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Phytohormones as Growth Regulators During Abiotic Stress Tolerance in Plants

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Phytohormones (PHs) play crucial role in regulation of various physiological and biochemical processes that govern plant growth and yield under optimal and stress conditions. The interaction of these PHs is crucial for plant survival under stressful environments as they trigger signaling pathways. Hormonal cross regulation initiate a cascade of reactions which finely tune the physiological processes in plant architecture that help plant to grow under suboptimal growth conditions. Recently, various studies have highlighted the role of PHs such as abscisic acid, salicylic acid, ethylene, and jasmonates in the plant responses toward environmental stresses. The involvement of cytokinins, gibberellins, auxin, and relatively novel PHs such as strigolactones and brassinosteroids in plant growth and development has been documented under normal and stress conditions. The recent identification of the first plant melatonin receptor opened the door to this regulatory molecule being considered a new plant hormone. However, polyamines, which are not considered PHs, have been included in this chapter. Various microbes produce and secrete hormones which helped the plants in nutrient uptake such as N, P, and Fe. Exogenous use of such microbes help plants in correcting nutrient deficiency under abiotic stresses. This chapter focused on the recent developments in the knowledge related to PHs and their involvement in abiotic stresses of anticipation, signaling, cross-talk, and activation of response mechanisms. In view of role of hormones and capability of microbes in producing hormones, we propose the use of hormones and microbes as potential strategy for crop stress management.

Keywords: phytohormones, plant growth regulators, abiotic stress, plant tolerance, biosynthesis

INTRODUCTION

Environmental changes either due to anthropogenic activities or due to abrupt seasonal changes in weather pose serious challenge of survival to plants. Since plants are sessile organisms, they have to face such environmental adverse conditions. Among various environmental changes, water deficit or drought, water logging, high salinity, low or high temperature, heavy metals, and solar radiation are detrimental for optimum plant growth and development (Raza et al., 2020; Hossain et al., 2021). Thus, leading to decreases in biomass and grain yields at a global scale (Achard et al., 2006; Gururani et al., 2015). In extreme environments, different types of abiotic stresses can co-occur. For example, salt stress is frequently interlinked with drought, which can be exacerbated by extreme temperatures (Ashraf and Foolad, 2007; Aslam et al., 2013; Slama et al., 2015; EL Sabagh A et al., 2019; EL Sabagh et al., 2021). The toxic effects of salt have a detrimental impact on the root expansion and control the ability to uptake both nutrients and water (Lambers, 2003; Awais et al., 2017). Plants have developed efficient sensing, signaling, and response mechanisms to cope with these detrimental stresses. One of the most conspicuous examples of these response mechanisms exerted by plants is represented by the PHs, which can be defined as cellular signal molecules that act as chemical messengers in plants under low concentrations, and have paramount functions in the regulation of the responses that plant show to abiotic stresses (Fleet and Sun, 2005; Davies, 2010; Williams, 2011). The signaling pathways are interconnected in a complex network that modulate physiological processes to quickly adapt to environmental stresses.

According to He et al. (2018), there are five general plant defense-related metabolites against abiotic stresses: the cuticle as the external protection, unsaturated fatty acids (UFAs) as membrane modulator and oxylipin precursor, reactive species scavengers, molecular chaperones (proteins and subcellular structures stabilization), and compatible solutes. These defensive metabolites are coordinated by a complex regulatory network that involves the participation of upstream signaling molecules as stress PHs, reactive oxygen species (ROS), hydrogen sulfide (H_2S), nitric oxide (NO), polyamines (PAs), phytochromes, and calcium, as well as downstream gene regulation factors, particularly transcription factors (TFs) (He et al., 2018). At present, nine types of PHs have been identified (Su et al., 2017), including auxins, the first phytohormone discovered (Darwin and Darwin, 1880), salicylates (SA), ethylene (ET), cytokinins (CKs), gibberellins (GAs), brassinosteroids (BRs), jasmonates (JA), abscisic acid (ABA), and strigolactones (SL), the last PHs to be discovered (Gomez-Roldan et al., 2008). Among these PHs, ABA, SA, ET, and JA have been recognized to have a central role in the plant's responses to environmental stresses (Peleg and Blumwald, 2011; Wasternack, 2014). Recently, Yadav et al. (2021) reviewed that phytohormones including ABA, BRs, CK, ET, GA, JA, and SA play crucial role in drought stress tolerance in plants through regulation of cellular functions at molecular levels through cell signaling. The SL and BR constitute a new plant hormone of increasing importance due to their involvement in the response against stresses such as extreme temperature and drought (Brewer et al., 2013; Ha et al., 2014; Nolan et al., 2020). Melatonin, a recently identified plant hormone, is involved in multiple physiological actions, such as growth, rooting, seed germination, photosynthesis, and protection against abiotic and biotic stresses (Maheshwari et al., 2015). Although polyamines are high in concentration and poorly translocated within the plant (conversely to PHs), they are necessary for plant growth under normal or stress conditions (Liu et al., 2007).

The homeostasis of PHs is controlled by regulation of metabolic pathways, transport, and cellular compartmentations (Pieterse et al., 2009; Iqbal, 2015b). Recently, mutants of hormone-biosynthetic pathways are generally used to understand integration of hormonal circuits into molecular processes associated with stress responses. Therefore, deciphering how plants can better tolerate environmental stresses with minimum or no reduction in their productivity is an important challenge

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Abbreviations: ABA, Abscisic acid; ABF, ABA-responsive factor; APX, Ascorbate peroxidase; ARF, Auxin response factor; AsA, Ascorbate; BRs, Brassinosteroids; CA, Cinnamic acid; CAT, Catalase; CKs, Cytokinins; CS, Chlorophyll synthase; DHA, Dehydroascorbate; DHAR, Dehydroascorbate reductase; ET, Ethylene; GAs, Gibberellins; GR, Glutathione reductase; GSH, Reduced glutathione; GSSG, Oxidized glutathione; H_2S, Hydrogen sulfide; IAA, Indole-3-acetic acid; IAM, Indole-3-acetamide; IAOx, Indole-3-acetaldoxime; IPA, Indole-3-pyruvic acid; IPT, Isopentenyl transferase gene; IPTs, Isopentenyl transferase; JAME, Jasmonic acid methyl ester; JAs, Jasmonic acids; MDHA(R), Monodehydroascorbate (reductase); MTA, Methylthioadenosine; NADPH, Nicotinamide adenine dinucleotide phosphate; NCED, 9-cisepoxy carotenoid di-oxygenase; NO, Nitric oxide; OPDA, Octadecanoid cis (+) 12 oxophytodienoic acid; Pas, Polyamines; PGPR, plant growth-promoting rhizobacteria; Phot, Phototropin; PHs, Phytohormones; PP2C, Protein phosphatase type-2C; PYL9, Pyrabactin-like receptor 9; RAF1, Rubisco accumulation factor 1; RNS, Reactive nitrogen species; ROS, Reactive oxygen species; SA, Salicylic acid; SAM, S-Adenosyl methionine; SOD, Superoxide dismutase; SL, Strigolactones; SnRK4, Sucrose non-fermenting-1-related protein kinase 4; TAM, Tryptamine; TFs, Transcription factors; UFAs, Unsaturated fatty acids; ZEP, Zeaxanthin epoxidase.

for researchers. **Figure 1** shows an overview of microbial phytohormone-mediated stress tolerance mechanisms in plants (Egamberdieva et al., 2017). This review aims to enhance the knowledge of the effects of abiotic stresses on endogenous PHs concentrations, and their role in plant physiology to elucidate the potential mechanisms of phytohormone-mediated abiotic stress responses in plants. This information can be used in forward-thinking solutions for developing climate smart crop cultivars in our dynamically changing world.

