributed to stamen development in *A. thaliana* L. (Cheng et al. 2009). JA antagonizes the biosynthesis of GA by inhibiting the activities and accumulation of GA20ox and GA13ox that are involved in the biosynthesis of GA. It has been indicated that the high level of JA inhibits GA biosynthesis in the stem of *Nicotiana attenuata* L. (Heinrich et al. 2013). Um et al. (2018) studied that JAZ interacts with DELLA repressor proteins, including SLENDER RICE 1 (SLR1), in GA signaling. The protein OsJAZ9 inhibits JA responses and stimulates GA responses in *Oryza sativa* L. showed antagonistic crosstalk between GA and JA. The combined application of JA and GA₃ on *Cicer arietinum* L. reduced cadmium contamination by increasing photosynthetic characteristics, enzymatic activities, osmolyte accumulation, and mineral nutrition (Ahmad et al. 2021).

Polyamines

Polyamines (PA) is a group of aliphatic amines that act as a plant growth regulator and participate in several developmental aspects of plants (Gonzalez et al. 2021). The exact signaling interplay between GA and PA is still not well understood. However, few studies reported that GA and PA coordinately play a role in plants growth and metabolic processes. The exogenous application of spermidine (Spd) improved drought tolerance in *Agrostis stolonifera* L. by improving RWC, chlorophyll content, antioxidant enzyme activities, endogenous PA levels, and reduced IAA and GA₃ accumulation level (Li et al. 2015; Krishnan and Merewitz 2017). Li et al. (2018) revealed that exogenous application of Spd alleviated drought stress in *Zea mays* L. by enhancing photochemical efficiency, synthesis of ATP, and endogenous PA, IAA, and GA₃ levels. Qin et al. (2019) also reported that the application of Spd stimulated floral induction in *Malus domestica* L. by increasing the activity of MdGA2ox2 that reducing GA₃ level. The flowering-related gene like LEAFY also increased by Spd. The spray treatment of PA and GA₃ on *Impatiens hawkeri* L. increased plant height, leaf numbers, plant biomass, and flower buds (Verdolin et al. 2021). The combined application of Spd and GA₃ improved endogenous PA contents, PA biosynthetic enzyme activities, developmental stages of flowering, and delayed flower senescence in *Rhododendron simsii* L. (Xu et al. 2021b). Zandona et al. (2021) found that exogenous application of GA₃ on *Calibrachoa sellowiana* L. breaks seed dormancy to promote seed germination and improve endogenous PA content.

Nitric Oxide

Nitric oxide (NO) is a key endogenous signaling molecule that regulates plant diverse physiological and biochemical processes (Wani et al. 2021a). Studies suggested that a possible interaction between GA and NO has existed that modulates various developmental events in plants, including seed germination, hypocotyl elongation, root growth, and growth of pollen tubes (Asgher et al. 2017). In *A. thaliana* L., NO up-regulates the GA signaling pathway that leads to improved protein storage in seed (Bethke et al. 2007). The NO-deficient *A. thaliana* L. mutant showed longer hypocotyl than wild-type ones. Interestingly, exogenous treatment of NO reduced hypocotyl length by enhancing the accumulation of DELLA protein and negatively affecting the GID1 receptor of GA (Lozano-Juste and Leon 2011). NO and other plant hormones, including GA, enhance aluminum stress tolerance in plants by maintaining their endogenous hormonal equilibrium (He et al. 2012). NO enhances the DELLA protein concentration and negatively impacts GA signal transduction (Freschi 2013). Moreover, NO and

GA₃ eliminated seed dormancy and induced germination in *Amaranthus retroflexus* L. (Kepczynski et al. 2017). NO is a crucial component in various plant hormone signaling networks, including GA, to moderate multiple metabolic functions in plants under adverse environmental conditions (Singhal et al. 2021).

