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REVIEW

Mitigating Strategies of Gibberellins in Various Environmental Cues and Their Crosstalk with Other Hormonal Pathways in Plants: a Review

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Abstract

Phytohormones are chemical substances that in minute concentration instruct a plethora of developmental and physiological responses in plants. These signal molecules synthesized within the plant body are referred to as plant growth regulators. The available literature revealed that manipulation of phytohormonal content could be a promising approach towards augmentation of environmental stress tolerance in crop plants. They play pivotal role in acclimatization against unstable environmental extremes. Gibberellins are plant hormones affecting germination, stem elongation, flowering, abolition of dormancy, determination of sex expression, leaf and fruit senescence, and enzymatic stimulation. The uncertainty in climatic condition and over expanding population has led to a heap of abiotic stresses in plants. Salinity, high temperature, chilling, freezing, heavy metals, drought, flooding, allelochemicals, and radiation are the stresses that hinder development of plants. The perception of these stresses by plants occurs in a highly coordinated and interactive manner by triggering the activation of a myriad of elaborate signaling networks in which phytohormones play a significant role. The present review describes biosynthesis, signaling, and the potential roles of gibberellins as a tool in mitigating stress, increasing growth, development, and tolerance in plants. In future, revelations evolving the comprehensive knowledge to understand the relationship of plant growth regulators and stress conditions are discussed. This review also enlightens the latest research progress in GA signaling and its crosstalk with other hormonal pathways, underlying the multitude role of DELLA proteins with components of other hormonal signaling pathways.

Keywords Phytohormones · Gibberellins · Abiotic stresses · Biosynthesis · Hormonal crosstalk

Introduction

In the present scenario of environmental conditions, plants grow continuously with the extreme levels of eliciting stresses. These stresses due to abiotic and biotic factors prevailing in the environment cause devastating effects on plants and lead to a loss in crop productivity globally (Rasool et al. 2018). There is approximately 55% decrease in the usual yield of chief crops (Bray et al. 2000). The plants are exposed to a vast range of environmental stresses viz. water deficit, freezing, heat, and salt stress which provide a complex and specified cellular and molecular response mechanism in a plant.

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Environmental stress factors pose negative effects on plant growth and metabolism and prove to be a major constraint in reducing the overall crop production (Mahalingam 2015). It is very interesting to investigate how plants perceive these stress elicitors, the way in which plants receive and respond to initial cues, and then their response and regulation at the genetic level (Yoshida et al. 2014). The increasing food demand leads towards deciphering novel and appealing strategies for the use of phytohormones as a method in producing stress-tolerant crops with high yields (Wani et al. 2016). Various intricate signaling processes in plants allow the initiation of crucial cellular and physiological adaptive responses towards stress.

Plants tolerance to stress involves diverse signaling molecules, stress recognizing receptor proteins, downstream signaling transducers, transcription factors, different genes, and metabolites involved in stress responses (Iqbal et al. 2011). Some plant species are stress-tolerant, while others are escapers or avoiders with wide physiological plasticity, adaptation, and acclimation mechanisms (Mickelbart et al. 2015). The stress-responsive metabolites, heat-shock proteins (HSPs), and hormonal homeostasis mitigate the harmful effects of heat injuries in the plants (Dobra et al. 2015). Alteration in hormone homeostasis and stability may be a consequence of heat stress tolerance in various crop plants (Bita and Gerats 2013). Engineering of improved crop plants using phytohormonal application could prove to a perfect platform for biotechnologists in devising stress tolerance mechanisms. The surveillance of stress signal significantly initiates the signal transduction cascades in plants where phytohormones work as the basal transducers (Novak et al. 2017).

Phytohormones act at the definite site of synthesis and imply accurate channel for transport to the site of action within the plant body to mediate key the response towards environmental stimuli in plant growth under both favorable and unfavorable conditions (Per et al. 2018). Phytohormones mediate both internal and external stimuli and coordinate diverse signaling cascades for better elicitation of response during stress tolerance (Kazan 2015). Gibberellins (GAs) are a class of tetracyclic diterpenoid, playing a pivotal role in growth and development, seed germination, dormancy, leaf expansion, stem elongation, flowering, sex expression, enzyme induction, senescence of leaf and fruit, and hormonal homeostasis (Hyun et al., 2016). They were first obtained from the metabolite products of pathogenic fungus, *Gibberella fujikuroi*, in the rice plant in 1938 (Santner et al. 2009). They are also involved in regulating plant growth and metabolism through stress tolerance pathways and are being used as a vital weapon in various modern agricultural practices. Recently, it has been surveyed that two GA transporters (nitrate transporter 1/peptide transporter family (NPF) and SWEET13/14 proteins) are involved in mediating long-distance movement and distribution of GA (Tal et al. 2016; Kanno et al. 2016).

A recent study on *Tilia miqueliana* seeds for consistent germination has been reported that during cold stratification, substances such as soluble protein, sugar, starch, and enzyme activities of protease and α-amylase were evaluated. The maximum values for both enzyme activities were observed in combined treatment of magnetically treated water-gibberellic acid (GA_3) and these changes could trigger the dormancy break and rapid germination (Yao and Shen 2018). Enhanced lodging resistance and biomass yield was correlated with increased production of GA in rice GA-deficient mutants with and high-GA producing lines (Okuno et al. 2014). Several studies have evinced that various hormones act in concert with each other, either synergistically or antagonistically, in an orchestrated manner to regulate a myriad of biological processes in plants (Peres et al. 2019). Genetic and molecular studies have unravelled that GA interacts with several hormonal pathways through a multifaceted network of interactions with downstream transcription factors or regulatory proteins from different families in explicating diverse developmental and adaptive responses (Ross et al. 2016).

In this review, we have tried to incorporate the knowledge that has been summarized over the last couple of decades regarding the ameliorating strategies of plants exposed to GA under varied environmental constraints through molecular approach. Attempts have been discussed towards highlighting the molecular events concerning the crosstalk between GA and other hormones in mediating array of developmental and stress adaptive mechanisms in plants.

Biosynthesis of Gibberellins

GAs is usually synthesized by methylerythritol phosphate (MEP) pathway in various plants (Hedden and Thomas 2012). In this pathway, trans-geranylgeranyl diphosphate (GGDP) is converted into bioactive GA (Hedden and Thomas 2012). Isopentenyl pyrophosphate (IPP) gets condensed in 20 carbons GGDP which acts as a biosynthetic precursor for GAs. Terpenoid pathway takes place in plastids and they become biologically active after modification in the endoplasmic reticulum and cytosol (Jaleel et al. 2007). The basic enzymes involved in yielding GAs from GGDP are terpene synthases (TPSs), cytochrome P450 monooxygenases (P450s), and 2-oxoglutarate-dependent dioxygenases (2ODDs) (Yamaguchi 2008; Hedden and Thomas 2012). Expression of three classes of dioxygenases enzymes, GA 20-oxidase (GA20ox), GA 3-oxidase (GA3ox), and GA 2-oxidases (GA2ox), is the main source of regulation of GA biosynthetic pathway during development and in different environmental cues. GA20ox and GA3ox are enzymes involved in triggering the production of bioactive GAs while GA2ox is the catabolic enzyme produces inactive GA products.