PHYTOHORMONES

Abscisic Acid

Abscisic acid was discovered in early 1960s and found that this phytohormone was responsible for breaking seed dormancy (Cornforth et al., 1965). Later on, it has been found that it has potential role in plant development and stress adaptive responses in plants (Guschina et al., 2002; Iqbal, 2015a). For example, ABA is involved in seed maturation and seed dormancy, and regulation of water in plant body through stomatal opening and closing, and adaptations of a plant to environmental stresses. Under water deficit conditions, ABA is biosynthesized in roots and transported to leaves *via* xylem thereby increase in concentration in the leaves. This increase of the ABA acts as a signal and start signaling cascade in guard cells to regulate cell turgor of guard cells (Danquah et al., 2013; Awan et al., 2017). In the abiotic stress response, the biosynthesis and redistribution of ABA cause stomatal closure and reduce transpiration rate, restricting cell growth (Peleg and Blumwald, 2011). ABA is quite famous for its functions in plant-water relations (Arkhipova et al., 2020).

ABA up-regulates hormone-responsive transcription factors, and in ABA signaling phosphatases and kinases play role in mediating fast responses to various abiotic stresses (Dar et al., 2017).

ABA biosynthesis pathway is derived from carotenoids (Nambara and Marion-Poll, 2005). Stress stimuli rapidly trigger ABA biosynthesis from β-carotene oxidative cleavage using 9-cis-epoxy carotenoid di-oxygenase (NCED) enzyme. The zeaxanthin epoxidase produces trans-violaxanthin, which gets converted to a 15-C compound called neoxanthin. After that, conversion of xanthoxin to abscisic aldehyde occurs, and then its oxidation leads to ABA production. The biosynthesis of ABA by the β-glucosidase homologs from ABA-GE has also been reported as an alternate pathway of ABA synthesis in some plant species exposed to abiotic stresses (Xu et al., 2013; Llanes et al., 2014).

Moreover, ABA not only mediate physiological responses through its own signaling, it also regulate physiological responses through interacting with other PHs in plants exposed to abiotic stresses (He et al., 2018). It is worth mentioning that ABA triggers and mobilizes an array of biochemical defenses such as biosynthesis of proline, antioxidants, ROS detoxifying enzymes, heat shock proteins, and unsaturated fatty acids along with the strengthening of cuticular waxes, which enable plants to ward-off adverse effects of abiotic stress to some extent (Ashraf and Foolad, 2007; Chen et al., 2013; Lee and Suh, 2015; Hoque et al., 2016; Huang et al., 2016; Liu et al., 2018; Yin et al., 2018; Singhal et al., 2021).

Ethylene

Ethylene is in gaseous form and involved in many vital morpho-physiological processes such as triple response in germinating seeds, developing flowers, ripening fruits, and triggering plant responses against environmental stimuli. Besides, ET regulates several stress-related biochemical responses of plants exposed to abiotic stresses such as heat, drought, chilling, salinity, heavy metals, water-logging, flooded, or submerged conditions (Awan et al., 2017). For instance, a close association between high ET level and freezing and cold stress was observed in *Arabidopsis* (Shi et al., 2012) and *Medicago truncatula* (Zhao et al., 2014), and regulation of ET homeostasis is crucial for sub optimal temperature stress (chilling and freezing) tolerance. High ET levels are help in salt stress tolerance as in salt tolerant *Arabidopsis* plants. The *ETIO1* (ethylene over producer) act positively in salt stress by maintaining Na^+/K^+ homeostasis and ROS production (Yang et al., 2017). Moreover, it plays a crucial role in altering plants' response to pathogen attack, external mechanical wounding, UV radiations, and nutrients deficiency. ET biosynthesis and accumulation were reported in many cases in response to damage or mechanical injury (Abeles et al., 1992; Kendrick and Chang, 2008).

The biosynthesis of ET, as shown in **Figure 2**, has been quantified in various plant tissues, wilting flowers, and ripening fruits in plants exposed to abiotic stresses (Kendrick and Chang, 2008). The underlying mechanism for ET biosynthesis gets initiated with S-Adenosyl methionine (SAM), which is the precursor of ET and is usually synthesized in large concentrations in various crops and fruit trees. An enzyme called 1- aminocyclopropane-1-carboxylic acid (ACC) synthase catalyzes the first chain reaction to convert SAM to ACC, and methylthioadenosine (MTA), which subsequently gets recycled to L-methionine. Owing to this recycling, L-methionine levels remain unchanged even when ethylene biosynthesis is at its peak. Moreover, the ET biosynthesis pathway is affected by ACC synthase enzyme, which is extremely labile and tends to limit biosynthesis rate and rises proportionally as that of ethylene levels in tissues, flowers, and fruits (Maheshwari et al., 2015).

Salicylic Acid

Among phenolic endogenous growth regulators, salicylic acid is one of the most vital growth regulators and has been characterized in almost all plant species belonging to diversified groups. The SA concentration has been reported to be 1 $\mu g\ g^{-1}$ of fresh biomass of rice, barley, and soybean crops. Its role as a regulator of an array of biochemical and physiological processes in plants has been identified. It helps in induction of systemic acquired resistance to various pathogens has been widely studied in plants (Misra and Saxena, 2009). However, in plants subjected to salinity and osmotic stresses, the SA role remained somewhat ambiguous in various plant species depending on the intensity and duration of osmotic stress. Simultaneously, SA exogenous application alleviated the adverse effects of salinity (Horváth et al., 2007).

During the 1960s, SA was synthesized from cinnamic acid (CA) by two biosynthesis pathways. One pathway involves a side chain of CA, which undergoes decarboxylation to produce benzoic acid, which is then subjected to 2-hydroxylation leading

