Chapter 9
Phytohormones as Fundamental Regulators of Plant–Microbe Associations Under Stress Conditions

Khushboo Choudhary, V. Vivekanand, and Nidhi Pareek

Abstract Stress conditions, be they abiotic or biotic, have detrimental impacts on agricultural yields. They also slow down bioremediation and lead to changes in ecosystems. These effects are primarily caused by rapid climate change due to various different factors and activities. To adapt to climate change conditions, plants have developed complex physiological and molecular mechanisms to prevent disaster. Phytohormones produced by root-associated microbes are essential for plant growth and also contribute to stimulation of plant tolerance of various stresses. Hormones act either by activating secondary messengers or via phosphorylation cascades involved in gene regulation. The roles of microbes under various types of environmental stress can be appreciated with a particular focus on production of phytohormones and their associations with host plants. Moreover, they also contribute to tolerance of biotic stresses such as pathogenic organisms via activation of induced systemic resistance and systemic acquired resistance mechanisms in plants. The combination of plants, plant growth–promoting microbes and phytohormones represents a tripartite consortium to provide a suitable environment for the spread of beneficial microbes, which, in turn, enhance plant growth. However, the association of such microbes with plants for management of stresses in agricultural systems still needs to be explored in greater depth.

Keywords Microorganisms · Phytohormones · Abiotic stress · Biotic stress

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9.1 Introduction

Plant species throughout the world are greatly affected by biological stresses (both biotic and abiotic) and by anthropogenic activities, preventing plants from reaching their full capacity for growth and production (Ogbe et al. 2020). An important step in plant defence is timely perception of stress conditions so they can be responded to quickly and efficiently. After detection, the constitutive basal defence mechanisms of plants lead to activation of complex signalling cascades that protect the plants from different stresses (Pandey et al. 2017).

Plants have developed very complex immune systems that enable them, as individual organisms, to tolerate not only individual stresses but also combinations of stresses. In plants, biotic and abiotic stresses prompt a broad range of defence responses at the molecular and cellular levels (Nejat and Mantri 2017). Better understanding of various tolerance strategies to maintain agriculture productivity by manipulation of environmental conditions can be helpful for exploiting the maximum genetic potential of crops (Egamberdieva et al. 2017).

Phytohormones are important growth regulators in specific plant organs. They have major effects on plant metabolism and play important roles in stress mitigation (Kazan 2013; Egamberdieva et al. 2017). Under conditions of biotic and abiotic stress, phytohormones control the allocation of resources to combat the most severe stress and activate several signalling pathways to control the balance of plant growth and defence responses (Yang et al. 2019). It is important to understand the similarities and differences in phytohormone signalling in agriculture production.

Phytohormones are a group of small quantities of growth regulators and signalling molecules, including abscisic acid (ABA), gibberellins (GAs), ethylene (ET), cytokinins (CKs), jasmonic acid (JA), auxins (AUXs), brassinosteroids (BRs), strigolactones (SLs) and salicylic acid (SA) (Kazan 2015). Some phytohormones—such as salicylic acid, ethylene, abscisic acid and jasmonates—are known for their positive roles in providing stress tolerance in plants (Pieterse et al. 2012). Salicylic acid, ethylene, abscisic acid and jasmonates are involved in crosstalk of auxins, gibberellin and cytokinin for regulation of plant defence response mechanisms (Nishiyama et al. 2013). It is essential to understand the complex communication of crosstalk between phytohormones (Khan et al. 2020).

Plant growth–promoting microbes can play beneficial roles, protecting plants from potential pathogens and providing adaptive benefits to plants, along with improving growth, health and production. Microbiomes are composed of many different types of microorganisms, viz. fungi, bacteria, archaea, protozoa and viruses (Mueller and Sachs 2015). Microbes modulate hormones level in plant tissues, and they have been found to have effects similar to those of exogenous phytohormone applications (Shahzad et al. 2016).

This chapter, based on the available literature on the effects of phytohormones on plant tolerance, seeks to improve understanding of microbial phytohormones and the impacts of their interactions with plants by defining their effects on plant morphological and physiological properties. The focus here is on plant-associated microbes, their physiology, their diversity and their involvement in plant tolerance of biotic and abiotic stresses.

