

# Role of Phytohormones in Stress Tolerance of Plants

Sajid Mahmood Nadeem, Maqshoof Ahmad, Zahir Ahmad Zahir,  
and Muhammad Ali Kharal

**Abstract** Environmental stresses, both biotic and abiotic, cause negative impact on plant growth and development, and plants need to adopt certain strategies for maintaining proper growth under stress conditions. These strategies include certain physiological, biochemical, and molecular mechanisms to cope with these stresses. These mechanisms include the production of hormones (phytohormones) and osmolytes. Phytohormones are organic molecules that affect various plant physiological processes like growth, development, and cell differentiation. Phytohormones regulate key physiological events under normal and stress conditions. They play a vital role for enhancing the ability of plants to adapt to the harsh environmental conditions by mediating a wide range of adaptive responses. These responses enable the plants to acclimatize to adverse soil conditions. Various types of phytohormones play an important function in plants individually or in coordination with each other. The nature and level of these hormones in plants are major factors that influence plant processes and functions. The present chapter describes the potential role of phytohormones for promoting plant growth and development under stress conditions. The major classes of plant hormones and their source of production have been described. Metabolism of phytohormones and their physiological responses with special reference to their concentration-dependent or negative impact on plant growth have been discussed in detail. The impact of these hormones on plant growth under stress conditions has been reviewed and discussed with selected examples. Also, the role of microbes in phytohormone production has been elaborated with examples. Future perspectives of the area have also been discussed.

**Keywords** Brassinosteroids • Gibberellins • Phytohormones • Stress tolerance

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S.M. Nadeem

University of Agriculture Faisalabad, Sub Campus, Burewala-Vehari, Pakistan

M. Ahmad • M.A. Kharal

Department of Soil Science, University College of Agriculture and Environmental Sciences,  
The Islamia University Bahawalpur, Bahawalpur, Pakistan

Z.A. Zahir (✉)

Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan

e-mail: [zazahir@yahoo.com](mailto:zazahir@yahoo.com)

## 1 Introduction

Stress conditions cause significant negative effect on crop productivity by disturbing plant processes owing to their impact on hormonal and nutritional imbalances. Some of the common stresses that cause negative impact on plant growth and development include salinity, drought, heavy metals, nutrient deficiency, and pathogens. These stresses affect the plant growth in one way or another. One stress may affect more than one plant processes by causing negative impact in a number of ways. For example, salinity affects plant growth by causing ion toxicity, oxidative stress, nutritional disorders, water stress, and hormonal imbalances (Munns 2002; Zhu 2007; Ashraf 2009; Nadeem et al. 2010a). In natural soil environment, plant develops certain mechanisms to cope with biotic and abiotic stresses in harsh environment. Multiple pathways of cellular signaling are activated to any given stimuli. These signals enhance the accumulation of phytohormones. Phytohormones are signaling molecules directing physiological and developmental processes in plants. The amount of hormones varies greatly depending upon certain biotic and abiotic factors. Even very low concentration of these hormones may cause significant impact on plant growth and development.

Hormonal signaling is critical for plant defenses against environmental stresses (Taiz and Zeiger 2010). Production of phytohormones plays central role in plant stress tolerance. The five major classes of phytohormones are auxin, cytokinins, ethylene, gibberellins, and abscisic acid. In addition to these well-known plant hormones, brassinosteroids, jasmonic acid, salicylic acid, and nitric acid have also been identified as chemical messengers present in trace quantities in plants (Rao et al. 2002). These hormones move throughout the plant body via the xylem or phloem transport stream.

Among these hormones, abscisic acid (ABA) is the most studied stress-responsive hormone that is involved in number of stresses including osmotic, drought, and cold stress (Peleg and Blumwald 2011; Wasilewska et al. 2008). Auxin is involved in the regulation of plant processes like organogenesis, embryogenesis, and vascular tissue formation (Petrasek and Friml 2009). Brassinosteroids, that is a new group of plant hormones, influence plant development processes like seed germination, flowering, and senescence (Rao et al. 2002).

These biochemical substances (phytohormones) are produced by plants (Santner et al. 2009), and it is a well-documented concept that phytohormones perform many functions in plants by influencing a number of physiological and biochemical processes of plant. These hormones also play an important role in mitigating the negative impact of various environmental stresses, both biotic and abiotic, on plant growth and development. These hormones integrate biotic and abiotic stress signals. Stress environment activates phytohormone signaling pathway that plays an important role in stress adaptation. It has been reported that adverse effect of salt stress on seed germination and plant growth was due to the decline in endogenous level of phytohormones (Wang et al. 2001; Debez et al. 2001). This argument was further supported when plant growth was enhanced under stress conditions by the exogenous application of phytohormones (Khalid et al. 2006; Egamberdieva 2009).

These and a number of other studies show that although plant itself has its mechanism to produce hormones to combat stress responses (Wasternack 2007; Xoconostle-Cazares et al. 2010; Kolaksazov et al. 2013), however its application from some other sources like inoculation with hormones producing bacteria and/or application of synthetic phytohormones may be useful for alleviating stress-induced impact on plant growth and development (Khan et al. 2004; Afzal et al. 2005; Egamberdieva 2009). This review highlights the importance of phytohormones in plant stress tolerance. The sources of phytohormones, its metabolism, and physiological impact of these hormones on plant growth particularly under stress environment have been reviewed and discussed in the following sections.

## 2 Sources of Phytohormones

Plant hormones or phytohormones are naturally occurring organic compounds that affect various physiological processes of plant. These hormones could be either synthesized by the plant or the microorganisms.

### 2.1 Plant Hormones

Plants have high plasticity for adaptation to certain environmental stresses by virtue of their specific mechanisms like their ability to synthesize endogenous hormones. Hormones are involved in response to certain environmental stimuli as well as for regulating internal development processes. Among phytohormones, auxin was the first hormone about which Charles Darwin in 1880 provided clue in his book entitled *The power of movement of plants*. Later on, in 1926, Dutch botanist Frits W. Went discovered auxin. L-Tryptophan is the precursor of the auxins, and root exudates are the main source of auxins in soil (Etesami et al. 2009).

These hormones serve as endogenous messengers against biotic and abiotic stresses. Initially, five plant hormones are identified including ethylene, abscisic acid, cytokinins, gibberellins, and auxins (IAA). These hormones are considered as classical phytohormones, and higher plants can synthesize all these five major classes of phytohormones. In addition to these well-documented hormones, brassinosteroids, jasmonic acid, polyamines, strigolactones, nitric oxide, and salicylic acid are also included in the list of phytohormones (Santner et al. 2009; Chen et al. 2009a). These hormones have been identified from a variety of plants (Table 1).

The synthesis of a plant hormone is tightly regulated and subject to positive or negative feedback mechanism and often affected by other hormones and environmental factors. A number of stress phytohormones can mediate stress tolerance in plants (Wasternack 2007). For example, drought tolerance limits the loss of water through abscisic acid-mediated closure of stomata (Xoconostle-Cazares et al. 2010). Also, an increase in content of jasmonates and salicylic acid in wheat has been observed under cold stress (Kosova et al. 2012; Kolaksazov et al. 2013).