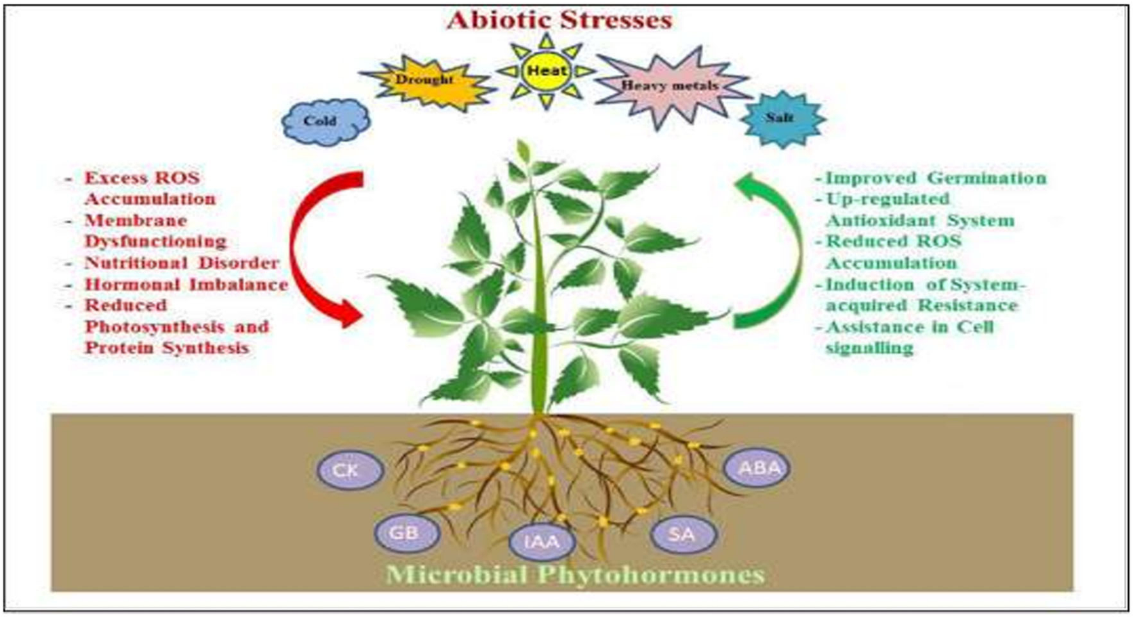

FIGURE 1 | An overview of mechanisms in microbial phytohormone-mediated plant stress tolerance. Several root-associated microbes produce CK, GA, IAA, SA, and ABA, which help plants to withstand stress by enhancing their antioxidant potential, by up-regulation of the antioxidant system and by the accumulation of compatible osmolytes thus reducing oxidative stress-induced damage; improving photosynthetic capacity and membrane stability; promoting cell division and stomatal regulation; stimulating the growth of root system, and acquisition of water and nutrients.

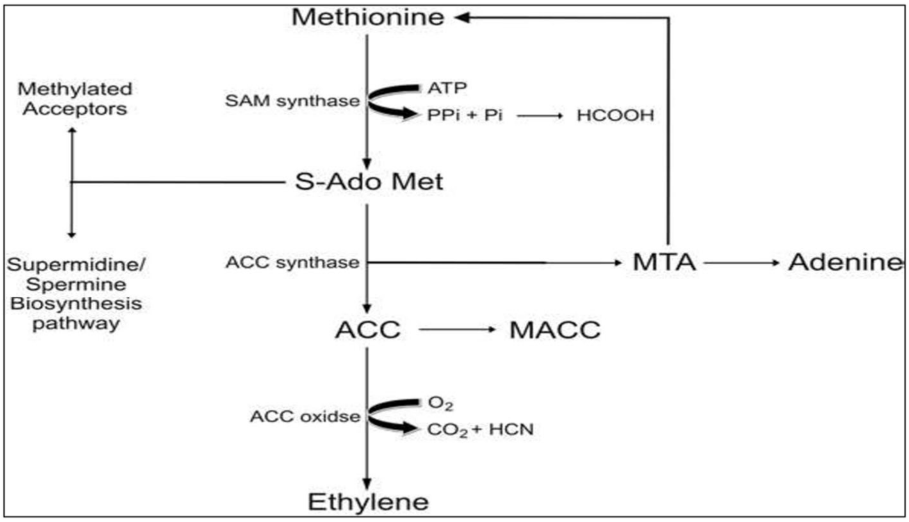

FIGURE 2 | Biosynthesis of ethylene in plant cells.

to the synthesis of SA in crops including tobacco (Yalpani et al., 1993) and rice (Silverman et al., 1995). However, it postulated that some other enzymes involved in this pathway are still unknown. The second pathway of SA biosynthesis involves CA, which gets subjected to 2-hydroxylation, leading to o-coumaric acid production, which is subsequently decarboxylated to biosynthesize SA. Trans-cinnamate-4- hydroxylate enzyme is responsible for catalyzing this reaction (Alibert and Ranjeva, 1971; Alibert et al., 1972). This pathway was firstly studied in seedlings of peas (Russell and Conn, 1967). However, the underlying mechanism of this pathway remains unclear.

Jasmonates

Jasmonates are a broad group, which are covering various compounds, such as jasmonic acids (JAs), jasmonic acid methyl ester (JAME), precursor of the JAs; octadecanoid cis (+) 12 oxophytodienoic acid (OPDA), amino acid conjugates, and metabolites such as 12-OH-JA and 11-OH-JA, and often these compounds are involved in plant responses to biotic and abiotic stresses. Jasmonates are found throughout the plant body; however, shoot apex, root tips, immature fruits, and young leaves like tender growing parts show remarkably high concentrations. The synthesizing pathway of JAs is said to be *via* the octadecanoid pathway, starting at linolenic acid and terminating at (+)-7-epi-JAs (Wasternack, 2007). The major plant organs of biosynthesizing Jasmonates are leaves and roots, while chloroplasts and peroxisomes are the sub-cellular primary sites of JAs biosynthesis (Cheong and Choi, 2003). Reports showed that development of the embryo and reproductive organs, determination of sex, seed germination and seedling development, root growth, fruit ripening, leaf movements and senescence, gravitropism, the formation of the trichome, and tubers are mediated by JAs (Wasternack and Hause, 2013; Wasternack, 2014). Further, signaling related to defense mechanisms of insects or pathogen are driven wounding is mediated by jasmonates.

JAs have a crucial role in abiotic stress tolerance; thus, studies were focused on these compounds because of their significant protective capacity on plants against stress (Takeuchi et al., 2011). For example, JAs-mediated plant responses are shown against drought stress, ozone stress (Sasaki-Sekimoto et al., 2005), UV-stress, salinity stress, cold stress (Yoshikawa et al., 2007), and temperature stress. In addition, JAs-mediated secondary metabolites production (Chen et al., 2006) is involved in plant movements related to adapt seasonal and circadian rhythms. Wasternack and Hause (2013) reported that jasmonates regulate microbe-associated symbiotic relationships, such as arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria (PGPR). The jasmonates involved signaling in abiotic stress regulation in *Carica papaya* (Mahouachi et al., 2007), citrus, and *Arabidopsis thaliana* (*A. thaliana*) (Arbona et al., 2010; Brossa et al., 2011) is well-confirmed. Moreover, the involvement of JAs in salt stress signaling in glycophytes such as tomato, barley, and others have been studied. However, the role of jasmonates in halophytic plants' response to salinity stress is yet to be explored. Certain laboratory experiments showed that changes in JAs profiles in response to different abiotic stressors were imposed using NaCl, mannitol/sorbitol, and water stress.

Gibberellins

The GAs are one of the longest and well-known groups of regulatory hormones integrated into numerous developmental processes of plants such as seed germination, inter-nodal elongation, induced flowering and fruit development (Islam et al., 2021). Recent studies have explored genetic basis and genes encoding GAs biosynthesis and deactivating enzymes using novel biochemical and genetic approaches (Yamaguchi, 2008; Pearce et al., 2015). More than 250 members in the GAs group are reported, though only a few of them are biologically active and play multiple roles in plant development. The cellular level regulation of the GAs is said to be complex. For example, the GAs metabolic pathway phases are regulated by enzymes in small multi-genic families; of those, each member plays a specific pattern of expression. However, two gene families encoding GAs, 20-oxidases (GA20ox) and GA3-oxidases (GA3ox) that catalyze the final steps in the synthesis of bioactive GAs, are strongly associated with GA biosynthesis (Hedden and Thomas, 2012).