9.2 Roles of Various Phytohormones in Plant Tolerance of Stresses

Various phytohormones are involved in plant tolerance of different types of stress (Tables 9.1 and 9.2; Figs. 9.1 and 9.2).

9.2.1 Cytokinins

Cytokinins are a very important group of phytohormones and are involved in many activities in plant growth and development, such as shoot and root meristem activity, regulation of organ size and development, shoot and root branching, and control of leaf senescence (Cortleven et al. 2019). Under conditions of water stress, especially in the grain-filling phase, it was observed that the ‘stay-green’ genotype has the potential to exhibit increased tolerance (Egamberdieva et al. 2017). It was shown that cytokinins enhanced tolerance of drought in transgenic cassava compared with that in wild type plants. Genes involved in biosynthesis of cytokinins are overexpressed, and their role in stress tolerance has been decoded (Zhang et al. 2010).

Exogenous application of cytokinins has been used to optimize internal cytokinin concentrations. It has also been documented that heavy metals, such as zinc and lead, severely inhibit seedling growth in chickpea through inhibition of gibberellic acid (GA_3) concentrations (Mohapatra et al. 2011). In one study, application of kinetin to chickpea stimulated plant growth and development under salt stress, and in another study, kinetin alleviated cadmium stress in eggplant by enhancing its antioxidant potential (Egamberdieva et al. 2017).

High cytokinin levels in plants increase resistance to pathogens, including fungi, bacteria and pest insects; the same is true of plant susceptibility to disease (Akhtar et al. 2019). The role of cytokinins in interactions with insects has been known for decades, and the discovery of cytokinin-mediated resistance to microbial pathogens in *Arabidopsis* and tobacco has been extended to other species (Dowd et al. 2017; Akhtar et al. 2019). There is experimental support for a possible dual role of fungi in modulating host immunity and optimizing nutrient supply (Akhtar et al. 2019). Similarly, bacteria cause cytokinin-induced resistance to bacterial pathogens in *Arabidopsis* (Großkinsky et al. 2016).

Table 9.1 Phytohormone-producing microbes and their actions against stress conditions in plants

Microbes	Stresses	Plants	Phytohormones	References
Bacillus licheniformis	Salinity stress	*Triticum aestivum*	Indole-3-acetic acid	Singh and Jha (2016)
Staphylococcus arlettae	Chromium (heavy metal) stress	*Helianthus annuus*	Indole-3-acetic acid, gibberellic acid, salicylic acid	Qadir et al. (2020)
Bacillus cereus, Bacillus megaterium, Trichoderma longibrachiatum, Trichoderma simmonsii	Drought and salt stress	*Glycine max*	Indole-3-acetic acid	Bakhshandeh et al. (2020)
Bacillus strains	Salinity stress	*Pennisetum glaucum*	Indole-3-acetic acid	Kushwaha et al. (2020)
Porostereum spadiceum	Salinity stress	*Glycine max*	Gibberellic acid	Hamayun et al. (2017)
Pseudomonas fluorescens	Water stress	*Vitis vinifera*	Abscisic acid	Salomon et al. (2014)
Arthrobacter woluwensis	Salinity stress	*Glycine max*	Abscisic acid, gibberellic acid, indole-3-acetic acid, jasmonic acid	Khan et al. (2019)
Micrococcus luteus	Drought stress	*Zea mays*	Cytokinin	Raza and Faisal (2013)
Sinorhizobium meliloti	Salinity stress	*Medicago sativa*	Indole-3-acetic acid, cytokinin	Provorov et al. (2016)
Serratia marcescens	Salinity stress	*Zea mays*	Salicylic acid	Lavania and Nautiyal (2013)
Gluconacetobacter diazotrophicus	Drought stress	*Oryza sativa*	Indole-3-acetic acid	Silva et al. (2020)
Bacillus aryabhattai	Heat stress	*Glycine max*	Indole-3-acetic acid, abscisic acid, gibberellic acid	Park et al. (2017)
Enterobacter sp.	Metal stress	*Hibiscus cannabinus*	Indole-3-acetic acid	Chen et al. (2017)
Rhizophagus irregularis	Drought, cold and salinity stress	*Digitaria eriantha*	Jasmonic acid	Pedranzani et al. (2016)

9.2.2 Auxins

Auxins are crucial phytohormones. They promote multiple growth and development events, such as elongation, cell division and differentiation (Asgher et al. 2015). Ljung (2013) described various modulations in synthesis transport metabolism and activity of auxins after plant exposure to stresses.