**Table 1** Phytohormones production by plants

Plant	Hormone	Reference
Barley ( <i>Hordeum vulgare</i> L.)	Indole-3-acetic acid	Ayvaz et al. (2012)
	Abscisic acid	Ayvaz et al. (2012)
Alpine ( <i>Arabis alpina</i> )	Jasmonate	Kolaksazov et al. (2013)
Wheat ( <i>Triticum aestivum</i> )	Jasmonic acid	Kosova et al. (2012)
	Ethylene	Datta et al. (1998)
	Abscisic acid	Zhao et al. (2001)
	Salicylic acid	Kosova et al. (2012)
Arabidopsis ( <i>Arabidopsis thaliana</i> )	Indole-3-acetic acid	Bartling et al. (1994)
	Gibberellins	Kobayashi et al. (1994)
	Abscisic acid	Xiong et al. (2001)
	Cytokinins	Takei et al. (2001)
	Auxin	Wang et al. (2015)
Rice ( <i>Oryza sativa</i> )	Gibberellins	Helliwell et al. (2001)
Maize ( <i>Zea mays</i> )	Gibberellins	Spray et al. (1996)
	Abscisic acid	Tan et al. (1997)
Bean ( <i>Phaseolus vulgaris</i> L.)	Brassinosteroids	Yokota et al. (1987)
Conifer ( <i>Cryptomeria japonica</i> )	Brassinosteroids	Watanabe et al. (2000)
Tomato ( <i>Lycopersicon esculentum</i> )	Brassinosteroids	Yokota et al. (2001)
	Ethylene	Mayak et al. (2004)
Chick pea ( <i>Cicer arietinum</i> )	Ethylene	Kukreja et al. (2005)
Potato ( <i>Solanum tuberosum</i> L.)	Salicylic acid	Coquoz et al. (1998)

Brassinosteroids are considered as the sixth group of phytohormones that was isolated from pollen of rape plant (*Brassica napus* L.) (Rao et al. 2002) and confers resistance to biotic and abiotic stresses (Sasse 2003; Mussig 2005). Brassinosteroids are present in plants at extremely low concentration, and their level varies in plant tissues with higher concentration of brassinosteroids in young tissues compared to mature ones (Yokota and Takahashi 1986). In addition to this, occurrence of jasmonic acid and salicylic acid is also reported in plants which are involved in various developmental processes like seed germination, root growth, and senescence (Creelman and Rao 2002; Chen et al. 2009b; Wasternack and Hause 2002, 2013).

Phytohormones move throughout the plant body and are distributed within plant tissues from cell to cell via the xylem or phloem transport stream. These hormones can cause significant impact on plant physiological processes. The excess amount of hormones may be stored in plant tissues as conjugates for further use. Plant gene and phytohormones interact with each other. Some genes activate the plant hormones, whereas certain hormones activate the genes as well. Many genes are involved in hormone perception and signaling pathways that control the production and activity of hormones by expression level of relevant gene. In plants, there are hormone receptors with high affinity responding to the phytohormones. The activities of phytohormones are affected by different parameters that include the properties and affinity of the receptors as well as the cytosolic  $\text{Ca}^{2+}$  (Weyers and

Paterson 2001). Most plant cells have receptors for different hormones. These cells recognize the hormones, and when a hormone meets the right receptor, it triggers a response.

The release of hormones is a normal physiological process of a plant during its life cycle and is also mediated by environmental conditions. After the release of hormones, these may act either close to or remote from their sites of synthesis to regulate responses to environmental stimuli (Davies 2004). Plant hormones operating at low concentration are able to translocate within the body and bind to a specific receptor protein.

## 2.2 Microbial Hormones

It is well established that two types of hormones are available to plants, one is endogenous production by plants and second is exogenous production by microorganisms. Like plants, a number of microorganisms residing in the soil also produce phytohormones; however, their pathways for hormone production may be different from plants. So far, a number of bacterial and fungal strains have been evaluated for their ability to produce phytohormones, and some selected examples have been mentioned in Table 2.

**Table 2** Microbial production of phytohormones

Microbe	Hormone	Reference
Bacterial phytohormones		
<i>Stenotrophomonas maltophilia</i> SSA	Indole-3-acetic acid, gibberellic acid, trans-zeatin riboside, and abscisic acid	Naz and Bano (2012)
<i>Pseudomonas mendocina</i> Khsr2, <i>Pseudomonas stutzeri</i> Khsr3, and <i>Pseudomonas putida</i> Khsr4	Indole-3-acetic acid, gibberellic acid, trans-zeatin riboside, and abscisic acid	Naz and Bano (2012)
<i>Bradyrhizobium japonicum</i>	Indole-3-acetic acid	Minamisawa and Fukai (1991)
<i>Bacillus subtilis</i> IB-22	Cytokinins	Kudoyarova et al. (2014)
<i>Pseudomonas putida</i>	Indole acetic acid	Gravel et al. (2007)
<i>Azospirillum</i> spp.	Abscisic acid, gibberellins	Cohen et al. (2009)
<i>Rhizobium phaseoli</i>	Gibberellins, indole-3-acetic acid	Atzorn et al. (1988)
<i>Bradyrhizobium japonicum</i>	Indole-3-acetic acid, gibberellic acid, abscisic acid	Boiero et al. (2007)
<i>Pseudomonas putida</i>	Indoleacetic acid	Patten and Glick (2002)
<i>Rhizobium leguminosarum</i>	Indole-3-acetic acid, ethylene	Dazzo et al. (2000)
<i>Pseudomonas putida</i>	Indole-3-acetic acid, ethylene	Mayak et al. (1999)
<i>Azotobacter chroococcum</i>	Gibberellin	Pati et al. (1995)
<i>Azospirillum brasilense</i>	Auxin, abscisic acid	Kolb and Martin (1985)
<i>Bacillus pumilus</i> , <i>Bacillus licheniformis</i>	Gibberellins	Gutierrez-Manero et al. (2001)

(continued)

**Table 2** (continued)

Microbe	Hormone	Reference
<i>Azospirillum brasilense</i>	Indole acetic acid (IAA) and gibberellic acid	Kumaran and Elango (2013)
<i>Pseudomonas</i> sp.	Indole acetic acid	Malik and Sindhu (2011)
Fungal phytohormones		
<i>Cladosporium</i> sp.	Gibberellins	Hamayun et al. (2010a)
<i>Penicillium citrinum</i>	Indole acetic acid	Khan et al. (2008a, b)
<i>Paecilomyces formosus</i> LHL10	Gibberellins, indole acetic acid	Khan et al. (2012a, b)
<i>Fusarium oxysporum</i>	Gibberellin and auxin	Hasan (2002)
<i>Phoma glomerata</i> LWL2 and <i>Penicillium</i> sp. LWL3	Gibberellins, indole acetic acid	Waqas et al. (2012)
<i>Aspergillus fumigatus</i> sp. LH02	Gibberellins	Khan et al. (2011b)
<i>Aspergillus fumigatus</i>	Gibberellins	Hamayun et al. (2009)
<i>Trichoderma atroviride</i>	Indole acetic acid	Gravel et al. (2007)
<i>Pisolithus tinctorius</i>	Indole-3-acetic acid	Frankenberger and Poth (1987)
Cyanobacteria/algal phytohormones		
<i>Nostoc</i> OS-1	Indole-3-acetic acid	Hussain et al. (2015)
<i>Nostoc</i> PCC 73102	Indole-3-acetic acid	Sergeeva Prasanna et al. (2002)
<i>Anabaena</i>	Indole-3-acetic acid	Prasanna et al. (2010)
<i>Oscillatoria annae</i>	Indole-3-acetic acid	Varalakshmi and Malliga (2012)
<i>Scenedesmus obliquus</i>	Indole-3-acetic acid	Correa et al. (2011)
<i>Haematococcus pluvialis</i>	Abscisic acid	Kobayashi et al. (1997)
<i>Chlorophyta</i> (Cyanobacteria)	Cytokinins	Ordog et al. (2004)
<i>Cyanophyta</i> (Cyanobacteria)	Cytokinins	Stirk et al. (2002)
<i>Dunaliella</i> sp.	Abscisic acid	Tominaga et al. (1993)
<i>Dunaliella salina</i>	Abscisic acid	Cowan and Rose (1991)
<i>Hydrodictyon reticulatum</i>	Brassinosteroids	Yokota et al. (1987)