GGDP in the plastids is transformed to ent-kaurene. Then, ent-kaurene is transported to the endoplasmic reticulum where it gets oxidized to GA_{12} which is the first GA produced and acts as a precursor of all types of GAs. Then, GA_{12} moves to cytosol were it is converted to GA_9 and GA_{53}. GA_9 by nonhydroxylation reaction produces GA_4 and GA_{53} while by hydroxylation reaction produces GA_1. GA_4 and GA_1 are bioactive GAs. Most bioactive GAs is found in prominently growing plant organs (Hedden and Thomas 2012). The diagrammatic representation of biosynthesis mechanism of bioactive gibberellins is shown in Fig. 1.

Signal Transduction Mediated by Gibberellins

There are various components which take part in signaling responses mediated by GAs. The bioactive GA enters the cell and binds to their soluble, nuclear receptor called gibberellin insensitive dwarf 1 (GID1). It causes a conformational change that triggers its interaction with a repressor called DELLA protein. DELLA is a class of nuclear proteins acting as transcriptional regulators having 2 domains, one is amino-terminal regulatory DELLA domain and the other one is carboxy terminal repressor GRAS domain (Colebrook et al. 2014). Further GA, GID1, and DELLA complex binds to SKP, Culin, F-box (SCF) ubiquitin ligase, which adds ubiquitin to the DELLA protein and ultimately initiates its degradation via the 26S proteasomal activity (Schwechheimer 2008). Degradation of DELLA protein will facilitate the release of transcription factors that will promote the expression of various genes involved in the GAs response. DELLA has been found to be a key mediator in other hormone signaling pathways showing an interrelationship of GA signaling with other hormonal mechanisms (Hou et al. 2010; Bai et al. 2012; Colebrook et al. 2014).

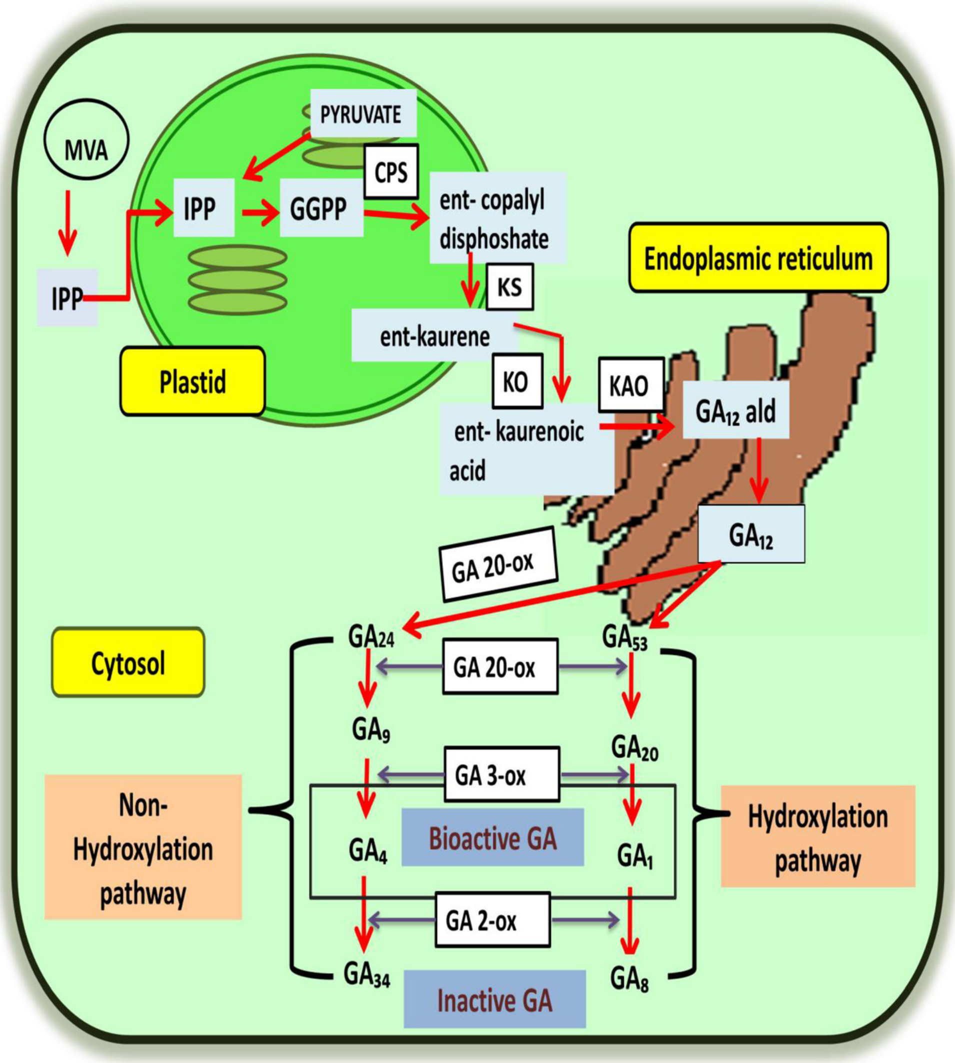

Fig. 1 Diagrammatic representation of biosynthesis of gibberellins in plants. CPS: ent-Copalyl diphosphate synthase; KS: ent-Kaurene synthase; KO: ent- Kaurene oxidase; KAO: ent-Kaurenoic acid oxidase; GA 20-ox: gibberellin 20-oxidase; GA 3-ox: gibberellin 3-oxidase; GA 2-ox: gibberellin 2-oxidase

Significant Role of Gibberellins in Mitigation of Various Stresses

GAs are important plant hormones that have been well studied for their strategies concerning stress alleviation. There are various physiological and anatomical parameters that are under the control of GAs action. A schematic representation of different roles governed by gibberellins in plants is shown in Fig. 2. An enormous research effort had been tailored towards deciphering the potential role of these phytohormones in stress tolerance and some of these recent studies have been outlined in this review. Mitigating role of gibberellins in various stresses in different plants is shown in Table 1 and Fig. 3.

Role of Gibberellins in Mitigation of Salt Stress

Salinity is major abiotic stress has affected 6% of the total land's surface area (Parihar et al. 2015) and 30% of the irrigated land negatively hampers growth and yield of plants (Fahad et al. 2015). It is responsible for the overproduction of ROS which hinders the cellular redox system in favor of oxidized forms. ROS creates oxidative stress that may be responsible for DNA mutation, enzymes inactivation, and lipid peroxidation leading to oxidative damage, cell death, and suppression of growth. Salinity stress disturbs the distribution of minerals, stability, and permeability of membrane, carbon, and nitrogen metabolism; decreases biosynthesis of chlorophyll (Hakeem et al. 2012); and increases ions toxicity and respiration rates (Liang et al. 2018).

GAs are reported to alleviate the deleterious effects of salinity by increasing the nitrogen-use efficiency, nitrate reductase activity, carbonic anhydrase activity, chlorophyll content, and absorption of mineral nutrient leading to improved plant yield (Criado et al. 2017). It has been reported that GAs enhance the growth of sugarbeet (Kandil et al. 2014), maize (Tuna et al. 2008), lettuce (Nasri et al. 2012), and tomato (Maggio et al. 2010) subjected to saline stress. GAs application to tomato plants caused increased stomatal conductance and improved water use efficiency of a plant at lower salinity level (Maggio et al. 2010). Hormonal priming by GA_3 augmented various germination characteristics of primed wheat seeds which may be corroborated to higher antioxidant enzymes profile of seeds subjected to stress (Tabatabaei 2013). In the case of higher concentrations of salt stress, GAs stimulates higher germination percentage owing to enhanced starch reserves transitions and amylase activity in cotyledons (Kaur et al. 1998; MacNeill et al. 2017).