Receptor protein of GA is nuclear localized GID1 and binding of GA with receptor protein help to interact with repressor DELLA protein. Protein-protein interacting domain of DELLA protein interact with F-Box protein which recruit SLY1 complex for its ubiquitination *via* SCF-E3 ligase complex. Upon ubiquitination, DELLA repressor protein is degraded by 26S proteasome and thus help in binding of transcription factor with promoter region of GA-inducible genes. Thus, GA mediate signaling by degrading repressor protein that bring about various biochemical and physiological responses. Thus, accumulation of GA in plant tissues either due to endogenous biosynthesis or due to exogenous application counteract negative effects of stresses and thus induce stress tolerance in plants. For instance, under water deficit conditions, decline in endogenous GA level by *GA2ox6* ectopic expression improved the seed yield and drought stress tolerance in rice (Lo et al., 2017). Moreover, GA regulate redox homeostasis through stimulating electron mobilization in *H. vulgare* (Mark et al., 2016). The involvement of GA in redox equilibrium helps plants to acclimatize in suboptimal growth conditions. *GRAS* transcription factors play crucial role in plant development and signaling including GA biosynthesis and signal transduction pathways. Liu et al. (2017) demonstrated that abiotic stress treatments like NaCl, H_2O_2, etc. enhanced the *GRAS40* expression in tomato. *SlGRAS40* interacted with auxin and GA pathways during vegetative and reproductive phases of tomato and transgenic expression of *SlGRAS40* plant and its expression induced the drouth and salt tolerance.

Auxins

Auxins are endogenous plant growth regulators, similar to CKs, and are mainly involved in root/shoot formation and relative growth (Sachs, 2005). Studies have shown that auxins work together with CKs in various cellular or physiological processes such as cell cycle progression, cell expansion, apical dominance, leaf development, and embryonic development during seed maturation (Tromas et al., 2009; Jurado et al., 2010). Indeed, auxins under environmental stresses influence the plant growth responses. In contrast, subsequent alterations in auxin homeostasis due to such environmental changes can result in distorted growth and development in plants, causing altered morphogenesis. Such stress-induced morphogenic responses are an acclimation strategy, which helps prevent or reduce the damaging effects of environmental stresses (Potters et al., 2009; Tognetti et al., 2012).

The genetic studies and *in vitro* assays claimed that Auxin biosynthetic pathways have one tryptophan (Trp)-independent and four Trp-dependent pathways, namely indole-3-acetamide (IAM) pathway, indole-3-acetaldoxime (IAOx) pathway, tryptamine (TAM) pathway, and indole-3-pyruvic acid (IPA) pathway (Woodward and Bartel, 2005; Taiz et al., 2015). Amongst them, the TAM and IPA pathways said to be contributed to plant development.

Similar to GA, receptor protein of auxin is also nuclear localized. Interestingly, receptor protein of auxin is a repressor protein. Binding of auxin with receptor protein or repressor protein recruits SCF^{TIR1}-E3 ligase which ubiquitinate repressor protein subsequently degraded by 26S proteasome. Degradation of repressor protein allowed to auxin response factors to bind with promoter region of auxin-inducible gene and thus mediate gene expression. Auxin response factor (ARF) family has been identified as transcription factors that mediated auxin's actions; for example, certain ARFs displayed crucial involvements in lateral root development (Wilmoth et al., 2005). A recent study reported that micro RNAs' collective function determined the quantity of lateral root growth, miR390 and TAS3-derived trans-acting short interfering RNAs and Auxin Responsive Factors forming auxin-responsive regulatory network (Marin et al., 2010). This complex auxin regulatory network has fine-tuned the vigor and elasticity of lateral root growth. However, the involvement of genes that mediate interactive environmental stresses toward growth responses is yet to be discovered.

Variety of abiotic stresses involved in auxin homeostasis, distribution, and their metabolism in the cellular environment. Two molecular mechanisms have been suggested for such alterations in auxin distribution under stress environments; changers in PIN gene expression, which is necessary for polar auxin transport, and inhibitory action of polar auxin transport generated *via* phenolic compounds accumulated during stress exposure (Kovtun et al., 2000; Potters et al., 2009). Moreover, stress-induced auxin metabolism is regulated by IAA degradation, which is catalyzed by peroxidases (Jain and Khurana, 2009). Thus, auxins can be considered as stress hormones having direct or indirect mediation, modifying the expression of certain stress-responsive genes; among the multi-functions of auxin in plants, the formation of lateral roots considered as of special significance as lateral roots play a key role in plant development regulating the architecture of the root system, stability of the plant and efficient nutrient and water uptake for the whole organism.

Cytokinins

The CKs are key PHs often considered ABA antagonists and auxin antagonists/synergists in various processes in plants responsible for plant growth, development, and tolerance against different abiotic stresses (Pospíšilová, 2003; Danilova et al., 2016). Besides, other hormonal pathways (e.g., ABA), CKs are activated when a plant is exposed to salt stress. By interacting with other plant hormones like auxins and ABA, CKs can considerably increase salt stress tolerance (Iqbal et al., 2006).

Plant endogenous CKs are adenine derivatives with either isoprenoid or aromatic side chains found in plants at a lower abundance (Sakakibara, 2006). The isoprenoid CKs can be distinguished as isopentenyl adenine (iP), trans-zeatin (tZ), cis-zeatin (cZ), or dihydrozeatin-type derivatives according to the hydroxylation and reduction of the side chain. The rate-limiting step of isoprenoid CK biosynthesis is catalyzed by isopentenyl transferase (IPTs). Rivero et al. (2010) generated transgenic tobacco carrying an *Agrobacterium tumefaciens* isopentenyl transferase gene (IPT). Similarly, the promoter of a senescence-associated receptor protein kinase (*SARK*) gene, from *Phaseolus vulgaris*, was constructed in front of the *IPT* gene. These transgenic plants (*PSARK*::*IPT*) are more tolerant of drought-induced leaf senescence, which results in a remarkable level of water stress tolerance. During water stress, a greater reduction in photosynthesis occurs in susceptible plants than the stress-tolerant transgenic plants due to the photosynthetic apparatus being degraded in suspectable plants under low photosynthesis conditions. Therefore, CKs may protect photosynthetic processes contributing to the stress tolerance in the transgenic plants (Rivero et al., 2010). In addition, recent studies on CK signaling have suggested that this hormone is indeed involved in plant salt stress responses shown in **Figure 1**. Synthetic CKs reverse the plants' drought-induced alterations and allow normal growth and developmental activities (**Figure 3**). Plenty of research findings suggest that CKs support normal growth and development under osmotic stresses and improve plants' drought tolerance ability. However, the precise molecular mechanism of CK-mediated drought tolerance is yet to be discovered.

Melatonin

In 1995, two groups of researchers simultaneously identified the presence of melatonin (N-acetyl-5-methox-ytrytamine) in vascular plants for the first time. Melatonin is a pleiotropic molecule with many diverse actions in plants (Wang et al., 2017). It is considered an antioxidant with important actions in the control of ROS (Raza et al., 2020) (**Figure 4**) and reactive nitrogen species (RNS), among other free radicals, and harmful oxidative molecules present in plant cells. In addition, plant melatonin is involved in multiple physiological actions, such as growth, rooting, seed germination, photosynthesis, and protection against abiotic and biotic stressors (Arnao and Hernández-Ruiz, 2015). The recent identification of the first plant melatonin receptor opened the door to this regulatory molecule being considered a new plant hormone. However, due to the diversity of its actions, melatonin has also been proposed as a plant master regulator.

Melatonin has a range of possible cellular and physiological effects, such as changes in intracellular Ca^{2+} and the permeability of membranes mediated by ion transporters, changes in the opening and/or closing of stomata carbohydrate, lipid, and nitrogen metabolisms, and also in osmoprotectant metabolites. Melatonin affects processes such as growth promotion, rooting induction, tropism, seed germination promotion, photosynthesis, optimizing efficiency, and leaf water/CO_2 exchange (Sharif et al., 2018). It also regulates other processes, such as ripening or senescence, the internal biological clock, and parthenocarpy. Finally, melatonin also acts as an endogenous plant bio-stimulator against abiotic or biotic stressors (Sun et al., 2014).