Among this microbial population, beneficial bacteria commonly known as plant growth-promoting rhizobacteria (PGPR) are the major contributor of phytohormones. These PGPR promote the plant growth and development by the production of phytohormones and act as biostimulators (Glick et al. 1998; Jimenez-Delgado 2004). A number of workers have reported the production of phytohormones by a significant population of bacteria (Arshad and Frankenberger 1998; Rao et al. 2002; Baca and Elmerich 2003; Khalid et al. 2006; Egamberdieva 2009). The type and amount of hormones produced by microorganisms are variable depending upon microbial community as well as suitable substrate or precursor available to the microorganisms. For example, Khalid et al. (2004) reported that among 30 bacterial isolates, 22 were able to use precursor of indole-3-acetic acid (IAA). They further reported that in the presence of IAA precursor, i.e., L-tryptophan, the bacterial efficiency

to synthesize IAA enhanced manifold. Likewise, mevalonic acid is the substrate for the microbial synthesis of gibberellins and abscisic acid; however, formation of different intermediate compounds during the growth phase of a microorganism determines what will be the final compound, i.e., a gibberellin or an abscisic acid. It is worth noting that the presence of a precursor in the environment can stimulate/enhance the synthesis of phytohormones and it may or may not be the basic requirement for microbial synthesis of hormones. A PGPR strain can also produce a phytohormone in the absence of a substrate in the soil environment as it has been observed in the case of IAA production by certain bacteria without precursor (Khalid et al. 2006).

Free-living bacteria and bacteria living in association with plants produce phytohormones. For example, free-living *Azospirillum brasilense* and symbiotic *Bradyrhizobium japonicum* have been reported to produce indole-3-acetic acid, gibberellic acid, and zeatin (Cassan et al. 2009). Similarly, an endophytic bacterium *Sphingomonas paucimobilis* ZJSH1 has also been found to produce indole acetic acid, salicylic acid, abscisic acid, and zeatin (Yang et al. 2014).

Apart from bacterial population, a number of fungi present in soil environment are also able to produce growth hormones. Akhtar et al. (2005) reported that 78, 83, 89, and 72 % fungal strains isolated from wheat, maize, potato, and tomato rhizosphere, respectively, were able to produce ethylene in the presence of L-methionine. Reports about phytohormone production by endophytic fungi are also available (Khan et al. 2008a, b; Hamayun et al. 2010a). Khan et al. (2011a) reported gibberellin production by endophytic *Aspergillus fumigatus* sp. LH02. Brassinosteroids have also been identified in unicellular green algae *Chlorella vulgaris* (Bajguz 2009; Stirk et al. 2013). Kim et al. (2005) reported more than 50 naturally occurring brassinosteroids from the entire plant kingdom.

### 3 Metabolism of Phytohormones

In an earlier study, Bont et al. (1979) observed that ethylene metabolism in *Mycobacterium* involves the epoxidation of the double bond by a mono-oxygenase. Wiegant and DE Bont (1980) found a new route for the degradation of ethylene glycol via acetaldehyde and acetate. They found that ethylene glycol was not an intermediate in ethylene metabolism.

It has been observed that in addition to synthesize IAA, some strains of *B. japonicum* are also able to catabolize IAA. Jensen et al. (1995) studied the catabolism of indole-3-acetic acid and 4- and 5-chloro-indole acetic acid by two strains of *Bradyrhizobium japonicum* (strains 61A24 and 110). They observed that both strains metabolized IAA with different efficacies and IAA was metabolized via dioxindole-3-acetic acid, dioxindole, isatin, and 2-aminophenyl glyoxylic acid (isatinic acid) to anthranilic acid. They reported that degradation of 4-Cl-IAA apparently stopped at the 4-Cl-dioxindole. The metabolism of IAA by peroxidases has been reported by oxidizing IAA via two different mechanisms: one is conventional mechanism that requires  $H_2O_2$  (Schulz et al. 1984) and the other one is not dependent on  $H_2O_2$  and requires  $O_2$  instead of  $H_2O_2$  (Savitsky et al. 1999).

Cytokinins are present in plants both as free base and the corresponding nucleosides and nucleotides. In earlier studies, first of all, Paces et al. (1971) demonstrated the oxidative cleavage of cytokinins in a crude tobacco culture. Later on Whitty and Hall (1974) named this cleavage as enzyme cytokinin oxidase. Mok et al. (2000) reviewed the synthesis and metabolism of cytokinin and reported that a number of enzymes were involved in cytokinin metabolism and these enzymes were not cytokinin specific. Cytokinin dehydrogenase is the enzyme that catalyzes irreversible inactivation of cytokinins. For years, it was assumed that molecular oxygen was essential for the activity of cytokinin dehydrogenase; however, the work of Galuszka et al. (2001) and Frebortova et al. (2004) showed that other electron acceptors, especially quinone types such as 2,3-dimethoxy-5-methyl-1,4-benzoquinone, also functioned efficiently other than oxygen. In addition to many plant species, the activity of this enzyme has also been reported in few lower organisms like moss, slime mold, and yeast (Gerhauser and Bopp 1990; Armstrong and Firtel 1989; Van Kast and Laten 1987).

#### **4 Physiological Effects of Phytohormones**

Phytohormones are naturally occurring substances that are produced by the plant and play a very important role in certain physiological processes of plant. These are released by the plant during its life cycle in normal conditions and also in response to some environmental stimuli. These signal molecules are present in trace quantities and are actively involved in many biochemical processes (Ogwenio et al. 2010). Among these hormones, ethylene, jasmonic acid, and salicylic acid play a role in biotic stress tolerance, and abscisic acid plays a role in regulating the abiotic stress tolerance (Ton et al. 2009; Bailey et al. 2009; Kavroulakis et al. 2007; Hadi and Balali 2010). However, some of these phytohormones are also equally effective for promoting biotic and abiotic stress tolerance in plants like jasmonates and salicylic acid (Hadi and Balali 2010; Hara et al. 2012; Khan and Khan 2013; Kazan 2015).

These hormones affect almost all the processes of plant life cycle and also play a critical role in plant defense system against environmental stresses both biotic and abiotic (Taiz and Zeiger 2010; Williams 2010). The effectiveness of the hormone depends upon its suitable concentration, its production at the right place and time, as well as its interaction with specific receptor. Depending upon their nature and concentration, they may cause positive and negative impacts on plant growth and development. They exert their influence on target cells where they bind transmembrane receptors, and depending upon the context, they are subject to positive or negative feedback control. Some of the major positive and negative impacts of these hormones on plant growth are discussed in the following sections.



## 4.1 Positive Effects

The role of phytohormones for accelerating plant growth and development is well documented. Hormones affect almost all physiological processes of plant. These hormones also enhance the plant resistance against unfavorable conditions and protect the plant from negative impact of a number of biotic and abiotic stresses. Among these hormones, ABA serves as an endogenous messenger in biotic and abiotic stress responses of plants (Adie et al. 2007; Ton et al. 2009). Gibberellic acids have been shown to have an effect on reactive oxygen and antioxidant activities (Tian et al. 2011; Wang et al. 2012).

Schumacher and Chory (2000) reviewed the role of brassinosteroids and reported that these hormones were required for a wide range of plant developmental processes including shoot and root elongation, seed development and germination, and development of vascular tissue. Gibberellic acids are also involved in stem and leaf elongation, flower induction, trichome, anther, seed germination, and fruit and seed development (Pharis and King 1985; Singh et al. 2002). Jasmonic acid (JA) induces resistance to a broad range of herbivores and is known to reduce the growth and survivorship of many insects. Fan et al. (2014) reported the role of JA to enclose the invading nematodes at the initial site of infection and then inhibit nematode multiplication and spread. The application of cytokinins also proved useful for regulating the plant response to environmental stress (Ha et al. 2012).