Foliar application of GA_3 (0.1 mM) and/or ascorbic acid (0.1 mM) to okra seedlings under NaCl stress aggravated various growth attributes. Furthermore, it was noted that the

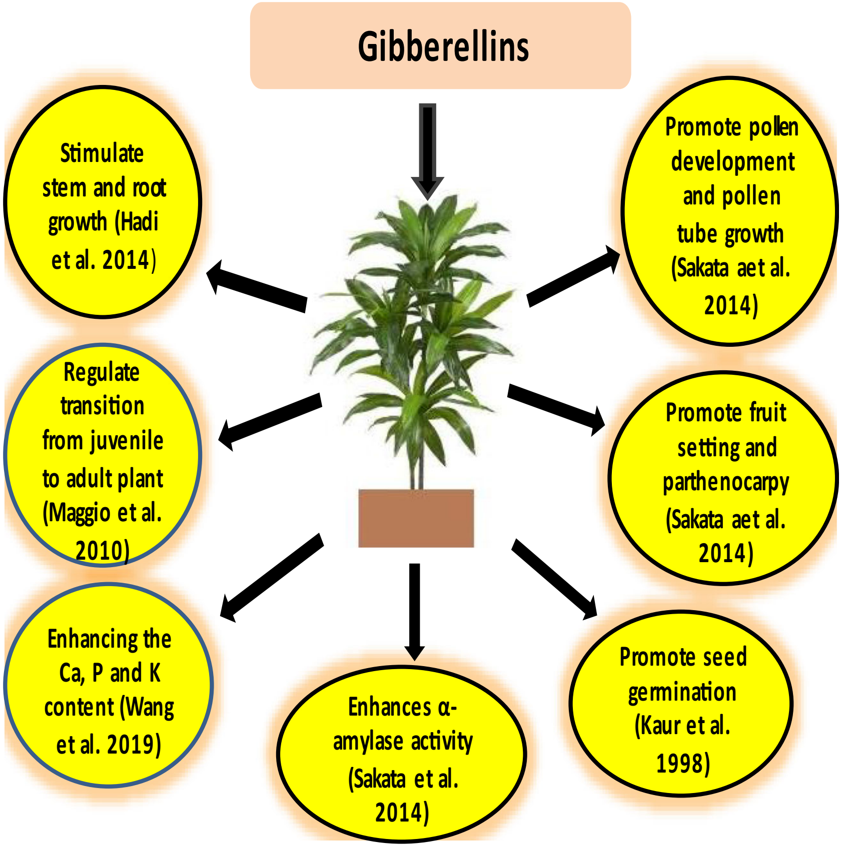

Fig. 2 Diagrammatic representation of various roles governed by gibberellins in plants

Table 1 Role of GA in mitigation of different stresses in plants

S.No.	Stress	Plants	Effects	Conc. of GA	Mitigating effect by GA	References
1.	Heavy Metal (Chromium)	*Pisum sativum*	Decreased seed germination, protein, nitrogen content, NR activity.	10 and 100 μM	Increased seed germination, plant length, protein, nitrogen content, NR activity.	Gangwar et al. 2011
2.	Heavy metal (Cadmium and Molybdenum)	*Hordeum vulgare*	Decrease sugars, protein content, radicles, α-amylase activity, acid and alkaline phosphatase	0.5 μM	Increased sugars, protein content, radicles, α-amylase activity of acid and alkaline phosphatase	Amri et al. 2016
3.	Heavy metal (Cadmium)	*Arabidopsis thaliana*	Chlorosis, inhibition of the root and shoot growth, increased lipid peroxidation and MDA content.	5 μM	Increase in root and shoot growth, decreased lipid peroxidation and MDA content	Zhu et al. 2012
4.	Heavy metal (Nickel)	*Triticum aestivum*	Decreased plant height, root length, fresh, dry weight, chlorophyll content, antioxidant enzyme activity and increased electrolyte leakage, MDA content.	10^{-6} M and 10^{-8} M	Increased plant height, fresh, dry weight, chlorophyll content, antioxidant enzyme activity and decreased electrolyte leakage.	Siddiqui et al. 2011
5.	Heavy metal (Cadmium)	*Brassica napus*	Decreased seed germination, fresh and dry weight, chlorophyll content and higher MDA content.	50 μM	Increased fresh and dry weight, chlorophyll content.	Meng et al. 2009
6.	Heavy Metal (Nickel)	*Glycine max*	Chlorosis, reduction in dry weights, chlorophyll Content, antioxidant enzymes activity and induce oxidative stress.	0.05 mM	Increased growth, root and shoot dry weights, chlorophyll Content, antioxidant enzymes activity.	Saeidi-Sar et al. 2007
7.	Heavy Metal (Nickel)	*Vigna radiata*	Reduction in shoot and root length, fresh weight and dry weight, photosynthetic pigments, chlorophyll content and induces oxidative stress.	10^{4} M	Increased shoot and root length, fresh weight and dry weight, photosynthetic pigments, chlorophyll content.	Ali et al. 2015
8.	Heavy Metal (Copper)	*Pisum sativum*	Induced oxidation and disrupted cellular homeostasis of cell	1 μM	Regulated thioredoxin/ferredoxin systems	Ben Massoud et al. 2018
9.	Heavy Metal (Cadmium)	*Parthenium hysterophorus*	Reduced plant growth and biomass	10^{-9}, 10^{-7}, and 10^{-5} M	Increased plant growth and biomass	Hadi et al. 2014
10.	Salt stress	*Brassica juncea*	Reduction in shoot and root length, fresh and dry weight, Leaf RWC, photosynthetic pigment, chlorophyll content while increase in electrolyte leakage, proline.	75 ml pot^{1}, conc. 75 mg 1^{1}	Increase in shoot and root length, fresh and dry weight, Leaf RWC, photosynthetic pigment, chlorophyll content reduction while electrolyte leakage decreased.	Ahmad 2010
11.	Salt stress	*Phaseolus vulgaris*	Reduction in fresh and dry weight, leaf area, photosynthetic pigments, protein, anthocyanin content, antioxidant enzyme activity while higher level of MDA, hydrogen peroxide (H_2O_2) content.	0.05 mM	Increased in fresh and dry weight, leaf area and leaf dry weight, photosynthetic pigments, protein anthocyanin content and activity of antioxidant enzyme.	Saeidi-Sar et al. 2013
12.	Salt stress	*Triticum aestivum*	Leaf area, photosynthetic pigments, carbohydrate, protein declined, Proline content increased.	100 mg L10)^{1} ml of 100 ppm)	Leaf area, photosynthetic pigments, carbohydrate, protein content increased.	Shaddad et al. 2013
13.	Salt stress	*Zea mays*	Leaf RWC, dry weight, chlorophyll contents, Electrolyte leakage increased.	50 ppm and 100 ppm	Leaf RWC, dry weight, chlorophyll contents increased while decreased Electrolyte leakage.	Tuna et al. 2008
14.	Salt stress	*Abelmoschus esculentus*	Decreased various growth attributes	0.1 mM	Increased levels of K, Ca, Mg and Fe and osmoprotectants	Wang et al. 2019
15.	Salt stress	*Oryza sativa*	Decreased levels of various lipids	10 μM	Upregulation of lipid biosynthesis	Liu et al. 2018
16.	Salt stress	*Glycine max*	Decrease in chlorophyll contents, root and shoot length and fresh and dry biomass, isoflavones content, endogenous ABA, SA and JA Content.	0.5 μM, 1.0 μM, and 5.0 μM	Increased chlorophyll contents, root and shoot length, plant fresh and dry biomass, isoflavones content, and endogenous ABA, SA and JA Content.	Hamayun et al. 2010
17.	Salt stress	*Beta vulgaris*	Decreased characters of seed germination and germination percentage, while mean germination time (MGT) increased.	0,100 and 200 ppm	Increased characters of seed germination and germination percentage, while mean germination time (MGT) decreased.	Kandil et al., 2014
18.	Low temp stress	*Oryza aestivum*	Leads to a drastic reduction in mature pollen and a severe decline in the seed-setting rate	10 μM	Promoted formation of mature pollen, increased seed-setting rate.	Sakata et al. 2014