One of the basic principles of any animal or plant hormonal function is a receptor responsible for interaction with the hormone and triggering downstream signaling chain elements. One of the most important limitations in studies on melatonin in plants is the lack of an identified receptor. This has also been a hurdle to considering melatonin as a plant hormone. However,

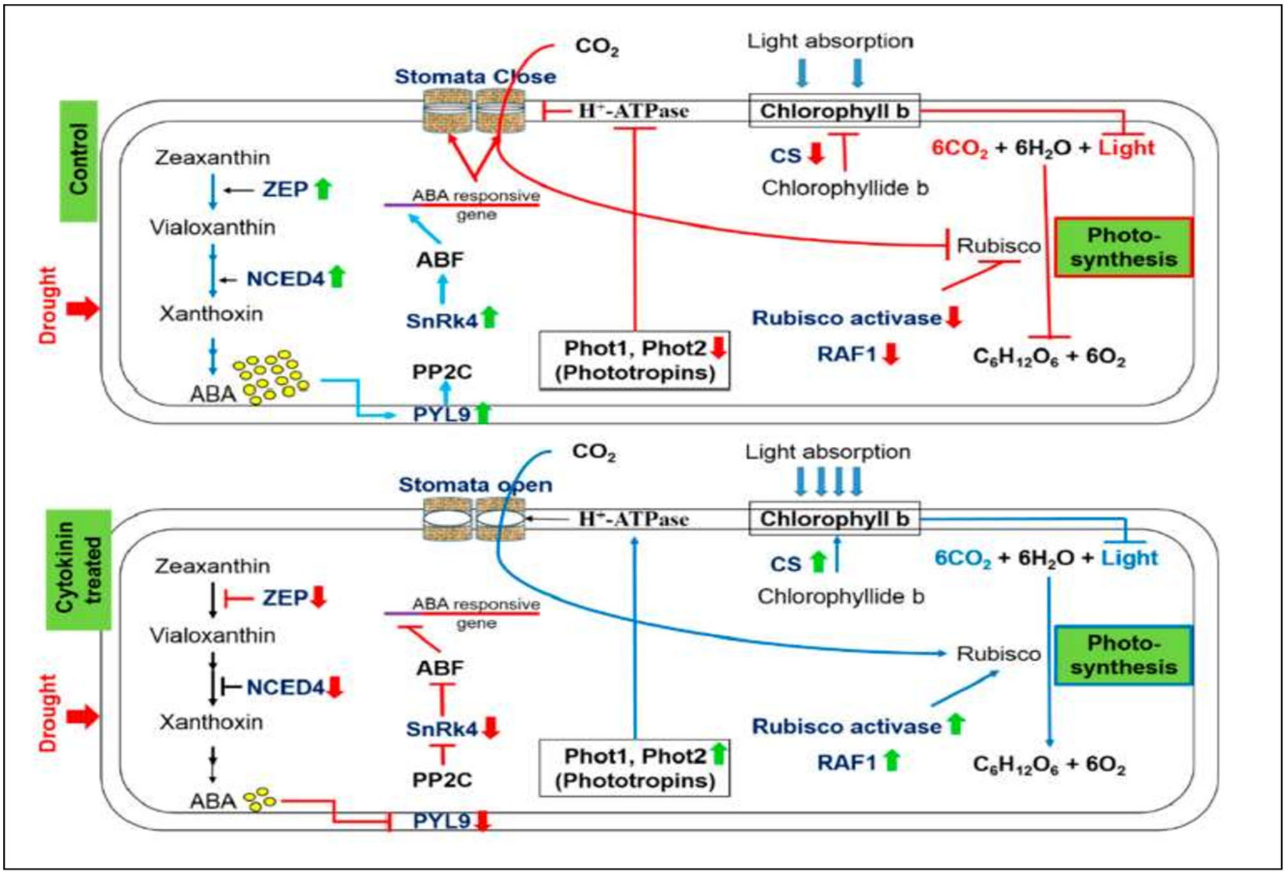

FIGURE 3 | The positive impact of synthetic CK on stomatal conductance, contents of chlorophyll b, and the process of photosynthesis under severe drought stress. Up (green) and down (red) arrows are the symbolic representations of increase and decrease, respectively. ZEP, Zeaxanthin epoxidase; NCED, 9-cis-epoxycarotenoid dioxygenase; ABA, Abscisic acid; PYL9, Pyrabactin-like receptor 9; PP2C, Protein phosphatase type-2C; SnRK4, Sucrose non-fermenting-1-related protein kinase 4; ABF, ABA-responsive factor; Phot, Phototropin; CS, Chlorophyll synthase; RAF1, Rubisco accumulation factor 1 (Gujjar et al., 2020).

similar to other plant hormones, identifying the receptor only came after obtaining many biochemical and physiological data relevant to melatonin (Zhang and Chang, 2016). The turning point came with the recent identification of CAND2/PMTR1, a phytomelatonin receptor in *A. thaliana*. Localized in the plasma membrane with a receptor-like topology, it interacts with the G-protein a subunit (*GPA1*), while its expression in different tissues is induced by melatonin. Phytomelatonin-receptor binding triggers the dissociation of Ggb and Ga, which activates NADPH oxidase-dependent H_2O_2 production (RBOH), enhancing Ca^{2+} influx and promoting K^+ efflux, finally resulting in stomatal closure. Like others, phytomelatonin is a plant hormone that controls stomatal closure through the CAND2/PMTR1-mediated signaling pathway, regulating H_2O_2 production. ABA application induced stomatal closure in CAND2 (a melatonin-insensitive phenotype in mutants lacking ATCAND2), suggesting that melatonin-induced stomatal closure has a receptor that is different from that for ABA while sharing some components with ABA signaling (e.g., Ga subunit, H_2O_2, and Ca^{2+} signals) (Guo et al., 2017; Arnao and Hernández-Ruiz, 2019).

Strigolactones

Strigolactones (SLs) are carotenoid derived PHs, which exuded from 80% of the plants that propose a symbiotic relationship with arbuscular soil mycorrhiza (Akiyama and Hayashi, 2006). These PHs were originally discovered as an "ecological signal" for parasitic seed germination and a symbiotic relationship among plants and beneficial microbes. The first natural SL (called strigol) was discovered as a germination stimulant of *Striga lutea*. This obligate hemiparasite plant requires a living host for germination and initial development, and subsequently, these compounds were collectively termed as strigolactones (Cook et al., 1972).