Auxin is a well-known group of phytohormones that plays a significant role in the initiation of primary root growth and promotion of root hair and lateral root formation (Takahashi 2013). The involvement of auxin in plant-microbe signaling is also known (Berg 2009). Recently, Kovaleva et al. (2015) observed that the addition of IAA to the nutrient medium increased the content of actin cytoskeleton (F-actin) in the apical and subapical zones of pollen tubes that might be responsible for the stimulation of pollen growth. This argument is supported by further observations such as the decrease in the content of endogenous IAA, inhibited germination, and/or blocked male gametophyte polar growth. It is also evident from the work of Tian et al. (2008) who observed that root inhibition due to high nitrate concentration was closely related to the reduction of IAA level in roots.

This positive impact of auxin is not only observed due to naturally occurring auxin compounds but also with the application of synthetic ones. It was observed from the work of Bajguz and Piotrowska-Niczyporuk (2014) that the application of natural as well as synthetic auxins caused significant impact on the growth, metabolite content, and antioxidant response of green alga (*Chlorella vulgaris*).

These phytohormones work individually and in coordination with each other and cause impact on plant physiological processes. An increase in ABA level has been observed in green algae when exposed to heat stress in the presence of brassinosteroids (Bajguz 2009). The synergistic role of ABA in regulating plant growth and development with brassinosteroids, gibberellic acid, and auxin has also been reported by workers (Zhang et al. 2009; Achard et al. 2006). Similarly, physiological activity of brassinosteroids is largely consistent with physiological influences

exerted by auxins. Stimulation of cell proliferation and endogenous accumulation of proteins, chlorophylls, and monosaccharides has been in algal cell by this synergistic interaction (Bajguz and Piotrowska-Niczyporuk 2013). Although the basic mechanisms of these interactions are not much clear however, it has been reported that these interactions are possibly mediated through various metabolic pathways (Kudryakova et al. 2013; Bajguz and Piotrowska-Niczyporuk 2014). Along with auxins and gibberellins, brassinosteroids promote cotton fiber initiation and elongation in the cultured ovule system (Sun et al. 2005; Shi et al. 2006).

These hormones in addition to controlling intrinsic growth also mediate adaptation of plant development to changing environmental conditions (Tuteja and Sopory 2008; Wolters and Jurgens 2009). Javid et al. (2011) reviewed the role of phytohormones in alleviating salt stress in crop plants. They concluded that the concentration of auxin, cytokinins, gibberellins, and salicylic acid decreased in the plant tissues under salinity stress, while an increase was observed in abscisic acid and jasmonate level. They demonstrated that changes in hormonal level is the cause of growth reduction under salinity stress and this negative impact can be diluted by the application of plant growth regulators. Cabello-Conejo et al. (2014) evaluated the phytoextraction capacity and growth of four Ni hyperaccumulating species (*Alyssum malacitanum*, *Alyssum corsicum*, *Alyssum murale*, and *Noccaea goesingense*) in the presence of four phytohormones (B, C, K, and P) based on gibberellins, cytokinins, and auxins. They observed that plant species were varied regarding biomass production and depend on the type of PGR and its rate of application. A significant increase in plant biomass and Ni accumulation was observed with the application of phytohormones, and most effective results were obtained in case of Ni accumulation with auxin-based product.

## 4.2 Negative Effects

Phytohormones cause positive effects on a number of plant processes; however, certain negative impacts on plant growth have also been observed due to these hormones. As discussed in previous sections, the effects on plant growth by phytohormones may be variable which depends upon their concentration, environmental factors, and physiological status/process of the plant. A phytohormone enhances plant growth up to a particular concentration, and growth inhibition may occur if concentration increases from that particular level. For example, ethylene that plays significant role in a number of plant processes also causes negative impact on plant growth and development due to its elevated level particularly under stress environment (Nadeem et al. 2010a). At low concentration, promotion of root growth while at high concentration inhibition of root elongation has been observed (Mattoo and Suttle 1991; Belimov et al. 2002). Ethylene plays an important role in legume-rhizobia association and causes significant impact on rhizobial infection in legumes (Penmetsa and Cook 1997). Inhibition of nodulation with ethylene has been observed whether it was applied directly as a gas or in the form of its precursor like

ACC (Yuhashi et al. 2000). This argument is further supported when nodulation was restored after treating with ethylene inhibitor (Guinel and Sloetjes 2000). Ethylene also affects the plant growth negatively by causing certain disorder or many other disorders such as leaf abscission, senescence, epinasty, and chlorophyll destruction (Shibli et al. 2007; Nadeem et al. 2010b). In addition to ethylene, indole acetic acid and abscisic acid are also known to modulate abscission (Suttle and Hultstrand 1993; Sexton and Roberts 1982).

Kukavica et al. (2007) observed that IAA inhibited the root elongation of hydroponically grown pea plants. IAA induced the disappearance of peroxidase isoforms and hydroxyl radical formation in the root and the root cell wall. Malik and Sindhu (2011) while studying the impact of co-inoculation of indole acetic acid producing *Pseudomonas* sp. with *Mesorhizobium* on chickpea (*Cicer arietinum*) growth and nodulation observed that exogenous seed treatment with higher concentration of IAA (10.0  $\mu\text{M}$ ) inhibited the growth of seedlings.

Similar response was also observed in the case of other hormones. For example, the phytotoxicity caused by some bacteria and fungi was due to the suppression of root growth by secretion of IAA at high concentration (Barazani and Friedman 1999a; Ditengou and Lapeyrie 2000). ABA positively affected the leaf size and bud dormancy and negatively influenced the size of guard cells and internode length (LeNoble et al. 2004). Severe inhibition of pollen germination and pollen tube growth was observed due to the application of gibberellins to grape flowers before or during anthesis (Kimura et al. 1996).

The phytohormones interact with each other, and this interaction may be a negative one, as observed in the case of jasmonic acid and gibberellins (Heinrich et al. 2013) where a high level of jasmonic acid antagonizes the biosynthesis of gibberellins. This decrease in gibberellins results in the inhibition of stem elongation of *Nicotiana attenuata*. They reported that this inhibition of gibberellins was due to high level of jasmonic acid.

## 5 Environmental Stresses and Plant Growth

The growth and productivity of plants are affected by various biotic and abiotic stresses. The plant growth is affected by osmotic stress, ionic toxicity, nutrient, and hormonal imbalances (Ashraf 2004; Munns et al. 2006; Ashraf and Foolad 2007). The important environmental stresses that effect plant growth and development include drought, salinity, high temperatures, freezing, flooding, and mechanical impedance.

Among environmental stresses, soil salinity is one of common problems of various arid and semiarid regions. Salinity causes an adverse effect on soil by degrading its quality, reducing the area of crop cultivation, and minimizing the crop yield (Sadiq et al. 2002). In arid and semiarid regions, 50 % reduction in the yield of major crops has been observed owing to salinity (Munns 2005; Keshtehgar et al. 2013). Growth inhibition is one of the primary impacts of salinity on plants that

might be due to its negative impact on photosynthesis as well as cellular disruption and oxidative disintegration under saline environment (Zhu 2007). Almost all morphological and physiological processes of plants are affected by salinity. In salty conditions, among various ions that cause a negative impact on plant growth, the effect of sodium is more pronounced that interferes the potassium uptake (Zhu 2007) that results in potassium deficiency in plant (Nawaz and Ashraf 2010). This increased Na/K ratio causes certain cellular and nutritional imbalances in plants like reduction in soluble sugars and essential nutrients (Ibrahim et al. 2006). Lowering of membrane stability of vital cell organelles was also observed due to high Na/K ratio (Gadallah 1999; Heuer 2003). In addition to Na<sup>+</sup>, higher chloride (Cl<sup>-</sup>) concentrations also disturb the plant metabolic activities by affecting the activities of certain enzymes. For example, plant loses its ability to maintain their osmotic pressure due to high chloride ion in the cytoplasm (Misra and Saxena 2009). In saline environment, inhibition of RNA and DNA synthesis has been observed due to reduced production of certain amino acids and respective nitrogenous bases required for this purpose (Chen et al. 2003; Song et al. 2006).