Table 1 (continued)

S.No.	Stress	Plants	Effects	Conc. of GA	Mitigating effect by GA	References
19.	Low temp stress	Potato tubers	Induced cold-induced sweetening of potatoes during postharvest storage		Exhibited decreased dormancy, increased sprouting and increased levels of reducing sugars	Xie et al. 2018
20.	Low temp stress	*Solanum lycopersicum*	Electrolyte leakage, MDA content, POD activity, proline and CAT activity increased.	0.2 mmol L^{1}	Decrease in electrolyte leakage, MDA content, POD activity, proline content, CAT activity decreased.	Ding et al. 2015
21.	Low temp stress	*Solanum lycopersicum*	Severity of chilling injury (CI) in fruit increased.	0.5 mM	Reduced chilling injury (CI) index	Zhu et al. 2016
22.	Low temp stress	*Anacardium occidentale*	Deteriorated the postharvest quality	180 mg L^{-1}	Enhanced postharvest quality by decreasing both mass and firmness loss without disrupting the physicochemical variables	Souza et al. 2016
23.	Drought stress	*Zea mays*	Leaf relative water content, dry weight, total chlorophyll concentration decreased, larger root:shoot ratio, Electrolyte leakage increased.	25 and 50 mg L^{1}	Leaf relative water content, dry weight, total chlorophyll content increased and Electrolyte leakage decreased.	Kaya et al. 2006
24.	Drought stress	*Zea mays*	Plant height, internode length, stem diameter, leaf chlorophyll index (SPAD values), cob length, seed weight, and cob diameter reduced	50, 100, and 150 mg L^{1}	Increase in plant height, internode length, stem diameter, leaf chlorophyll index (SPAD values), cob length, seed weight, and cob diameter	Akter et al. 2014
25.	Allelopathic stress (Juglone)	*Lepidium sativum*	Inhibition in seed germination, Root and shoot growth, fresh weight and dry weight	1 mM	Seed germination, Root and shoot growth, fresh weight and dry weight were alleviated.	Terzi and Kocacalıskan, 2009

combined treatment of GA_3 + ascorbic acid in NaCl-stressed seedlings greatly increased the levels of K, Ca, Mg, and Fe in leaves and roots and osmoprotectants like proline and soluble protein (Wang et al. 2019). Enhanced accumulation of organic solutes like glycinebetaine and proline was encountered in *linum* plants treated with GA_3 and calcium chloride ($CaCl_2$) exposed to Nacl toxicity which might have involved in osmotic adjustment in plants (Khan et al. 2010). Combined treatment of $CaCl_2$ and GA_3 improved carbonic anhydrase activity of plants fed with Nacl, which could have regulated the rubisco levels leading to enhanced net photosynthetic rate in plants. Salinity hamper plant growth by decreasing the GA production in plants, and exogenous GA application could augment growth by enhancing endogenous GA content (Saeidi-Sar et al. 2013). GA-mediated growth in stress resulted in enlarged leaf area, initiation of cell division and/or cell elongation, increased photosynthetic rate, and upregulated invertase activity.

Kandil et al. 2014 found that soaking sugarbeet seeds in GA_3 at 100 and 200 ppm could significantly increase averages of final germination percentage (FGP), mean germination time (MGT), coefficient velocity (CV), seedling vigor index (SVI), energy of germination (EG), emergence rate (ER), and speed of germination (SG) under saline conditions. It was reported that increased salt concentration could decrease FGP, CV, SVI, EG, ER, and SG while increase MGT. GA applied to salt-fed plants decrease rates of water loss and gradually raise the water potential of leaves and increase rates of carbon gain which may ultimately lead to enhanced biomass production in plants (Ahmad 2010). Exogenous application of GA could greatly increase leaf elongation rates (LER) under stress and nonstress conditions caused due to higher cell elongation and production rates in 2 genotypes of *Festuca arundinacea* (Xu et al. 2016). Quantitative PCR analysis demonstrated that gene *EXPA7* was downregulated by salt treatment in both the genotypes whereas it was upregulated by GA under nonstress conditions.

GA_3 (17 μM) induced salt tolerance by enhancing the levels of cytokinin (CK), and auxin in *Sorghum bicolor* plants has been reported (Forghani et al. 2018). The authors used GA_3 inhibitor, paclobutrazol, and GA_3-treated plants in the experiment and suggested that altered levels of GA_3 caused different allocation pattern by modulating the ratios of CK/GA_3, Indole acetic acid/GA_3, and total polyamines/GA_3. Rice plants exposed to salt stress significantly decreased levels of various lipids including monogalactosyldiacylglycerol, digalactosyldiacylglycerol, and phospholipid lipids + sulfoquinovosyl diacylglycerol. The seeds pretreated with 10 μM GA_3 prior to salt stress maintained high lipid levels by upregulating gene monogalactosyldiacylglycerol synthase (OsMGD) (Liu et al. 2018). The three wheat cultivars (Gascogen, Zagros, and Kuhdasht) exposed to foliar sprayed GA_3 (50 mg L^{-1}) under saline condition caused 58.03%