Several strigolactone analogs, including GR5, GR7, and GR24 (a compound with the highest activity), have been chemically synthesized in many plants, and succeeding characterizations have described their functional roles in various developmental processes, including root development, shoot branching, leaf senescence, reproductive development, and controlling the architecture of plant organs (Gomez-Roldan et al., 2008; Kapulnik et al., 2011; Kohlen et al., 2011; Ruyter-Spira et al., 2011). Like other plant hormones, the major functions of SLs are the development, and its interaction with auxin dominates

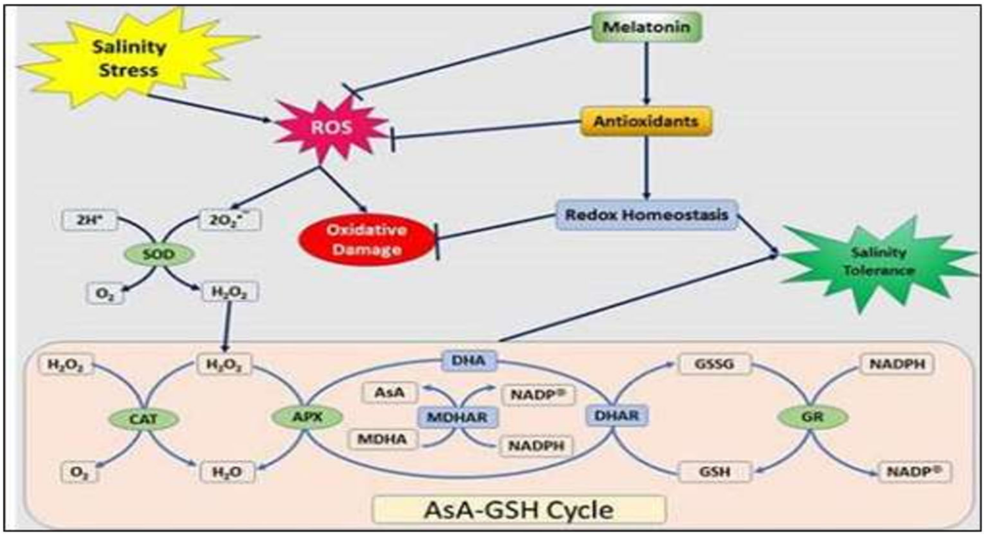

FIGURE 4 | Schematic presentation of the ascorbate–glutathione cycle and a model depicts the melatonin-induced alleviation of NaCl-caused oxidative stress in peanut plants. ROS, reactive oxygen species; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; AsA, ascorbate; MDHA(R), monodehydroascorbate (reductase); NADPH, nicotinamide adenine dinucleotide phosphate, DHA, dehydroascorbate; DHAR, dehydroascorbate reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; and GR, glutathione reductase (ElSayed et al., 2020).

in the SL-regulated developmental processes (Hayward et al., 2009). SLs are apocarotenoids derived from carotenoid cleavage mediated by Carotenoid cleavage dioxygenase (CCDs) enzymes (Booker et al., 2005). The first step of biosynthesis occurs in the plastids with the help of three plastids localized enzyme D27, CCD7, and CCD8 utilizing-trans-β-carotene in plastids producing caprolactone (CL) (Alder et al., 2012). Carlactone is then further oxidized by cytochrome P450 monooxygenase MAX1 or other homologous genes into different forms of SLs by few other unidentified steps catalyzed by novel, unknown enzymes. SLs are involved in the symbiosis relationship of plants and microbes in the rhizosphere. They activate hyphal branching and enhanced the growth and energy metabolism of symbiotic arbuscular mycorrhiza fungi after being exuded from the root.

Furthermore, SLs impact the quantitative development of root nodule symbiosis with symbiotic nitrogen-fixing bacteria (Rochange et al., 2019). The extent of SLs production in plants is strictly regulated and dependent on the stresses that plants confront at various stages of their development. Several studies confirm the importance of SLs in regulating multiple physiological and molecular processes during the adaptation of plants to different abiotic stresses such as salinity, drought, nutrient starvation, temperature, and pathogenic assail (Marzec et al., 2013). Evidence for crosstalk between SLs and other PHs in responses to abiotic stresses suggests that SLs actively participate within regulatory networks of plant stresses.

Recently, Ling et al. (2020) reported that exogenous application of GR24 in seedling of rice resulted in better growth, increased POD and SOD activity, and improved net photosynthetic rate, stomatal conductance, and intercellular CO_2 concentrations. These results show that GR24 may alleviate the damage of rice caused by salt stress, improve the adaptability to high-saline environments, and provide a relatively stable yield. The plant produces high amounts of SLs under nutrient deficiency conditions that lead to suppressing shoot branching and stimulating symbiosis (Gomez-Roldan et al., 2008; Umehara et al., 2008). SLs also showed to play a crucial role in nitrogen and phosphorous deficiency, inducing modification of root and shoot architecture and promoting the symbiosis of rhizobial bacteria and AM fungi (Marzec, 2016). As reported above, the significance of SLs has been well-recognized in several stress conditions as salinity, drought, temperature, and nutrient deficiency; however, their establishments as stress-related PHs demand extensive research.

Brassinosteroids

Brassinosteroids (BRs) are polyhydroxylated steroid PHs. They regulate several physiological and biochemical processes in the plant, such as cell elongation, cell division, photomorphogenesis, xylem differentiation, growth, and reproduction (Nolan et al., 2020). The BRs exist in free and conjugated, and nearly 69 and 5 conjugated and free BRs have been identified (Bajguz, 2011). The BRs are diverse in nature and biological activity. Among the BRs, brassinolide (BL) has been documented as the most active BR, and it was isolated and purified from *Brassica napus* pollen (Grove et al., 1979). The BRs are closely related to auxins, through the modulation of its transport, coordinating the tropic responses of plant organs (Li et al., 2005), and promoting lateral root primordial initiation during lateral root development (Bao et al., 2004). The endoplasmic reticulum most likely served as the site for BRs synthesis. The formation of a protein complex comprising enzymes (metabolon) to efficiently route the substrate to specified enzymes in a single biosynthetic pathway has been anticipated in plants only, and

BRs biosynthesis occurs through cyto-chromeP450 (CYP), a triterpenoid pathway (Ralston and Yu, 2006; Choe, 2007; Chung et al., 2011). Hydroxylation of membrane-induced campesterol initiates the BR synthetic pathway (Choe et al., 1998). The intermediates gradually become more polar with hydroxyl group addition on side chain on C-22, C-23, and C-2, C-3, C-6 on steroid rings, respectively (Vukašinović and Russinova, 2018).

Unlike other PHs, BRs are used in contiguity to synthesizing cells rather than long-distance transport. Nevertheless, BRs crosstalk with PHs such as auxin exerts a long-distance effect (Symons et al., 2008; Vriet et al., 2013). The BRs metabolism involves various processes, including acylation, glycosylation, and sulphonation, to maintain the desired levels of bioactive BR in the cells (Saini et al., 2015). The BRs signaling is initiated by leucine rich repeat receptor like kinase (LRR-RLKs) BRI1 which is membrane bound. BRs signaling used two strategies initiation of phosphorylation cascade by kinases and degradation of repressor protein BIN2 and thus allowing transcription factors to bind with DNA binding elements for gene expression. Thus, BRs signal is also amplified during signal transductions. That's why a small amount of BRs is sufficient to initiate developmental programs under normal or stress conditions (Nolan et al., 2017). Numerous studies have documented the abiotic stress tolerance in plants with exogenous application of BRs (Kagale et al., 2007; Bajguz and Hayat, 2009; Yuan et al., 2010; Anjum et al., 2011; Divi et al., 2016). Nevertheless, the BRs need in minimal quantity like other PHs. Therefore, plant responses to exogenous BRs treatment are concentration-dependent. A high BR application rate is found to inhibit the plant growth, while the opposite is observed at lower concentrations (Chaiwanon and Wang, 2015; Belda-Palazon et al., 2018). The abiotic stresses enhanced ROS generation leading to oxidative stress, while BRs help regulates the cellular ROS level under stressful environments. For instance, 28-homobrassinolide application to *Brassica juncea* L. plants subjected to combined temperature and salt stress enhanced enzymatic antioxidant activities (SOD, CAT, APOX, DHAR, and MDHAR) and ROS homeostasis (Kaur et al., 2018). Likewise, in *Lycopersicum esculentum*, BRs application ameliorated the supra optimal temperature-induced photosynthesis inhibition and augmented the carboxylation and activities of the antioxidant system (Ogweno et al., 2007). Recently, Fàbregas et al. (2018) demonstrated that overexpression of *BRL3* (vascular BR receptor) promotes drought responses without penalizing growth in *Arabidopsis*. In another study, Serna et al. (2015) documented the alleviation effects of BRs on lettuce salt-stressed plants. They found that BRs were involved in the partial reversion of NaCl accumulation in cells. Moreover, some critical agronomic traits in crops are potentially regulated by BRs, such as plant height, leaf angle, and inflorescence structure (Yamamuro et al., 2000; Hong et al., 2003; Sakamoto et al., 2006; Yang et al., 2018). Altogether, these studies demonstrate that BRs are potent PHs due to their versatile functions, and support the important role of BRs as anti-stress agents. Besides the great progress in the last decade in BRs research, many questions remained unanswered. The complete understanding of the dynamics of BRs homeostasis and its interactions with other PHs will add key knowledge that will allow the modulation of various useful traits in plants and address current challenges in agriculture.