Table 9.2 Genetic delude of plant hormones from various transgenic plant origins and their roles in stress tolerance by plants

Phytohormones	Associated genes	Function	Function in plants	References
Abscisic acid	*LOS5*	Regulation of abscisic acid biosynthesis	Increased abscisic acid levels in transgenic *Zea mays*	Wani et al. (2016)
Cytokinin	*CKX*	Cytokinin inactivation	Drought resistance in *Arabidopsis thaliana*	Werner et al. (2010)
Ethylene	ACC synthase gene	Catalysis of the rate-limiting step in ethylene biosynthesis	Reduced ethylene levels with good drought resistance in *Zea mays*	Habben et al. (2014)
Indole-3-acetic acid (auxin)	*YUCCA6*	Indole-3-acetic acid biosynthesis	Drought resistance	Ke et al. (2015)
Brassinosteroids	*AtHSD1*	Brassinosteroid biosynthesis	Salinity resistance, enhanced growth and development	Tiwari et al. (2020)
Abscisic acid	*NCED*	Abscisic acid biosynthesis for feedback control	Stomatal conductance, enhanced drought resistance	Wani et al. (2016), Estrada-Melo et al. (2015)

ACC 1-aminocyclopropane-1-carboxylase

Auxins play important roles, directly or indirectly, in promoting heavy metal tolerance. Heavy metals have a negative effect on biosynthesis of auxins (Hu et al. 2013). The toxic effect of lead on sunflower plant growth was minimized by addition of a low concentration of auxin, which stimulated an increase in root volume, surface area and diameter (Fässler et al. 2010).

Plants are exposed to many different microbes around them, with disease being the exception rather than the rule for plants. The occurrence of disease is relatively infrequent because plants are able to detect potential pathogens in their vicinity and induce a basal host defence that prevents most environmental microbes from colonizing them and causing disease (Kunkel and Harper 2018).

Auxins plays important roles in numerous plant–microbe associations. Several plant-associated microbes—nitrogen-fixing symbionts, plant growth–promoting rhizobacteria (PGPRs), pathogens etc.—produce auxin hormones (Yin et al. 2014). When grown in a culture medium, some plant pathogenic bacteria (such as *Pseudomonas savastanoi*, *Pantoea agglomerans*, *Dickeya* sp. and *Xanthomonas campestris*) produce auxins (McClerklin et al. 2018; Kunkel and Harper 2018). Enhancement of the auxin stratum in contagious host tissue prompts a number of different processes associated with pathogenesis, such as inhibition of host protection, epiphytic colonization, stimulation of host cell division and pathogen development in plant tissue (Kazan and Lyons 2014). In many cases, the pathogen itself produces auxin, and auxin can be seen as a virulence factor in this interaction. However, in other interactions, the pathogen stimulates auxin accumulation or auxin

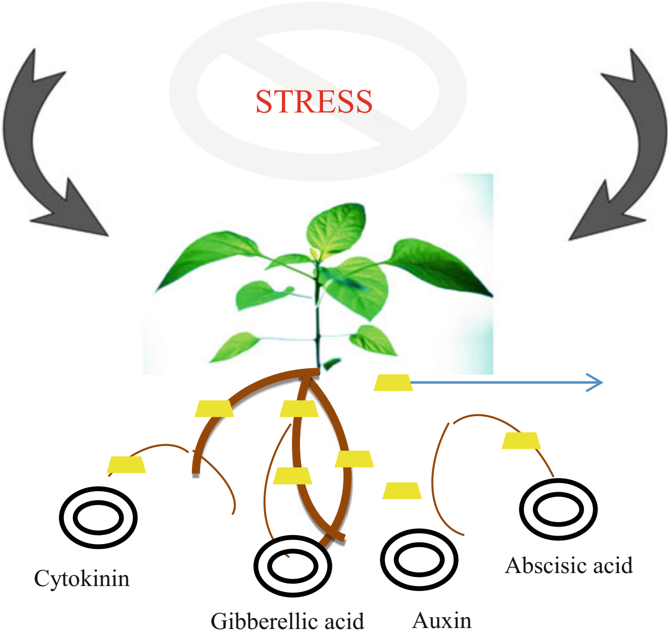

Fig. 9.1 Mechanisms of microbial phytohormone–mediated plant stress tolerance. Various root-associated microbes produce several phytohormones, which help plants to withstand stress by enhancing their antioxidant potential