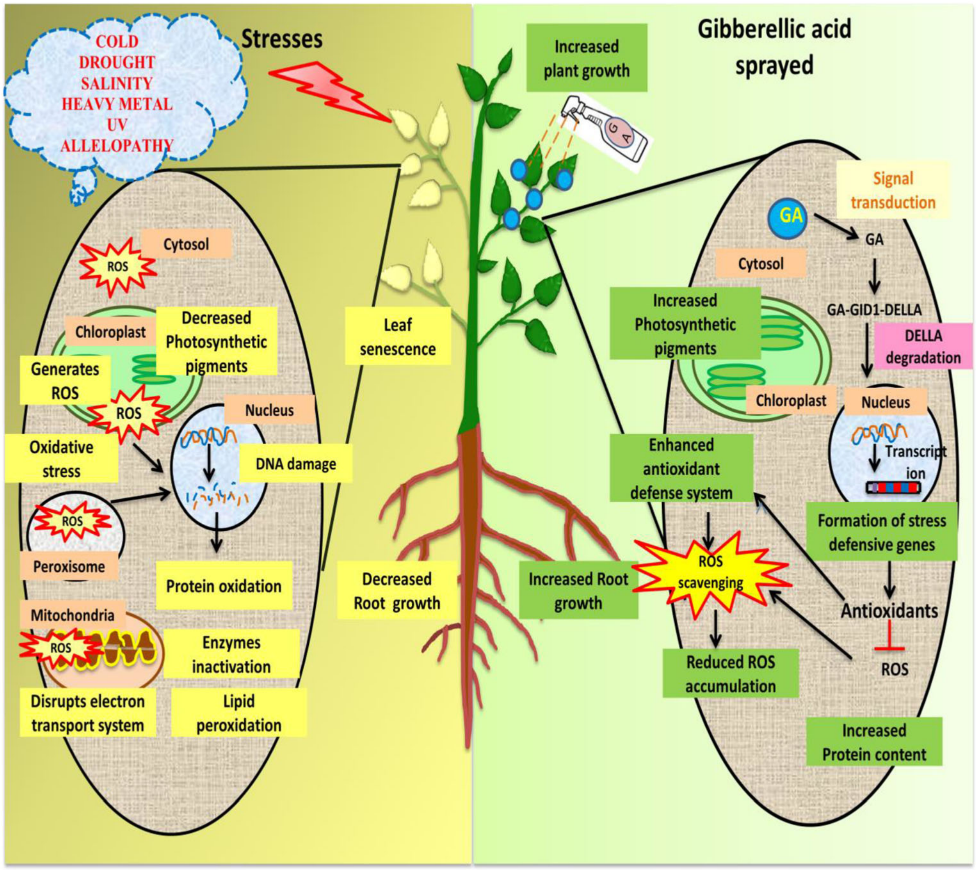

Fig. 3 Schematic representation of detrimental effects of stresses and their mitigation by gibberellins in plants. **a** Various deleterious effects caused by different stresses which leads to alteration in various physiological parameters and enhance production of ROS species in different cellular compartments of the cell and cause oxidative stress which ultimately leads to DNA damage, lipid peroxidation, enzyme inactivation etc. in plants. **b** The gibberellic acid mediated stress alleviating strategies in plants by enhancing production of various stress defensive genes and antioxidants which acts as ROS scavengers and reduce ROS accumulation and leads to better growth of plants

increase in rubisco carboxylase activity and decreased proline content (Manjili et al. 2012).

Role of Gibberellins in Mitigation of Heavy Metal Stress

Industrial activity and anthropogenic lifestyles caused a continuous increase in water and soil pollution by heavy metals, and pose a threat to life (Bücker-Neto et al. 2017; Marichali et al. 2014). Heavy metals aggregated beyond a critical value result in oxidative stress leading to disrupted plant growth and yield (Vishwakarma et al. 2017). Heavy metals like cadmium (Cd), chromium (Cr), nickel (Ni), zinc (Zn), aluminum (Al), and arsenic (Ar) impose obstruction in various physiological attributes (Hameed et al. 2016) and cause a reduction in growth (Bonanno et al. 2017).

Cd toxicity is harmful to many metabolic pathways and it leads to reduced root and shoot growth, ROS formation like hydroxyl radicals, H_2O_2, and superoxide radicals that cause oxidative damage in plant cells, chlorosis, and leaf rolling (Asgher et al. 2014). Cr reduces seed germination, growth, and photosynthesis inhibiting nutrient uptake, changes water balance, and affects nitrogen and sulfur metabolism (Singh et al. 2016). Excess amount of Ni caused deleterious effects on seedling growth and seed germination, inhibition of mitotic activity which reduces root growth, photosynthesis suppression due to disruption in chloroplast structure, dysfunctional electron transport, and impairment of chlorophyll synthesis (Rizwan et al. 2017).

GA plays a significant part in the defense mechanism of plants against Cd stress (Masood and Khan 2013). GA is proved to be effective in enhancing the mitotic activity, carbohydrates metabolism, protein and RNA contents, and ultimately increased tolerance against Cd (Mohamed and Abdel-Razik 2005). Amelioration of toxic effects of Cd and Molybdenum (Mo) contaminants by GA_3 in barley was reported (Amri et al. 2016). Authors enumerated that GA_3 (0.5 μM) facilitated elevated activities of 4 hydrolytic enzymes (α- and β-amylase, acid, and alkaline phosphatase) paralleled with increased sugar and amino acid content in the endosperm. These results assist in the restoration of mobilization of protein and starch reserves from endosperm to roots during germination. In *Arabidopsis thaliana*, GA_3 alleviated toxicity of Cd by inhibiting the accumulation of nitric oxide and assertion of a Cd transporter gene IRT1, and ultimately resulted in less Cd accumulation and an increased Cd resistance (Zhu et al. 2012). Mustard plants grown under Cd stress undergo oxidative stress resulting in increased ethylene production along with decreased photosynthesis. However, plants supplemented with 10 μM gibberellins and 100 mg sulfur kg^{-1} soil increased sulfur assimilation, glutathione production, and photosynthesis but decreased ethylene levels (Masood et al. 2016).

Soybean seedlings with Ni toxicity were grown without ascorbic acid and/or GA_3, and Ni uptake was decreased by roots to some level and improved antioxidant enzyme activities. Authors assumed that GA_3 probably alleviates the effects of Ni stress (Saeidi-Sar et al. 2007). Pre-sowing seeds of wheat with GA_3 and calcium alone or in combination assisted in the reversal of disrupted growth attributes induced by Ni toxicity (Siddiqui et al. 2011). It was manifested that plants fed with GA_3 and calcium were effective in enhancing antioxidant activity and accumulation of proline which were apparently involved detoxification of Ni.

Pea seedlings exposed to exogenous GA under Cr toxicity evidenced improved seed germination and seed growth as compared to stressed plants due to the enhanced mobilization of nitrogenous components from cotyledons to the developing axis (Gangwar et al. 2011). GA-mediated alleviation of toxicity was allocated to recovered antioxidant activity and better nitrogen assimilation rate. Saleem et al. 2015 investigated the effect of GA in ameliorating Cr contamination in sunflower plants. The results pointed out that the combined application of GA and pressmud declined the Cr uptake from the soil, and reversed Cr toxicity by further improving various growth attributes.

GA_3 at 1 μM concentration in *Pisum sativum* plants maintained thioredoxin/ferredoxin systems and provided protection from oxidation exposed to copper stress (Ben Massoud et al. 2018). They also showed that GA_3 ameliorated cellular homeostasis by regulating the redox state of glutathione and cysteine and maintained levels of thiols and carbonyls. Exogenous application of GA on rice plants increased endogenous GA content while decreased translocation of iron (Fe) to shoots by inhibiting OsYSL2 gene expression, involved in Fe transport. Results clearly pointed out that GA amends homeostasis of Fe in rice plants via negative regulation of Fe translocation from root to shoot of plants (Wang et al. 2017).

Various literatures encourage the utilization of GA in phytoremediation of heavy metal-contaminated soils. Foliar application of GA on *Parthenium hysterophorus* plants grown under Cd-contaminated soil showed a significant increase in plant biomass correlated with the ability of GA_3 to promote cell division (Hadi et al. 2014). Similarly, Sun et al. 2013 evaluated the combined effect of GA_3 and Tween-80 on *Tagetus patula* plants under Cd contamination. According to the authors, GA_3 positively promoted growth and biomass of *Tagetus* plants.