For plants, water availability is considered as a major dictating factor for their production. Under salinity stress, due to the increase in soil osmotic potential, soil water becomes unavailable to plants and extraction of water from soil becomes difficult (Nawaz et al. 2010) that result in the disturbance of certain cellular and metabolic activities of plants that leads to improper plant growth and development (Munns 2005). Under water-deficit conditions, plant growth is adversely affected due to alteration in many key physiological processes related to growth and reproduction (Manivannan et al. 2008). Plants respond promptly to water stress, and the consequences of even a short-term drought at any growth stage cause negative impact on plant's whole life cycle. Drought affects almost every morphological, physiological, and biochemical aspect of plant and poses severe limitations for crop production (Aroca 2012). The literature revealed that drought mainly affects key processes regarding cell division, water relations, nutrient uptake, nutrient assimilation, energy transfer, carbon fixation, and photosynthesis (Yamance et al. 2003; Gomes et al. 2010; Taiz and Zeiger 2010; Asrar and Elhindi 2011). The reduction in water contents of cytoplasm restricts the cell division, elongation, and differentiation primarily due to decrease in turgor pressure, metabolic activity, and inhibition of energy transfer (Taiz and Zeiger 2010). The inhibition of cell multiplication adversely affects the vegetative and reproductive growth due to lower biomass accumulation leading to stunted root and shoot growth, poor flowering, and fruit development (Asrar and Elhindi 2011). Under water-deficit conditions, plants show limited nutrient uptake and become nutrient deficient. Several reports indicate that under water shortage, plants show significant reduction in all macro- and micronutrients in roots and shoots, especially nitrogen, potassium, and phosphorus (McWilliams 2003; Subramanian et al. 2006; Asrar and Elhindi 2011).

Temperature affects every physical, chemical, and biological process in living cells. A slight increase or decrease in temperature can cause irreversible damage to crop plants. High temperature is the most extreme form of temperature stress which

is challenging the plant's survival in extreme climatic conditions. Plants under high temperature stress show a variety of responses at cellular and molecular level. High temperature adversely affects the growth, phenology, biochemistry, physiology, and anatomy of plant (Wahid et al. 2012).

Like other stresses, the effect of high temperature on plant growth can be observed at any stage from germination to seed production. Ren et al. (2009) reported that high temperature inhibits the germination due to alteration in expression of protein profiles. At germination, plants are more sensitive to temperature change that severely inhibits the seedling emergence and its development (Egli et al. 2005). Specific enzymes involved in germination are denatured by high temperature that inhibits the growth of germinating embryos (Wahid et al. 2012). Photosynthesis is also affected by heat stress as high temperature destroys the mesophyll cell followed by deshaping and swallowing of chloroplasts, stroma, and lamella, severely affecting the activity of photosystem II (Carpentier 1999).

The chilling injury refers to the extreme low temperature but slightly above freezing point, while freezing injuries occur when freezing temperature prevails and solutions in plants start freezing followed by crystallization resulting in complete ceasing of biochemical machinery and rupture of membrane structures (Sokolnik 2012). The disturbance in biochemical mechanisms also results in the production of reactive oxygen species (ROS) that induces oxidative stress, as low temperature hinders the functioning of oxido-reductive enzymes, e.g., catalase inhibition leads to higher accumulation of  $H_2O_2$  and free radicals (Los and Murata 2004; Sun et al. 2010).

At present, due to the rapidly increasing industrialization and urbanization, environmental pollution is becoming a serious issue. The most toxic pollutants that prevail in the environment are heavy metals that are toxic to every living, and reports showed that almost every ecosystem has been contaminated with these pollutants (Wei and Yang 2010; Azizullah et al. 2011). The release of heavy metals in soil and water is becoming a serious limitation for crop production not only in area surrounding the industrial locations, but heavy metal stress is also becoming a serious issue even in remote areas as the injudicious and blind use of chemicals for crop production severely contaminated the soils with heavy metals (Hjortenkrans et al. 2006; Nada et al. 2007). These heavy metals pose cytotoxic, genotoxic, and mutagenic effects on plants. Most of heavy metals are actively uptaken by plants and transferred into food chain resulting in serious health issues in animals and humans as well (Flora et al. 2008).

The above discussion showed that plants faces a number of stresses in soil environment. All these stresses affect the plant growth and development by causing negative impact on various plant physiological processes. These stresses also interact with each other, and the intensity of their impact may be increased. The intensity of these stresses may vary with plant species as well as growth stage. One stress may be more detrimental at particular growth stage, and control of this negative effect at that stage could be beneficial for proper plant growth and development.

## 6 Mitigation of Stress-Induced Impacts on Plant Growth Through Phytohormones

The use of plant growth regulators is an effective approach to promote plant growth and development. Owing to their growth promotion abilities, phytohormones are being used effectively for enhancing crop production under normal as well as stress conditions. There are certain reports which show their effectiveness in agricultural production (Saeedipour 2013; Bano and Yasmeen 2010; Kovaleva et al. 2015; Afzal et al. 2005).

### 6.1 Mechanism of Action

A variety of mechanisms are adopted by plants to cope with stress conditions. Among these, one of the effective and comprehensive mechanisms includes the biosynthesis of plant growth regulators or phytohormones. Production of these organic metabolites is a primary tool for plants to mediate a wide range of adaptive response systems (Santner et al. 2009) and be involved in regulating various plant processes under normal as well as adverse soil conditions necessary for normal plant growth and development (Kaya et al. 2009).

The phytohormones cause impact on all phases of the plant throughout its life cycle. Movement of phytohormones throughout the body takes place via the xylem or phloem transport stream. In order to exert their response, phytohormones bind transmembrane receptors or endoplasmic reticulum. Hormonal concentrations and tissue sensitivity regulate the physiological process that causes profound effects on plant growth (Taiz and Zeiger 2010). In response to stress conditions, plants tend to accumulate high concentrations of phytohormones like auxins and IAA (Javid et al. 2011; Wang et al. 2001). This high concentration of hormones might be helpful for mitigating the negative impact of stress. For example, under low soil water potential, auxins accumulation in plant roots takes place which are transported to leaves. At the surface of cell membrane of stomatal cells, these auxins bind to receptors that result in enhanced stomatal conductance (Babu et al. 2012). It is reported that IAA has influence on oxidative phosphorylation in respiration and enhances oxygen uptake. It has been assumed that growth enhancement by IAA might be due to increased energy supply.

Gibberellin biosynthesis is also greatly influenced by developmental and environmental stimuli that disturb the level of hormone in the plant (Yamaguchi and Kamiya 2000; Olszewski et al. 2002). A decrease in endogenous level of gibberellic acid (GA) and reduced crop yield have been observed under salinity stress (Xie et al. 2003; Hamayun et al. 2010b). It might be due to decrease GA biosynthesis in plant and due to the activity of oxidases that cause distraction of hormones in plant. Similarly, there are many reports which show that in order to get immunity against stresses, plants accumulate significant amount of cytokinins in their body. Regulation of carbon and nitrogen assimilation with the accumulation of cytokinin that

enhanced drought tolerance in rice has been reported by Reguera et al. (2013). Rivero et al. (2007) also reported tobacco tolerance against drought through accumulation of cytokinins. It has been hypothesized that cytokinins enhance wheat salt tolerance through interacting with other plant hormones by regulation and detoxification of toxic ions and reactive oxygen species. Abscisic acid and cytokinins interact antagonistically causing opposite effects on various plant developmental processes including stomatal conductance, seed germination, and cotyledon expansion (Blackman and Davies 1984; Thomas 1992). It is also reported that high CK accumulating in plants show improved nutrient efficiency during nutrient deficiency (Rubio-Wilhelmia et al. 2011). It has been observed that cytokinins influence the nitrogen metabolism (Sakakibara et al. 2006) by enhancing nitrate reductase activity in plants (Sykorova et al. 2008).