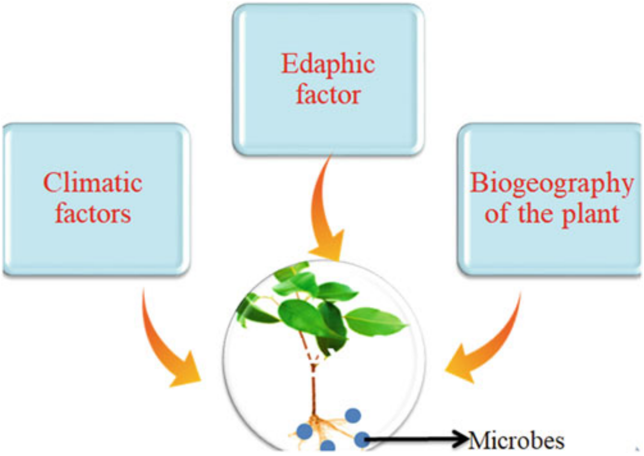

Fig. 9.2 Factors affecting plant-associated microorganisms

signalling in the host, which has evolved to modulate host auxin biology through the action of a viral factor (Kunkel and Harper 2018).

9.2.3 *Abscisic Acid*

Like other phytohormones, abscisic acid is known to play a crucial role in plants by improving stress impedance and adaptation. It is a naturally occurring member of the sesquiterpenoids, a group of major phytohormones involved in regulation of development. Several reports have described the role of abscisic acid in integrating signalling during stress exposure with subsequent control of downstream responses (Wilkinson et al. 2012). Stress response gene regulation through abscisic acid promotes and regulates signalling under abiotic stresses (Sah et al. 2016).

Abscisic acid has been described as controlling root development and water content under drought stress conditions (Cutler et al. 2010). However, during stress, a sudden increase in abscisic acid concentrations can cause growth retardation and modulate tolerance responses to stress. Even so, there is information indicating a useful effect of abscisic acid in countering the side effects of stresses, including cold stress, chilling, salinity and drought stress (Egamberdieva et al. 2017).

Exogenous utilization of abscisic acid under drought stress conditions to promote the activities of antioxidants to ameliorate stress passivity has been proposed as an effective tool for stress mitigation (Bano et al. 2012). Exogenous application of abscisic acid under drought stress conditions to improve carbon metabolism, stress tolerance and protein transport was found to significantly affect the proteome of tea plants (Zhou et al. 2014).

The major roles of abscisic acid in plant protection against pathogenic microbes are multifaceted. Abscisic acid–induced stomatal closing by regulation of guard cell ion flux in response to pathogenic attacks is important in preventing penetration of bacterial pathogens through the foramen (Lu and Yao 2018). The main components of abscisic acid–mediated stomatal function (immunity) are the serine protein kinase Open Stomata 1 (OST1), the regulatory component of the abscisic acid receptor and 2C-type protein phosphatase (Lim et al. 2015). A flagellin peptide from *Pseudomonas syringae*, a member of the pathogen-associated molecular patterns (PAMPs), induced stomatal closure through stimulation of SLAC1/SLAH3 in guard cells in an OST1-dependent manner (Chen et al. 2020). Su et al. (2017) reported that MKK4/5-MPK3 is an interdependent function in the organic acid metabolism cascade that mediates stomatal function (immunity) with abscisic acid.

9.2.4 *Gibberellic Acid*

Gibberellins are important plant development regulators and part of a large family of tetracyclic diterpenoids, which play vital roles in aspects such as lateral shoot growth, seed dormancy and establishment of floral organs (Olszewski et al. 2002). Khan et al. (2004) observed increased fruit production, leaflet development, and potassium, nitrogen and phosphorus levels in tomatoes as a result of exogenous application of gibberellic acid.