Role of Gibberellins in Mitigation of Low Temperature Stress

Temperature stress is one of the major concerns for plant scientists worldwide due to frequent climatic changes. Low temperature stress declines photosynthetic ability and efficiency of plants by altering the exchange of gases, synthesis of chloroplast chlorophyll fluorescence (Anwar et al. 2018). The horticultural crops cultivated in regions of tropical and subtropical areas undergo through a serious storage problem imposed due to chilling injury. Chilling stress enhances the accumulation of ROS, and plants' ability to scavenge ROS during and after treatment reflects the resistance and adjustment to low temperature (Zhao et al. 2011). The activation of machinery of various antioxidant enzymes in different crop plants has proved to be an important aspect in conferring chilling stress tolerance. Various literatures are documented on the effect of low temperature on crop plants like *Pyrus malus*, *Corylus avellana*, and *Arabidopsis thaliana* seeds and indicated that gibberellins content is influenced more in cold-treated seeds than noncold-treated seeds (Derkx et al. 1994).

In tomato plants under cold stress, exogenous GA triggered the expression of GA catabolic gene, GA2ox1, and enhanced expression of C-repeat/dehydration-responsive element-binding factors (CBF1) transcription factor which provides tolerance by GA catabolism (Zhu et al. 2016). It was also noted that GA upregulated the accumulation of endogenous SA by isochorismate synthase (ICS) pathway. Tomato fruits treated with GA showed elevated endogenous GA_3 content providing tolerance to chilling injury, while fruits treated with paclobutrazol (GA biosynthesis inhibitor) decreased endogenous GA_3 content exacerbating chilling injury (Ding et al. 2015).

Growth repression is a significant approach of plants towards abiotic stress tolerance by producing bioactive GA to promote degradation of DELLA (Achard and Genschik 2009). Tomato fruit exposed to cold during storage when treated with exogenous GA showed the downegulation of DELLA gene (Zentella et al., 2007). Exogenous GA triggers the DELLA proteins degradation by the mechanism of ubiquitin-proteasome system and increase in stress tolerance (Achard et al. 2009). GA_3 treatment could significantly increase hydroxyl radical scavenging activity and ferrous ions chelating activity in cucumber hypocotyls and radicles under suboptimal temperature, which could be partly responsible for lower lipid peroxidation (Li et al. 2011).

In tomato fruit, GA_3 applied exogenously mitigated chilling injury by inhibiting electrolyte leakage and reduced MDA content, increased proline content, and increased antioxidant enzymes activities which ultimately helps to delay fruit ripening, increase firmness, and improve the life of peach fruit in cold storage (Dagar et al. 2012). The application of exogenous GA_3 elevated the level of SOD activity in gladiolus cut flower during storage (Saeed et al. 2014). In *Arabidopsis thaliana*, GAs applied exogenously under cold stress helps in breaking rosette by increased differentiation and enlargement of tissues. Moreover, the bioactive GAs increased just prior to radicle emergence in germinating seeds of *Arabidopsis thaliana* (Ogawa et al. 2003). In rice plants, GA reduced low temperature mediated male sterility and increased number of mature pollen grains, and higher seed set was reported (Sakata et al. 2014). Reduced expression of GA biosynthetic genes GA20ox3 and GA3ox1 in developing anthers under low temperature was also observed.

Xie et al. (2018) reported that the potato tubers exposed to GA exhibited decreased dormancy, increased sprouting, and increased levels of reducing sugars by regulating gene expression of ADP-glucose pyrophosphorylase (AGPase), granule-bound starch synthase (GBSS), *b*-amylase (BAM1/2), UDP-glucose pyrophosphorylase (UGPase), and invertase inhibitor (INH1/2) which could help ameliorate cold-responsive effects. The authors also suggested that GA could prove to be an effective tool in controlling cold-induced sweetening of potatoes during postharvest storage. Exposure of GA_3 (100 ppm) to 3 cultivars of *Solanum lycopersicum* namely Fayrouz, Aziza, and N23-48 under low temperature (10 °C) enhanced stress tolerance (Haroun et al. 2018). Authors made an assumption that new bands of protein in DNA fingerprinting formed which are might be involved in stress tolerance. These results suggested that low temperature stress could be attenuated by application of GA which plays a beneficial role in stress protection.

Nowadays, GA is exploited to alleviate chilling injury symptoms under low temperature storage on horticultural crops and fruits. GA_3 elevated the levels of antioxidant enzymes like catalase (CAT) and superoxide dismutase (SOD) and reduced those of peroxidase (POD) and polyphenol oxidase (PPO) in toon sprout exposed to postharvest chilling stress. Moreover, it reduced malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) content while maintaining the reducing sugar, soluble sugar, and proline levels in toon sprout (Zhao et al. 2018).

Souza et al. (2016) evaluated the effects of preharvest treatment of aminoethoxyvinylglycine and GA_3 on postharvest quality and life of cashew apples during cold storage and demonstrated that GA improved postharvest quality of apple by decreasing both mass and firmness loss without disrupting the physicochemical variables. Whereas, aminoethoxyvinylglycine effect on physiology and quality of apple was inconsistent.

Role of Gibberellins in Mitigation of Drought Stress

Drought stress is one of the major abiotic constraints which could severely affect growth and metabolism of a variety of plant species (Boaretto et al. 2014). Plants exposed to drought show impaired physiological, anatomical, and biochemical parameters such as plant growth, photosynthesis rate, turgor reduction, stomatal conductance, and damages to cellular organelles ultimately leading to a decrease in plant growth and productivity (Tripathi et al. 2016). During drought stress, the water available in the soil decreases to crucial levels and atmospheric conditions which constantly lead to enhanced loss of water. Plants tolerance to drought stress greatly differs from one plant species to the other. Drought results in oxidative stress and a substantial increment in levels of various stress adaptive molecules like flavonoids and phenolic acids. Disrupted balance of the endogenous hormone exposed to drought-stress conditions hampered various physiological attributes and increased embryo abortion (Hasanuzzaman et al. 2012).

Application of growth hormones exogenously is found to be effective in drought management. Application of GA_3 (50 mg L^{-1}) to maize plants was effective in alleviating detrimental effects of drought by enhancing plant height, internodes length, and grain yield by 78.8% (Akter et al. 2014). In this study, authors evidenced that exogenous application of phytohormones during the early growth stage could have augmented endogenous phytohormonal levels which have supplied the plant with energy to mitigate stress. They also found that phytohormonal application at the vegetative stage was more effective than at reproductive stage in ameliorating adverse effects of drought (Akter et al. 2014).

GA_3 is found to be helpful in stimulating the growth of wheat, maize, and tomato plant exposed to drought stress. The drought stress affects both elongation and expansion of plant cell; it was observed that cell division and cell elongation increased by applying GA_3 exogenously due to increment in endogenous GA content under drought stress (Rodriguez et al. 2006).

GA_3 at 32.2 mg l^{-1} concentration applied by foliar spray in *Capsicum annuum* has the ability to alleviate water stress condition by enhancing various physiological parameters. It was also noted that plants treated with GA_3 increased more in height than control plants (Pérez-Jiménez et al., 2016). In maize plants under drought conditions, decreased Ca^{2+} levels in leaves as compared to nonstressed plants were observed. Although, plants treated with GA_3 showed enhanced Ca^{2+} levels and augmented membrane stability (Kaya et al. 2006). The application of GA_3 on *Zea mays* in water deficit conditions increased the growth period, vegetative growth, cell division, and cell elongation (Al-Shaheen and Soh, 2018). The gibberellins produced by *Azospirillum lipoferum* were able to ameliorate the deleterious effects of drought stress in *Zea mays* plants (Cohen et al. 2009). In this study, maize plants treated with fluridone (inhibitors of abscisic acid (ABA) and prohexadione-Ca (Inhibitor of GA synthesis) in combination or alone reduced growth despite high ABA levels suggesting that both ABA and GA played an essential role in stress alleviation mechanism in *Azospirillum*.