## 6.2 *Phytohormones and Plant Stress Tolerance*

Endogenous and exogenous applications of phytohormones play a significant role in enhancing plant ability to maintain their growth under stress conditions. In addition to endogenous plant hormones, exogenous application of phytohormones also plays an important role in improving plant tolerance against adverse conditions (Table 3). A number of reports are available that are demonstrating the positive effects of endogenous and exogenous application of phytohormones on plant growth and development (Fan et al. 2014; Afzal et al. 2005; Fassler et al. 2010; Kumar et al. 2014; Shaddad et al. 2013).

Auxins are well-known phytohormone that play an important role in plant tolerance against various environmental stresses like salinity, waterlogging, and soil acidity (Salama and Awadalla 1987; Ribaut and Pilet 1991; Gadallah 1994, 1995). In many plants and under certain environmental conditions, endogenous phytohormone production may be lower which is not sufficient to mitigate the negative impact of stress environment (Wyn Jones and Storey 1981; Yancey 1994; Subbarao et al. 2001). Exogenous application of phytohormones under such conditions may be helpful in reducing adverse effects of stress (Makela et al. 1998a, b; Yang and Lu 2005). For example, exogenous application of auxins caused significant increase in crop yield by reducing the adverse effect of water stress (Abdoli et al. 2013a, b). Similar response was also observed in the case of heavy metal stress where the application of IAA minimizes the negative impact of heavy metal toxicity on plant growth by regulating metal accumulation and decreasing oxidative damage (Gangwar and Singh 2011; Gangwar et al. 2014). It is achieved by enhancing the activity of antioxidant enzymes as reported by Kumar et al. (2012a, b). They demonstrated that regulation of heavy metal uptake by auxin application was due to enhancement in enzymatic and nonenzymatic antioxidant activity. In water-deficit environment, the closing of stomata reduces the CO<sub>2</sub> fixation that disturbs the photosynthetic activity of the plants (Chatrath et al. 2000); however, reverse has been observed by application of IAA under such condition (Khalid et al. 2013).



**Table 3** Effect of phytohormones on plant growth

Crop	Hormone	Response	Reference
Tomato ( <i>Lycopersicon esculentum</i> )	Jasmonic acid	Proved as a useful disease control agent by inhibiting the multiplication of nematode and enclosing the invading nematodes at the initial site of infection	Fan et al. (2014)
	Salicylic acid	Decreased disease symptoms and 73 % reduction in the infection symptoms on the potato tubers were observed. With increase in concentration from 0.2 to 2 mM, the number of potato tubers was enhanced	Hadi and Balali (2010)
Petunia ( <i>Petunia hybrida</i> L.)	Auxin and cytokinin	Stimulation of polar growth due to the intensification of the cytoplasm flow. Auxin and cytokinin regulate the pollen tube polar growth via their effects on actin polymerization and spatial organization	Kovaleva et al. (2015)
Black gram ( <i>Phaseolus mungo</i> L.)	Indole acetic acid	Reduction in protein content and nitrate reductase activity were observed that was alleviated by IAA application and crop yield improved	Guru Devi et al. (2012)
Maize ( <i>Zea mays</i> )	Cytokinins	Enhanced germination and pollen tube growth of maize ( <i>Zea mays</i> L.) under sodium chloride salinity	Dhingra and Varghese (1985)
	GA3 and IAA	Seed priming with phytohormones enhanced germination and radicle and plumule length. 8 h was more effective than 16 h in all aspects	Saeedipour (2013)
	GA3 and IAA	EDTA significantly reduced the plant growth and dry biomass, while application of phytohormones improved it. Combined application of EDTA, GA3, and IAA was more effective, and significant increase in Pb uptake and its translocation into shoot were observed	Hadi et al. (2010)
	Indole-3-acetic acid, gibberellic acid, and <i>trans</i> -zeatin	Significant improvement in growth and their P status. GA3 and <i>t</i> -Z promoted shoot/root growth and morphological changes. IAA affected the chemical composition of the rhizosphere	Wittenmayer et al. (2008)
	Auxins	Diluted the impact of cold stress by reducing the morphological and physiological changes in cold-stressed plants	Battal et al. (2008)



Pepper ( <i>Capiscicum annuum</i> )	Indole-3-acetic acid	An increase in spermine and a decrease in putrescine in leaves of pepper were observed with IAA application	San-Francisco et al. (2005)
Sunflower ( <i>Helianthus annuus</i> )	Indole-3-acetic acid	Significant increase in Zn uptake and alleviation of toxic effects of Pb and Zn on plant root and shoot growth. Enhanced phytoextraction potential of treated plants	Fassler et al. (2010)
	Cytokinins	Enhanced phytoextraction by improving biomass production that might be due to stimulation of cell division and shoot initiation	Tassi et al. (2008)
Hyperaccumulating species ( <i>Alyssum corsicum</i> , <i>Alyssum malacitanum</i> , <i>Alyssum murale</i> , and <i>Noccaea goesingense</i> )	Gibberellins, cytokinins, and auxins	Enhanced Ni extraction efficiency and improved growth and biomass production of tested species	Cabello-Conejo et al. (2014)
Coriander ( <i>Coriandrum sativum</i> L.)	GA3 and 2,4-D	Improved growth parameters and decreased proline contents were observed with increasing concentration of applied hormones	Kumar et al. (2014)
Wheat ( <i>Triticum aestivum</i> )	Abscisic acid and benzyladenine	Decrease in IAA and GA and increase in proline and ABA under water stress. Application of said hormones played a role in osmoregulation by the production of proline. ABA was more effective at the later stages while benzyladenine at early stages	Bano and Yasmeen (2010)
	Gibberellins	Seed soaking with gibberellins enhanced the seedling vigor under salinity stress	Afzal et al. (2005)
	Gibberellic acid	Improved Ca <sup>2+</sup> and K <sup>+</sup> uptake and enhanced growth and yield parameters of wheat	Iqbal and Ashraf (2013)
	Jasmonic acid	Enhanced activities of antioxidant enzymes and the concentration of antioxidative compounds to reduce the excessive reactive oxygen species	Qiu et al. (2014)
	Auxins	Grain yield improved under drought stress by the application of auxins	Abdoli et al. (2013a, b)
	Auxins	Improvement in plant antioxidant defense system occurred that reduced the negative impact of heavy metal stress	Kumar et al. (2012a)
	Gibberellins	Enhanced root and shoot dry matter. Chlorophyll and carotenoid contents improved	Turkylmaz (2012)

(continued)

**Table 3** (continued)

Crop	Hormone	Response	Reference
Rice ( <i>Oryza sativa</i> )	Auxin	Application of IAA precursor L-TRP improved the growth and yield. Enhanced the uptake and translocation of cadmium	Farooq et al. (2015)
<i>Roselle (Hibiscus sabdariffa)</i>	Auxins	Enhanced carbohydrate accumulation in grains	Javid et al. (2011)
Strawberry ( <i>Fragaria ananassa</i> )	Gibberellic acid	Improved photosynthetic pigments, growth, and osmotic relations under salinity stress	Ali et al. (2012)
Groundnut ( <i>Arachis hypogaea</i> )	Gibberellins	Application of phytohormone improved the fruit quality	Qureshi et al. (2013)
	Gibberellins	Positively increased growth and yield parameters	Khan et al. (2011a, b)