Polyamines

Polyamines (PAs) are small aliphatic nitrogenous bases produced as a result of cellular metabolism. The PAs have not planted hormones, but due to their involvement in regulating several growth and development processes and responses to abiotic stress in plants, they have been proposed as a new category of plant growth regulators (Liu et al., 2007; Chen et al., 2019). Initially, the ability of PAs to bind with anionic macromolecules was supposed to link with their biological functions, which lead to the consideration of PAs as polycations having distinctive structural roles. However, later may study demonstrated that PAs act as regulatory molecules in key cellular processes such as cell division, cell differentiation, DNA and protein synthesis, and gene expression (Seiler and Raul, 2005; Alcázar et al., 2010; Igarashi and Kashiwagi, 2010; Childs et al., 2017). Furthermore, PAs are involved in various physiological processes in plants including embryogenesis, organogenesis, reproductive development, leaf senescence, and fruit maturity.

Moreover, the several studies have reported the protective role of PAs against environmental stresses (see reviews Alcázar et al., 2010; Gill and Tuteja, 2010; Minocha et al., 2014; Chen et al., 2019). Spermidine (Spd), spermine (Spm), and Putrescine (Put) are the major PAs in plants, while cadaverine (Cad) and diamino propane (Dap) are less studied in plants. The PAs are present in conjugated (covalent and non-covalent bounded) or free form (Gholami et al., 2013). The main product of PAs biosynthetic pathway is Put, which serves as the precursor for Spm and Spd (Xu et al., 2009). In plants, Put biosynthesis occur in three different routes: *via* Arginine by arginine decarboxylase (ADC) (the most frequent route), *via* ornithine (Orn) by ornithine decarboxylase (ODC), and citrulline (Cit) by citrulline decarboxylase (CDC) (Chen et al., 2019). The PAs catabolism is contingent on the action of diamine oxidase, and PA oxidase and PAs metabolism is closely associated with several other metabolic pathways in plants. The H_2O_2 produced due to PA oxidation is involved in signal transduction and plant responses to biotic and environmental stresses (Freitas et al., 2017; Mellidou et al., 2017; Sariyev et al., 2020). The PA biosynthetic pathway is linked to ethylene synthesis, sharing the same precursor (S-adenosylmethionine) and competing. Further, PAs metabolism is closely associated with nitric oxide generation (Pál et al., 2015), which triggers a signal transduction process related to plant growth. The distribution of PAs is organ and tissue-specific in plants. For instance, Put is the most abundant PA found in leaves, while the higher level of Spd is present in other plant organs (Reginato et al., 2012; Takahashi et al., 2017).

Polyamines are implied in response to different abiotic stresses. Generally, transgenic plants overexpressing PA biosynthetic enzymes, such as spermidine synthase, arginine decarboxylase, and S-adenosylmethionine synthetase, showed the protective roles of polyamines under abiotic stress conditions. Moreover, exogenous application of PAs showed increased stress tolerance in several plant species (Alcázar et al., 2010; Qi et al., 2010; Minocha et al., 2014).

THE BENEFICIAL EFFECTS OF PGPR-MEDIATED PHYTOHORMONES IN PLANTS UNDER ABIOTIC STRESSES

Abiotic stresses such as drought, high soil salinity, flooding, heat, cold, oxidative stress, and heavy metals not only deteriorate environmental resources but also reduce crop growth and productivity by reducing nutrient uptake (EL Sabagh et al., 2020b; Javeed et al., 2021). The plant nutrients remarkably influence the physiological and biochemical functions of plants (Raza et al., 2020), and the deficiency of the essential nutrients slows down the growth and development, even go-ahead to the death of plants (Bennett, 1993; Balakrishnan, 1999). Plant breeding and genetic engineering approaches are the best techniques to develop stress-resistant plants, but limited success is achieved in this field despite significant efforts.

Increasing nutrient availability and uptake for plants is one way to alleviate nutrient deficiency under abiotic stress conditions. Plant growth-promoting rhizobacteria (PGPR) are the potential candidates to protect plants by colonizing within the rhizosphere and producing antimicrobial metabolites (antagonistic). The PHs produced by such a community of bacteria provide plant health and immunity by regulatory hormones (Maheshwari et al., 2015).

PGPRs associated with plant roots improve plant productivity and immunity through various mechanisms like overproduction of beneficial PHs, consequently increases the root surface area and numbers of root tips, enhances the uptake of nutrients from soils, and reduces the stress-related damages (Kloepper et al., 2004; Çakmakçi, 2016). The PGPR helps fix atmospheric N_2 into biologically available N compounds and produce growth-promoting hormones and prevent the infestation of plant pathogens or increased resistance power of plants against pathogens (Bottini et al., 2004; Compant et al., 2005).

Due to the production and degradation of the major groups of plant hormones, plant growth promotion is facilitated by PGPR *via* diverse mechanisms. However, plant root exudates have many potential substrates for rhizobacterial growth, including plant hormones or their precursors. Rhizobacterial mediation of plant hormone status shows local effects on root elongation and architecture, mediating water and nutrient capture, and affects plant root-to-shoot hormonal signaling that regulates leaf growth and gas exchange. Combining rhizobacterial traits (or species) influences plant hormones and status, thereby, modifying root architecture (to capture existing soil resources) to make additional resources available (e. g., nitrogen fixation, phosphate solubilization), which may enhance the sustainability of crops (Maheshwari et al., 2015).

In addition to different environmental stresses in crop production and the adverse effects of the chemical fertilizers on the environment, environmentalists push worldwide to reduce chemical fertilizer levels below those recommended for optimum yields. However, such reductions would represent nutrient stress on plants. Hence, the use of PGPR is a great option that facilitates crop productivity with reduced fertilizers. Shaharoona et al. (2008) reported that the use of PGPR strain with 75% recommended doses of N-P-K fertilizers produced the equivalent yield of wheat (*Triticum aestivum* L.) that were obtained with the full dose of N-P-K fertilizers (100%) in the absence of PGPR.

Extracellular plant growth-promoting rhizobacteria (ePGPR) and intracellular plant growth-promoting rhizobacteria (iPGPR) are PGPR classes. The ePGPRs exist within the rhizosphere or in the spaces between the root cortex cells, while the iPGPRs generally exist inside the specialized modular structures of root cells. The bacterial genera under the ePGPR class are *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas,* and *Serratia* (Viveros et al., 2010). The iPGPR belongs to the family of Rhizobiaceae that includes species of *Allorhizobium*, *Bradyrhizobium*, *Mesorhizobium,* and *Rhizobium* (Bhattacharyya and Jha, 2012).