Role of Gibberellins in Mitigation of Allelopathic Stress

Plants are also exposed to allelopathic stress in nature through interaction with other plants. The phenomenon of allelopathy involves either directly or indirectly and either beneficial or deleterious effects of a plant or microorganisms on another plant by releasing chemicals in the environment (Rice 1984). Chemicals involved in allelopathy are called as allelochemicals including various low molecular weight secondary metabolites obtained from plants and microorganisms which play a significant role in the plant to plant interaction.

Various studies have reported that allelochemicals can help to stimulate or inhibit germination and growth of the plant (Scavo et al. 2018), inhibit antioxidant enzymes activity, increased free radical levels which results in higher membrane lipid peroxidation, and alter membrane potential, which greatly declines the scavenging activity of activated oxygen and cause damage to plants membrane (Hussain et al. 2017). It can also influence various respiration and photosynthesis by damaging photosynthetic machinery and decreasing photosynthetic pigment, and decrease stomatal conductance and transpiration (Latif et al. 2017). Allelochemicals like 2-benzoxazolinone (BOA) in tomato (Yadav et al. 2018a) and cinnamic acid (CA) in maize (Yadav et al. 2018b). The phytohormonal application can prove to be an efficient mitigating strategy towards the devastating effect of allelochemicals (Yadav et al. 2019).

Mitigation by GAs is effectual in allelopathic stress caused by juglone (5-hydroxy-1, 4- naphthoquinone), an allelochemical released by walnut. Juglone exhibited reduction in seed germination of several plant species such as tomato, cucumber, alfalfa, radish, and watermelon (Terzi, 2008, 2009; Kocaçalı_kan et al., 2009). GA and kinetin can overcome allelochemical stress of juglone on germination and growth (Terzi and Kocacalıskan, 2009). The exogenous supplement of GA in seeds resulted in overcoming juglone stress by altering low GA concentration and proves to be beneficial for intercropping of the species which are juglone sensitive in the same field as walnut trees (Terzi and Kocacalıskan 2009). These results concluded that application of GA exogenously mitigates allelopathic stress in plants.

Gibberellins Crosstalk with Different Hormonal Pathways

The developmental events occurring in the plant life cycle imply synchronized amendments in molecular mechanisms of plant growth through intricate networking and coordinated involvement of diverse hormonal cues. In the past couple of years, various studies have confirmed that the interactions between various phytohormones are the rule rather than the exception in integrating and remodeling growth by stress resistance (Kohli et al. 2013). It has been well confirmed that auxin promotes GA biosynthesis and plays a significant role in growth of plant (Golldack et al. 2013). Hormones like auxin, GA, and CK are the central participants in regulating growth under stress conditions as during unfavorable conditions, ABA and ethylene (ET) decrease growth by altering the action of GA, auxin, and CK (Peleg and Blumwald 2011). Various research efforts have been deciphered towards investigating DELLA protein as a central hub in mediating plethora of other hormonal signals in various developmental and adaptive responses in plants (Table 2).

The interaction among brassinosteroids (BRs) and GAs is well documented (Peres et al. 2019). BRASSINAZOLE-RESISTANT 1 (BZR1) and BRASSINOSTEROID-INSENSITIVE 1 EMS-SUPPRESSOR1 (BES1) are a positive transcription factor in BR signaling. It has been reported that GA biosynthesis is regulated by BR as a result of interaction of BZR1/BES1 and DELLAs, transcription factor involved in GAs and BR signaling. The DELLA proteins interact with the BZR1/BES1 at the “GRAS” domain and inhibit the DNA-binding activity of BZR1 (Bai et al. 2012). It was noted that increased levels of BZR1 at the promoters of its targeted gene were observed by an increase in GA probably due to GA induced DELLA degradation (Li et al. 2012). Various alterations in expression of GA biosynthetic genes were observed in mutant BR signaling in *Arabidopsis thaliana* may be due to disruption in bioactive GA synthesis (Li et al., 2012; Li and He 2013; Unterholzner et al. 2015). In rice, elongation of cell mediated by BR is initiated by the GAs synthesis by upregulation of expression of GAs biosynthesis genes *D18*/*GA3ox-2* (Tong et al. 2014). The transcription factor, PHYTOCHROME INTERACTING FACTOR4 (PIF4), involved in regulating light responses plays a role in GA-BR signaling by interacting with DELLA and BZR1 proteins (Oh et al. 2012, 2014). DELLA proteins are negative regulators of PICKLE/ENHANCED PHOTOMORPHOGENIC1 (PKL/EPP1), a factor involved in chromatin-remodeling which limits cell elongation. PKL/EPP1 acts with PIF3 and BZR1 in promotion of hypocotyl growth (Zhang et al. 2014).

Auxin, another hormone, promotes hypocotyl growth. Auxin signaling pathway involves the expression or repression of transcription factor auxin response factors (ARFs) by the degradation of AUX/IAA family proteins. Plants treated with paclobutrazol, an inhibitor of GA synthesis, showed inhibition in hypocotyls growth by auxin (Chapman et al. 2012); however, in *della* mutants treated with paclobutrazol, reduced hypocotyls growth was not observed interpreting that both BR and auxin are sensitive to DELLA accumulation (Lilley et al. 2013).

GA-ABA interconnection helps in maintaining the equilibrium between seed germination and dormancy which plays a pivotal role in stress tolerance. Both these hormones show antagonistic relationship leading to high GA and low ABA levels under favorable and low GA and high ABA levels under unfavorable environmental conditions in seeds. In unfavorable conditions, increased ABA levels lead to downstream activation of transcription factors like ABSCISIC ACID INSENSITIVE 3 (ABI3) and ABI5, which negatively regulate seed germination (Piskurewicz et al. 2008). On the

Table 2 Della crosstalk with other hormonal signals in regulating various developmental functions in plants