Gibberellic acid was found to trigger plant development under several different types of abiotic stress, such as salinity, drought and cold (Ahmad 2010). Increased plant water levels and reduced stomatal resistance were observed in gibberellic acid–treated tomato plants grown in saline stress conditions. Gibberellic acid influenced uptake and partitioning of ions in roots and shoots, promoting growth and maintaining plant metabolism under ordinary and stress conditions (Maggio et al. 2010; Iqbal and Ashraf 2013). An increase in osmatic components was observed in plants exposed to salt stress, and their content was further increased through gibberellin acid treatment. Endogenous use of gibberellin influenced osmatic stress in plants and preservation of tissue water content (Egamberdieva et al. 2017).

In *Arabidopsis thaliana*, gibberellic acid enhanced resistance to the bacteria *Pseudomonas syringae* and conferred disease immunity to the fungus *Alternaria brassicola* (Yimer et al. 2018). Softening during storage and development of *Alternaria* black spot disease, caused by *Alternaria alternata*, are the main post-harvest factors that reduce the storability and quality of *Diospyros* fruit. Pre-harvest application of gibberellic acid significantly enhanced fruit storage, as evaluated through fruit preservation and levels of *Alternaria* black spot (Maurer et al. 2019).

9.3 Plant-Associated Microbes

In the environment, vigorous and healthy plants live in association with various plant microbes consisting of all types of microorganisms—including fungi, archaebacteria, bacteria and protists—which create complex microbial consortia and influence plant development, health and productivity (Hassani et al. 2018). These microbes are present on the surfaces of leaves, sprouted seeds, roots and fruits, or they live inside the plants (Hardoim et al. 2015). Plants have developed their own adjustments to mitigate most stresses (abiotic and biotic) in their environments. They also depend on their associated microbes to help them survive and protect themselves against microbial attacks (Turner et al. 2013).

The relationships between plants and their associated microbial communities are not unidirectional; the host plants also provide novel metabolic capabilities for their associated microbes, leading to adaptations to specialized niches that have either positive, neutral, or variable impacts on plant health (Thrall et al. 2007). The microorganisms that promote plant development are plant growth–promoting bacteria (PGPBs), ectomycorrhizal fungi, arbuscular mycorrhizal fungi and vesicular arbuscular mycorrhizae, which live in association with plants and moderate levels of phytohormones.

9.3.1 Plant Growth–Promoting Bacteria

Plants are close allies with a numerous variety of bacteria, which play important roles in their development, disease prevention and stress tolerance. A number of beneficial bacterial strains, defined by Kloepper and Schroth (1981) as plant growth–promoting bacteria, have been isolated from the phyllospheres, rhizospheres and endospheres of a wide variety of plant types (Rilling et al. 2019). Some bacteria have become intracellular endophytes that assist in plant–microbe co-development (Bulgarelli et al. 2013). Among these bacterial taxa are PGPRs, which exert beneficial effects on plants via indirect and direct mechanisms. Beneficial rhizobacteria are used by plants to increase their water and nutrient uptake, and their biotic and abiotic stress tolerance. Although many soil bacteria species have been studied to encourage plant growth, the systems of processes by which bacteria perform their beneficial activities are usually not easy to elucidate. The molecular bases of the plant–bacteria interaction mechanisms accountable for physiological changes is now starting to be identified, mainly through new 'omics' approaches (Backer et al. 2018).

9.3.1.1 Phytohormones Produced by Plant Growth–Promoting Rhizobacteria

Phytohormones produced by PGPRs are key performers in regulating plant development. They also act as molecular signals in response to environmental factors that limit plant development or become lethal if otherwise uncontrolled (Fahad et al. 2015). Many rhizosphere bacteria species are able to secrete hormones for root uptake or maintenance of hormone balance in plants to enhance growth and biotic and abiotic stress responses (Backer et al. 2018).