Gibberellins play an important role in plant growth and development owing to their impact on seed germination, root/shoot elongation, as well as flowering and fruit patterning (Fleet and Sun 2005; Shani et al. 2013). Gibberellins are significantly focused phytohormones by researchers to be used as stress protectant (Basalah and Mohammad 1999; Hisamatsu et al. 2000). An enhancement of wheat growth has been observed under saline condition by the application of gibberellins (Parasher and Varma 1988). According to the findings of Maggio et al. (2010), exogenous application of gibberellic acid under stress conditions reduces the stomatal resistance and increases water use efficiency. Afroz et al. (2005) reported the improvement in photosynthetic efficiency and nitrogen metabolism of salt stress mustard plant due to the application of gibberellins. Yield enhancement due to seed priming with gibberellin is attributed to the regulation of ion uptake and their partitioning (Kumar and Singh 1996; Iqbal and Ashraf 2010). Kaya et al. (2006) demonstrated that maize drought tolerance can also be improved by the application of gibberellic acid. According to their findings, it was due to enhancing chlorophyll and leaf water content as well as maintaining membrane permeability and nutrient concentrations in plant body. This can also be obtained by enhancing the activity of antioxidant enzymes against reactive oxygen species (Falkowaska et al. 2010). Plants under high temperature stress show increased acidulation of extracellular solution and decreased proteolysis level that can be regulated by the application of gibberellins (Aleksandrova et al. 2007).

The fundamental role of cytokinins is considered to maintain the indeterminate property of shoot apical meristems (Davies 2004; Hopkins and Huner 2008). Cytokinins also regulate the assimilate partitioning, sink strength, and source/sink relationships (Kuiper 1993; Ronzhina and Mokronosov 1994; Roitsch 1999). Like other phytohormones, cytokinins also affect the plant responses to environmental stresses, and this effect may be a direct and indirect one (Wilkinson et al. 2012). For example, under drought stress, the decrease in cellular contents of cytokinin results in an increase of abscisic acid (Davies and Zhang 1991) which caused the closing of stomata resulting to low photosynthetic activity of the plant (Rivero et al. 2010). In certain cases, stress-induced cytokinin synthesis like in tobacco (Rivero et al. 2009), cotton (Kuppu et al. 2013), and peanut (Qin et al. 2011) protects the plants from adverse effects of different stresses that cause negative impact on plant physiology (Reguera et al. 2013). Barciszewski et al. (2000) also reported the plant tolerance against salinity and drought due to accumulation of cytokinins. Other workers also reported the role of exogenous application of cytokinins in plant stress tolerance (Wang et al. 2001; Gupta et al. 2003; Yang et al. 2003) which is considered as an economical and easy strategy for inducing stress tolerance in many crops (Torres-Garcia et al. 2009). For example, seed priming with cytokinin is reported to increase germination and seedling survival under salt stress (Iqbal et al. 2006). Improvement of wheat seedlings and potato plants with cytokinin application under salt stress has been observed (Naqvi et al. 1982; Abdullah and Ahmad 1990). Cytokinins also act as protectant agent against plant pathogens as reported by Ketabchi and Shahrtash (2011), where the application of cytokinin significantly reduces the negative impact of *Fusarium moniliforme* on maize seedlings.

Plants synthesize different phytohormones under stress conditions depending upon the strength of their defense mechanism. The exogenous application of different phytohormones has been proven as an effective method to cope with stressful environments. It is concluded that the exogenous application of phytohormones to stress-sensitive plants can induce stress tolerance in plants.

## 7 Enhancing Plant Stress Tolerance Through Phytohormone-Producing Microbes

As described earlier, plant growth regulators (PGRs) or phytohormones are organic compounds and produced by plants in very minute quantities and translocated to different tissues. These PGRs play a primary role in the coordination of physiological processes related to growth, reproduction, and stress management. In rhizosphere, a number of microbes also synthesize these hormones as signaling agents for phyto-stimulation (Egamberdiyeva 2005). For example, auxins are important group of phytohormones, which are synthesized by soil microbes in abundance. Under stress conditions, inoculation of PGR-synthesizing microbes enhances the stress tolerance of plants. Use of PGR-synthesizing microbes as biofertilizers has been proven as a highly effective technique for enhancing crop production under normal as well as stress conditions (Ahemad and Kibret 2014). A number of microbial strains produce a variety of phytohormones including IAA, gibberellic acid, proline, and zeatin (cytokinins). All these hormones play a pivotal role in the enhancement of plant growth and productivity not only under normal conditions but also under stress conditions especially salinity, drought, temperature, and oxidative and photogenic stresses (Cassan et al. 2009). The role of PGPR for promoting plant growth owing to their ability to produce phytohormones has been reviewed in Table 4.

Literature indicates that PGR-synthesizing rhizobacteria greatly help in protecting plants under stressful conditions (Khalid et al. 2006; Egamberdiyeva 2005; Nadeem et al. 2010b). A number of bacterial strains are capable of synthesizing different phytohormones (Lugtenberg and Kamilova 2009). Commercially available PGRs are also being used exogenously to induce different plant responses and enhance plant growth under stress conditions. But, these artificially synthesized PGRs are not only very expensive but are also less efficient than PGRs from microbes (Khalid et al. 2006). Under stress, the use of PGR-producing microbes as biofertilizer is reported to improve plant growth and production by the ameliorating action of phytohormones, secreted by rhizospheric microbes, that helps plant to regulate their osmotic potential, hormonal balance, and level of toxic ions in cytoplasm.

Leinhos and Bergmann (1995) reported that phytohormone-producing microbes enhance plant growth and induce drought tolerance in plants by producing IAA that is taken up by plants and performs a significant role in alleviation of adverse effects of drought on plants. San-Francisco et al. (2005) also reported in pepper plants that inoculation of auxin-producing microbes enhanced the growth and physiology of pepper plants growing under nutrient stress conditions. The induction of stress tolerance was attributed to the production of free polyamines and enhanced levels of

**Table 4** Effect of phytohormone-producing microbes on plant growth

Crop	Microbe	Response	Reference
Maize ( <i>Zea mays</i> )	<i>Stenotrophomonas maltophilia</i>	Significant improvement in growth occurred. Root and shoot proline content enhanced under normal and salinity stress	Naz and Bano (2012)
	<i>Azospirillum lipoferum</i>	ABA and GA inhibitors negatively affected the growth of plants; however, inoculation with phytohormone-producing bacteria completely reversed this effect. The relative water contents of inhibitor-treated plants and drought-stressed plants were significantly lower, and this effect was completely neutralized by inoculation	Cohen et al. (2009)
Rice ( <i>Oryza sativa</i> ) and wheat ( <i>Triticum aestivum</i> )	<i>Nostoc</i> OS-1	Efficiently colonized the roots of both crops and improved growth	Hussain and Iqbal (2015)
Wheat ( <i>Triticum aestivum</i> )	<i>Pseudomonas aurantiaca</i> , <i>Pseudomonas extremorientalis</i> TSAU6, and <i>Pseudomonas extremorientalis</i> TSAU20	Significantly increased root growth. Response was more significant under salinity stress	Egamberdieva (2009)
	<i>Bacillus subtilis</i> IB-22, <i>B. subtilis</i> IB-21	<i>B. subtilis</i> IB-22 increased amino acid rhizodeposition, while <i>B. subtilis</i> IB-21 did not significantly affect amino acid concentrations and failed to accumulate cytokinins in culture media	Kudoyarova et al. (2014)
Soybean ( <i>Glycine max</i> L.)	<i>Rhizobium</i> spp.	Through production of IAA, <i>Rhizobium</i> inoculation enhanced water and micronutrients by improving root growth. Overall plant growth was improved	Etesami et al. (2009)
	<i>Penicillium funiculosum</i>	Significant enhancement in soybean growth parameters. Less endogenous abscisic acid and elevated jasmonic acid contents in treated plants under salt stress	Khan et al. (2011a)
Corn ( <i>Zea mays</i> L.) and soybean ( <i>Glycine max</i> L.)	<i>Aspergillus fumigatus</i> sp. LH02	Significant improvement in growth parameters including shoot length and shoot fresh and dry biomass under salt stress. Chlorophyll contents and photosynthetic rate also enhanced	Khan et al. (2011b)
	<i>Azospirillum brasilense</i> Az39, <i>Bradyrhizobium japonicum</i> E109	Inoculation with PGPR singly or in combination promoted seed germination, nodule formation, and early development of corn and soybean seedlings	Cassan et al. (2009)