In stress conditions, the growth and development of plants are stimulated by the functions of PGPR. It has been reported by Mantelin and Touraine (2004) that the development of the profuse root in response to PGPR stimulatory effects can directly improve the growth and development of plants. The production of PHs like IAA, CKs, and GAs under drought, nutrient deficiency, salinity, and metal toxicity stresses changes the root structure (Adesemoye et al., 2008).

Plants uptake more nutrients from the soil due to higher root surface area, contributing to the promotion of plant growth (Vessey, 2003). Moreover, it also increases the nutrients (N, P, and K) uptake efficiency of plants due to the PGPR production (Mayak et al., 2004; Turan et al., 2012). PGPB strains improve the N_2 fixation and survive plants under stressed soil conditions reported in many previous studies (Gupta et al., 2014; Nadeem et al., 2014).

The PGPR can neutralize or decrease the stress-related hormones (ethylene by bacterial ACC deaminase activity), which are produced in plants under stressed soils, and reduce the inhibitory effects of various pathogens in the forms of bio-control agents, root colonizers, and environmental protectors, resulting in improve growth and development of plants. PHs produced by PGPR are major signaling molecules employed in the enhancement of crop production. IAA in the majority and other hormones such as ABA, CK, ET, etc. (natural, semi-synthetic, and synthetic) proved beneficial by stabilizing plant immunity, biocontrol, and crop productivity. The role of phytohormone in seed dormancy, seedling emergence, elongation, somatic embryogenesis, initiation, and enhancement brings the immense need to manage increasing food production to account for sustainable agriculture. Phytohormone is exploiting endogenously and exogenously in the maintenance of several physiological traits of plants. It has been revealed that some PGPR secretes novel signaling molecules that also promote plant growth. The use of rhizobacteria signaling in promoting plant growth offers a new window of opportunity, especially to provide novel biological products for enhancing plant growth and development in a sustainable manner (Maheshwari et al., 2015).

Salinity is one of the most significant abiotic stress that hinders crop yield by causing damage to plant growth and development (Abdelhamid et al., 2019; EL Sabagh et al., 2020a).

Under the saline condition, plants uptake essential nutrients from a diluted source in the presence of highly concentrated non-essential nutrients such as calcium, iron, magnesium, sodium, and chlorine (Fageria et al., 2011; Liu et al., 2020; Monsur et al., 2020). In salt-affected soils, the uptake and use efficiency of nutrients (phosphorus, potassium, and boron) are low due to the negative interactions with higher concentrations of cations and anions. Hence, plants grown in salt-affected soils require a higher amount of nutrients than plants grown in normal soils. Legumes grown in salt-affected soils also adversely affect the biological nitrogen fixation. Jha and Subramanian (2013) reported from a greenhouse study on rice that PGPR inoculated plants under saline conditions increased the uptake of N (26%), P (16%), K (31%), and decreased the uptake of Na (71%) and Ca (36%) resulting exhibited higher germination, survival, dry weight, and plant height as compared to non-inoculated control plants in the same condition.

The PGPR contributed significantly to reduce the nutrient build-up in the soil (Mantelin and Touraine, 2004; Adesemoye et al., 2008). Soil fertility is enhanced due to the levels of nitrogen fixation in legumes. Nitrogen-fixing bacteria metabolize the root exudates and make available nitrogen to synthesize amino acids in plants. The PGPR is the resultant effect of the symbiosis of rhizobia and legume plants. Nitrogen fixation ability depends on the free-living bacteria like Azospirillum, Burkholderia, and Stenotrophomonas (Dobbelaere et al., 2003). Sulfur is an important macronutrient released from sulfate through oxidation of bacteria for the plants (Banerjee and Yesmin, 2002).

For optimum growth and development of plants, phosphorus (P) is an essential macronutrient, although P is limited to most of the world's soil. Plants uptake P mainly in the form of soluble inorganic phosphate, but P forms insoluble complexes (unavailable for plant roots) with Al and Fe, and Ca and Mg in acidic and alkaline soils, respectively. A limited amount of bioavailable P in the soil shows extensive abiotic stress in plants. In this situation, naturally, PGPR microbes present in the soil or artificial inoculation of PGPR strains as a biofertilizer solubilizes the insoluble P, and increases P availability to plants or helps to develop more lateral roots and root hairs in making more surface area for absorption of inorganic P and other nutrients (Gyaneshwar et al., 1999). The most efficient phosphate solubilizing bacteria are Rhizobium, Bacillus, and Pseudomonas, and fungi are Aspergillus and Penicillium.

Ehteshami et al. (2007) reported that the phosphate-solubilizing microorganisms could perform positively in promoting plant growth and P uptake in maize crop under water deficit conditions that lead to the development of improved stress tolerance in plants. The use of PGPB salt-stressed tomato plants increased P uptake (Mayak et al., 2004). The PGPR increased the uptake of P in peppers under high and low-temperature stress (Martin and Stutz, 2004). Wheat seeds inoculated with *Pseudomonas indica* and *Azotobacter chroococcum* increased the uptake of mineral nutrients, especially Zn (Abadi and Sepehri, 2016). Egamberdiyeva (2007) reported that PGPR inoculation such as *Pseudomonas alcaligenes* PsA15, *Bacillus polymyxa* BcP26, and *Mycobacterium phlei* MbP18 in maize under nutrient-deficient condition promoted growth and uptake of N, P, and K.

Iron (Fe) toxicity is a severe constraint of rice production in wet conditions. The *Bacillus* strains can mitigate Fe toxicity symptoms (Asch and Padham, 2005; Terré et al., 2007). PGPR produces siderophores to sequester ferric ions from the soil and supplies them to the plants under iron-limiting stress conditions (Compant et al., 2005). Production of siderophores by PGPR increases nutrient uptake under mineral shortage may, in turn, favor heavy metals sequestration (Khan et al., 2009). Pishchik et al. (2002) reported that barley seeds inoculated with the commercially available PGPR *Klebsiella mobilis* increased the grain yield by 120%, and decreased two-fold Cd contents in grains when plants are grown in cadmium-contaminated soil. This may be due to free Cd ions can be bound by bacteria into complex forms that cannot be taken up by the plants. Therefore, inoculation of PGPR can be considered an innovative and cost-effective alternative to the availability of nutrients under different abiotic stresses.

CONCLUDING REMARKS

Abiotic stresses hinder plant growth and development at all phenological stages, particularly at the seed germination and reproductive growth stages. In most of the negative effects in plants caused by abiotic stresses, nutrient deficiency is highly significant. Plants tolerant to abiotic stresses have better ability to preferentially uptake nutrients either due to endogenous hormonal regulation or due to interaction with root zone microbes which release variety of hormones. In view of role of phytohormones in different plant physiological processes, exogenous application of these hormones can improve stress tolerance in plants. In addition, application of hormone producing microbes might have multiple effects in alleviating adverse effects of abiotic stresses on plants. It do not only promote the growth but such application improved the nutrient availability in soil, help in uptake of nutrient and induce stress tolerance in plants. Application of PHs in abiotic stressed-plants is a well-known strategy for crop stress management. The PHs are classified into several classes, and each class has a specific role against specified abiotic stress. Although biosynthetic pathways and signaling pathways of different hormones are known, hormonal cross regulation is poorly understood. Future research needs to explore the molecular mechanisms of different PHs and their cross regulation in alleviating adverse effects of abiotic stresses on plants. In the future, the use of advance biological tools such as genomics, proteomics, transcriptomics, and bioinformatics in this area of research will help in exploring detailed mechanism of abiotic stress tolerance in plants and role of PHs in this regard.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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