S.NO.	Hormone	Genes involved	Function	Regulation/ expression	References
1.	Abscisic acid	ABSCISIC ACID INSENSITIVE 3 (ABI3) ABSCISIC ACID INSENSITIVE 5 (ABI5), SOMNUS	Seed germination	Negative, inhibits	Lim et al. 2013
2.	Brassinosteroid	BRASSINAZOLE-RESISTANT 1 (BZR1) and BRASSINOSTEROID-INSENSITIVE1 EMSSUPPRESSOR1 (BES1)	Hypocotyl cell elongation	Negative	Bai et al. 2012
3.	Brassinosteroid	PHYTOCHROME INTERACTING FACTOR4 (PIF4)	Regulates light responses	Negative	Oh et al. 2012, 2014
4.	Brassinosteroid	PICKLE/ENHANCED PHOTOMORPHOGENIC1 (PKL/EPP1)	Chromatin-remodeling limiting cell elongation	Negative	Zhang et al. 2014
5.	Auxin	AUXIN RESPONSE FACTORS 6 (ARF 6)	Hypocotyl cell elongation	Negative	Chapman et al. 2012
6.	Ethylene	ETHYLENE-INSENSITIVE 3 (EIN3), HOOKLESS1 (HLS1) and RELATED TO APETALA2.3 (RAPT2.3)	Formation of apical hook	Negative	Marın-de la Rosa et al. 2014
7.	Jasmonic Acid	JASMONATE ZIM DOMAIN1 (JAZ1) MYC2	Defense to herbivory and nectrotrophs	Positive	Heinrich et al. 2013
8.	Jasmonic Acid	JASMONATE ZIM DOMAIN1 (JAZ1) MYC2 GLABROUS1 (GL1), GLABROUS3 (GL3) and ENHANCER OF GL3 (EGL3)	Trichome development	Negative, inhibits	Qi et al. 2014
9.	Jasmonic Acid	SESQUITERPENE SYNTHASE GENES (TPS21 and TPS11)	Formation of sesquiterpene	Negative, inhibits	Hong et al. 2012
10.	Cytokinin	TYPE-B ARABIDOPSIS RESPONSE REGULATORS (ARRS)	Photomorphogenetic responses	Negative, inhibits	Marın-de la Rosa et al. 2015
11.	Strigolactone	DWARF14 (D14), DWARF3/MAX2/ RMS4, and DWARF53 (D53)	Axillary bud outgrowth	Negative, inhibits	Zhou et al. 2013

other hand, when the conditions are favorable, ABA levels decrease and GA synthesis is initiated, causing degradation of RGL2 and promoting seed germination (Piskurewicz et al. 2008). There is a connection found between ABA-mediated abiotic stress responses with the DELLA proteins in *A. thaliana* (Achard et al. 2006). In ABA-receptor mutant, *abi1-1*, no DELLA accumulation was observed when supplemented with ABA recommended that reduction in growth by ABA is not exclusively DELLA-dependent but requires signaling of ABI1 (Colebrook et al. 2014). Gene *XERICO* is transcriptional downstream, targeted by DELLA, and has been suggested to repress negative regulator of ABA biosynthesis (Ariizumi et al. 2013). Recently, a study evidenced that DELLA, ABI3, and ABI5 forms a complex that transcribes the gene SOMNUS (SOM) that is a negative regulator of seed germination (Park et al. 2011; Lim et al. 2013). Under unfavorable conditions, DELLA/ABI3/ABI5 complexes are accumulated which activates SOM which in turn synthesize ABA and inhibit GA synthesis and decrease seed germination (Kim et al. 2008; Lim et al. 2013).

GAs and CK shows antagonistic regulation of varied developmental pathways depicting increased SAM activity by CKs and limited by GA. In a recent study, it was underlined that DELLA proteins and type-B ARABIDOPSIS RESPONSE REGULATORS (ARRs), a transcription factor of CK signaling, are needed for the maintenance of root meristem and photomorphogenic responses (Marı’n-de la Rosa et al. 2015).

DELLA proteins are involved in ET signaling by interacting and degrading the activity of transcription factors ETHYLENE-INSENSITIVE 3 (EIN3) and EIN3-like (EIL), positive regulators of ET signaling (An et al. 2012). GA and ET with cooperative action control apical hook development, where expression of HOOKLESS1 (HLS1; an N-acetyltransferase) and RELATED TO APETALA2.3 (RAPT2.3; a TF belonging to the group VII ETHYLENE RESPONSE FACTOR) is initiated by binding of EIN3/EILs proteins; DELLA repress this response by inhibiting proteins EIN3/EILs (Marı’n-de la Rosa et al. 2014). ET signaling activation under salt stress has shown promoting tolerance to stress by stimulating the function of DELLAs by CTR1-dependent ET response pathway occurring downstream EIN3 (Achard et al. 2006). Submerged rice plants facilitate gibberellins biosynthesis by increased *GA3ox* expression as well as catabolism of ABA and also showed high ET accumulation (Colebrook et al. 2014). Enhanced bioactive GA due to ethylene response factor (ERF) domain proteins SNORKEL1 and SNORKEL2 is reported due to ethylene accumulation in submerged plants (Hattori et al. 2009). Under cold stress CBF1/DREB1b, member of the AP2/ETHYLENE-RESPONSIVE ELEMENT-BINDING PROTEIN (EREB) promotes resistance by the acquisition of DELLAs through ET signaling and reduce growth (Achard et al. 2008).

The exact interaction between GA and strigolactone (SL) is still underdeveloped (Omoarelojie et al. 2019). The data reported that GA show antagonism on SL mediated regulation of ABC-type transporters (Lantzouni et al. 2017). In rice, it was reported that DELLA protein SLENDER RICE1 (SLR1) interacts with SL receptor DWARF14 (D14) in SL-dependent manner and regulates downstream SL signaling pathway (Nakamura et al. 2013).

DELLA proteins are also involved in mediating interaction between GA and jasmonic acid (JA) by binding to JAZ1, repressors of JA signaling, thereby competing with transcription factor MYC2 which regulates JA-dependent transcriptional responses (Hou et al. 2010; Wild et al. 2012). In necrotrophic pathogens, JA provides resistance and growth inhibition, through DELLA signaling (Yang et al. 2012; Heinrich et al. 2013). JA signaling stimulated the expression of REPRESSOR OF GA1-3 (RGL3), which competes with MYC2 for binding to JAZ1 and JAZ8. Thus, RGL3 show positive role in mediating JA regulated resistance (Wild et al. 2012). Recently, a report supported the evidence that DELLA and JAZ proteins are degraded by GA and JA respectively, in order to activate the complex WD-repeat/bHLH/MYB to initiate trichome development in *Arabidopsis* (Qi et al. 2014).

The regulation from source to sink is maintained by GA both in nonstressed and stressed conditions via various physiological modifications in which GA induce production of SA. Mutants of SA, the sid2 mutants were found vulnerable to stress but were unaltered by GA when applied exogenously (Alonso-Ramı’rez et al., 2009, 2009; Kohli et al. 2013). These observations suggest that GA play a crucial role in coordinating with several other hormonal pathways and mechanisms subjected to plants stress tolerance.

Conclusion and Future Prospectives

The continuous increase in food demands for expanding population and exhausted natural resource, and climatic uncertainty is a matter of great concern. The abiotic stresses are significant constraint restraining productivity of crop worldwide. Therefore, there is a necessity to produce tolerant varieties of crop to cope with food security and scarcity. In recent years, there are fewer studies conducted dealing with biosynthesis, signaling, and physiological action of phytohormones; however, the significant role of phytohormones in regulating responses to deleterious environmental cues is still not well documented.

This review reflects that gibberellins act as one of the efficient plant growth regulators that amend various plant growth responses. Although, genes involved in GA-mediated stress resistance are known but still, there is a gap which needs to be filled in order to generate stress-tolerant varieties in field. Despite the immense progress in various genomic technologies for the elucidation of detailed and integrative knowledge for exploration of key components governing GA responses, still various challenges are in the path for engineering of stress-tolerant varieties through various breeding programs. Findings of different reports call for further investigation and analysis of the DELLA protein-mediated responses and how these proteins affect the signaling of different phytohormones other than GA. The applications of this phytohormone in future hold great potential as a management tool for providing tolerance to agricultural crops against the continuous environmental constrains which will help to extend potential crop yield in future. Further in future, it becomes necessary to unveil our focus towards multiple stress conditions as different stress conditions are likely to prevail simultaneously in field conditions by applying varied molecular techniques.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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