(continued)

**Table 4** (continued)

Crop	Microbe	Response	Reference
Fodder ( <i>Galega orientalis</i> Lam.)	<i>Rhizobium galegae</i> , <i>Pseudomonas</i> sp.	Application of IAA producing <i>Pseudomonas</i> with IAA absent <i>R. galegae</i> enhances rhizobia-legume interactions acting as “rhizobium helper bacteria”	Egamberdieva et al. (2010)
Indian mustard ( <i>Brassica juncea</i> )	<i>Pseudomonas</i> sp. and <i>Bacillus megaterium</i>	Enhanced plant growth and protected the plant from Ni toxicity. Nonsignificant effect on Ni extraction, however, produced significant biomass	Rajkumar and Freitas (2008)
Cucumber ( <i>Cucumis sativus</i> )	<i>Paecilomyces formosus</i> LHL10	Significantly enhanced cucumber growth parameters. Dilute the negative impact of salinity by accumulating proline and antioxidants and maintaining plant water potential	Khan et al. (2012a, b)
	<i>Burkholderia</i> sp.	Significantly enhanced cucumber growth parameters. Soluble sugar and crude protein contents were significantly higher in inoculated plants	Kang et al. (2010)
	<i>Phoma glomerata</i> LWL2 and <i>Penicillium</i> sp. LWL3	Under stress, growth was affected that was regulated by endophytes inoculation through altering abscisic acid, jasmonic acid, and salicylic contents	Waqas et al. (2012)
Tomato ( <i>Lycopersicon esculentum</i> )	<i>P. putida</i> and <i>T. atroviride</i>	Inoculation caused significant improvement in the fresh weight of both root and shoot in the presence of L-tryptophan	Gravel et al. (2007)
Chickpea ( <i>Cicer arietinum</i> )	<i>Pseudomonas</i> sp., <i>Mesorhizobium</i> sp.	Co-inoculation significantly increased nodule number and nodule biomass. The response was more significant in case of co-inoculation compared to <i>Mesorhizobium</i> -inoculated plants alone	Malik and Sindhu (2011)

spermine and decreased levels of putrescine that efficiently regulated the mineral uptake in plants and reduced the stress intensity. Similarly, Wilmowicz et al. (2008) reported that several microbes were capable of producing abscisic acid, which is a vital phytohormone. The inoculation of such microbes to plants resulted in significant improvement in reproductive growth including flowering and fruiting (Zhang et al. 2006). Under stress conditions, microbial-derived phytohormones also help plants to withstand stress-induced oxidative destruction through maintaining the equilibrium between antioxidants and ROS (Arbona et al. 2005).

Under high nitrate supply plant shows reduced root growth due to nitrate stress. However, the introduction of IAA producing microbial inoculants increases the concentration of endogenous IAA which improves root growth under nitrate stress (Forde 2002; Tian et al. 2008). Liu et al. (2007) reported that the uptake of bacterial synthesized phytohormones increased the heavy metals chelation which reduced the severity of heavy metal stress on plants. Ahmad et al. (2014) reported the inoculation with auxin-producing halo-tolerant PGPR. Ahmad et al. (2013) improved the productivity of mung bean grown under salinity stress.

Some soil microbes synthesize phytohormones from their precursors and release the soil solutions that are taken up by plants. The abundant availability of these precursors enhances the ability of plants to produce larger concentrations of phytohormones. Zahir et al. (2010) reported that the inoculation of auxin-producing rhizobacteria and application of L-tryptophan (a precursor of auxin) alone and in combination enhanced the endogenous auxins and significantly improved yield of maize. The combined application was more effective for promoting plant growth and yield. Similar results were obtained by Arkhipchenko et al. (2005) as growth and biomass production were significantly improved in legume fodder when applied with L-tryptophan-synthesizing microbes under drought conditions. L-tryptophan results in higher production of auxins in plant's body resulting in improved water relations and vascular conductance (Barazani and Friedman 1999b; Taiz and Zeiger 2000).

Under stress conditions, the production of ethylene is a fundamental phenomenon that obstructs major plant physiological processes. Ethylene is a growth regulator, and higher production of this restricts plant growth and induces early senescence (Nadeem et al. 2010a). On the other hand, soil microbes having 1-aminocyclopropane-1-carboxylate (ACC) deaminase restrict the activity of ethylene, produced under stress conditions. Several microbes have the ability to biosynthesize ACC-deaminase and help the plants in maintaining adequate levels of ethylene (Glick et al. 2007; Nadeem et al. 2007; Ahmad et al. 2011). Cheng et al. (2007) reported that the application of soil microbes having the ability to produce ACC deaminase was found to enhance plant growth under low temperature and salinity stress.

It may be concluded that phytohormones are unique substances involved in plant growth and stress regulation. However, the biosynthesis of these substances varies from species to species as not all the plants can produce ample concentrations of these hormones under stress conditions. In this case, soil microorganisms take part in plant stress tolerance mechanisms and provide them with already synthesized phytohormones which are highly effective for plant growth promotion under stress conditions so that plants can grow and produce better even under hostile conditions without any laborious input.

## 8 Conclusions and Future Prospects

The above discussed review shows the importance of plant growth regulators in plant growth promotion. In soil environment, plant faces various biotic and abiotic stresses that affect a number of plant physiological processes. To cope with these stresses, plant develops certain strategies, and the production of hormones is one of them. These phytohormones play an important role in plant growth and development by accelerating plant processes. Not only the endogenous plant hormone but its exogenous application and microbial synthesized phytohormones are equally effective for promoting plant growth. It is also evident from the above discussed review that these phytohormones also interact with each other and this interaction may be positive or negative. Most of the negative responses by phytohormones are due to high concentration that directly affects the particular plant process or antagonizes the production of other hormones that results in impaired plant growth. This elevated level of growth hormone might be due to the result of some environmental stimuli or overproduction of a particular hormone by inoculated strains.

The work of a number of researchers discussed here shows that concentration of a hormone, its use for particular purpose, as well as application of phytohormone-producing strain are some of the major factors that should be kept in mind for improving plant growth and development under normal and stress conditions. In order to clear our understanding about these aspects, there is a huge gap that should be filled by conducting research on gross root level. Research should be focused on rate and timing of phytohormone application, their stability, as well as their bio-availability in soil environment. The selection and evaluation of potential strains that have the ability to produce phytohormones need further research so that a suitable strain for a particular purpose can be used effectively.

By using biotechnological and molecular approaches, efforts could also be focused in developing genetically engineered plants that have the ability to synthesize particular hormones which enable them to withstand and maintain their growth in adverse soil conditions. These transgenic plants would be able to grow under various conditions with minimal yield losses.

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