Salicylic Acid

Salicylic acid (SA) is a small phenolic compound that plays a regulatory role in various physiological processes of plants (Hayat and Ahmad 2007). GA and SA are essential in plants' various growth and physiological processes. Recent studies emphasize that a complex network of interaction existed between two hormones, but still, limited literature has been found. SA inhibits seed germination in *Zea mays* L., *A. thaliana* L., and *Hordeum vulgare* L. Further, SA and WRKY genes regulate the activity of α -amylase. GA promotes α -amylase production in aleurone cells but is inhibited by SA. In the aleurone cells of *Hordeum vulgare* L. seed, the expression of HvWRKY38 is downregulated by GA but upregulated by ABA and SA (Xie et al. 2007). The application of GA₃ on *A. thaliana* L. minimized the inhibitory effect of salt and heat stresses and improved seed germination, seedling growth, and expression of isochorismate synthase1 and PR1 genes involved in the regulation of biosynthesis and function of SA (Alonso-Ramirez et al. 2009). The seedlings of *Solanum lycopersicum* L. treated with SA mitigated chilling injury by enhancing antioxidant enzyme activities and regulating GAs metabolism (Ding et al. 2016). The exogenous application of SA on *Carthamus tinctorius* L. ameliorated salinity stress by improving mineral nutrient content, endogenous IAA and GA levels and expression of SOS1 and NHX1 genes (Shaki et al. 2019). The co-application of GA₃ and SA on *Brassica juncea* L. enhanced growth and yield parameters, including seed yield and oil content (Ijaz et al. 2019). In *Ajuga integrifolia* L. SA application increased plant biomass and phytochemical production, including phenolics, flavonoids and antioxidants, while GA₃ behave antagonistically to downregulate their production (Abbasi et al. 2020). The exogenously applied GA₃ promoted the biosynthesis of SA, resulting in a high level of SA that improved plant defense responses against environmental cues (Emamverdian et al. 2020). Furthermore, the combined application of GA₃ and SA on *Echinacea purpurea* L. improved plant height, biomass, yield, and oil content (Hasan-beigi 2021).

Strigolactones

Strigolactones (SLs) are a group of carotenoid-derived plant growth regulators that modulate many physiological processes, including root development and shoot

branching (Wani et al. 2021b). GA and SLs may interact to regulate plant growth and developmental aspects, but their complex crosstalk is poorly understood. It has been found that GA is considered a regulator of SLs biosynthesis. Moreover, GA signaling regulates SLs biosynthesis by controlling the SLs biosynthetic gene expression (Ito et al. 2017; Marzec 2017). SLs stimulate the interaction between SLs receptor DWARF14 (D14) and a DELLA protein SLENDER1 (SLR1), exhibiting crosstalk between GA and SLs signaling pathways (Nakamura et al. 2013). The *Oryza sativa* L. GA biosynthetic mutant was insensitive to a synthetic analogue of SLs treatment, while the wild type responded to that treatment (Marzec 2017). GA and SL synergistically controlled the expression of GA2ox2 and SUPPRESSOR OF max2 1-LIKE8 (SMXL8) genes to regulate seedling growth of *A. thaliana* L. (Lantzouni et al. 2017). The defect in the biosynthesis or signaling of SLs resulted in dwarfism in *Oryza sativa* L. but could be restored by GA₃ treatment. The transcription level of cell division and cell elongation-related genes was enhanced by GA₃ treatment leading to increased shoot elongation (Zou et al. 2019).

Conclusion and Future Prospective

The constant rise in food demand due to expanding population, depleted natural resources, and climatic uncertainty is a major concern worldwide. Among the natural calamities, abiotic stress is a significant factor that adversely affects the growth and productivity of economically important crops. Plant growth regulators play a significant role in providing tolerance against abiotic stresses and improving the growth and production of crop plants. One of the important and widely discussed phytohormones is gibberellins, which are essential in improving various aspects of the horticultural crop's plant growth, development, and post-harvest life. Gibberellins enhance the abiotic stress tolerance in crop plants by modulating many gene expressions which influence the levels of antioxidants (enzymatic and non-enzymatic), osmolytes, and several other proteins and enzymes. Gibberellins interact with other plant growth regulators to improve plant growth and physiological processes. From the above-reviewed literature, it may be concluded that exogenous application of gibberellic acid increased morphological traits, physiological and metabolic processes, and yield and quality components of crop plants under diverse environmental conditions. However, in the future, there is a need to conduct further research on this hormone to explore its potential role and use it as a management tool for increasing the growth, productivity, and shelf life of valuable crops. Furthermore, the

comprehensive knowledge to understand the relationship of gibberellins with other phytohormones under salt stress conditions are need to be widely investigated.

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Declarations

Conflict of interest The authors announce that no competing interest exists.

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