PGPRs that produce auxins have been characterized through transcriptional changes in hormones and have been found to enhance root biomass, confer protection, stimulate root lengthening and cell wall modification, reduce stomatal size and induce expression of auxin-inhibiting genes that improve plant growth (Spaepen et al. 2014; Ruzzi and Aroca 2015; Llorente et al. 2016). Rhizobacteria can produce relatively large amounts of gibberellic acid, leading to improved plant shoot development (Jha and Saraf 2015). Production of cytokinins by rhizobacteria can also lead to increased root exudate production by plants, potentially increasing the numbers of rhizobacteria associated with the plants (Backer et al. 2018). The hormone ethylene plays a crucial role in plant stress tolerance (Nadeem et al. 2014). PGPRs produce 1-aminocyclopropane-1-carboxylase (ACC) deaminase, which decreases ethylene output in plants (Vejan et al. 2016). Several studies have demonstrated increased stress (biotic and abiotic) tolerance in plants inoculated with rhizobacteria that produce ACC deaminase. This appears to occur when the rhizobacteria are able to raise the level of ethylene to a sufficient level to reduce plant development, as has been shown with *Camelina sativa* (Ahemad and Kibret 2014; Pérez-Montaño et al. 2014; Ruzzi and Aroca 2015; Heydarian et al. 2016).

9.3.1.2 Enhancement of Plant Development by Plant Growth–Promoting Rhizobacteria Under Stress Conditions

The mechanisms regulating stress tolerance in plants are convoluted and complex, as plants are sessile organisms, which have no choice as to where they live (Wani et al. 2016). Development of biotic and abiotic stress tolerance in crop plants through lineal breeding is a time-consuming and expensive procedure, and genetic engineering raises issues related to moral and social ethics.

The roles of beneficial microorganisms are now being exploited for stress management and development of climate change–tolerant agriculture (Backer et al. 2018). *Bacillus amyloliquefaciens* is a biological control agent, used against *Rhizoctonia solani*, which enhances tolerance through increased defence mechanisms in plants. Modulation of phytohormone signalling in colonized plants has revealed sustained maintenance of elicitors, production of secondary metabolites and moderation of the balance between reactive oxygen species (ROS) and ROS scavengers (Srivastava et al. 2016). *Enterobacter asburiae* enhances resistance to viral disease (tomato yellow leaf curl virus) by enhancing expression of defence-related genes and antioxidant enzymes such as lyase, catalase, peroxidase and superoxide dismutase (Li et al. 2016). Thus, by performing biocontrol functions, rhizobacteria defend plants against pathogens by prompting biochemical and molecular defence responses inside the plants (Lugtenberg and Kamilova 2009).

PGPRs can promote induced systemic resistance (ISR) in their host plants by triggering expression of pathogenesis-related genes, mediated via phytohormone signalling pathways and defence regulatory proteins, to arm plants against future pathogen attacks (Pieterse et al. 2014). *Pseudomonas putida* MTCC5279 was shown to ameliorate drought stress in *Cicer arietinum* (chickpea) plants by regulating ROS scavenging efficiency, membrane integrity and osmolyte (betaine, proline and glycine) accumulation.

Stress tolerance is positively regulated by bacteria through differential expression of genes involved in ethylene biosynthesis (*ACO* and *ACS*), stress response (*LEA* and *DHN* (dehydrin)), ROS scavenging by antioxidant enzymes (*CAT*, *APX*, *SOD* and *GST*), transcription activation (*DREB1A* (dehydration responsive element binding) and *NAC1*), salicylic acid (*PR1*) and jasmonate signalling (*MYC2*) (Tiwari et al. 2016).

Application of thuricin-17, produced by *Bacillus thuringiensis* NEB17, to *Glycine max* (soybean) under drought conditions resulted in root modifications such as greater root length and increased total N_2 content, nodule biomass and root abscisic acid content (Prudent et al. 2015).

9.3.2 Arbuscular Mycorrhizal Fungi Associated with Plants

In natural ecosystems, growth of numerous plants in nutrient-poor soils is viable because they form symbiotic associations with microorganisms for their mutual benefit (Liao et al. 2018). Associations between arbuscular mycorrhizal fungi (which belong to the Glomeromycotina subphylum) and more than 70% of land plants, including the most economically important crops—such as potato, rice and soybean—are considered to be some of the most prevalent and significant symbiotic associations in nature (Brundrett and Tedersoo 2018).

Formation of intracellular fungal structures and the degree of fungal dispersal inside plant roots are tuned dynamically by the plants, and this may prevent excessive colonization and loss of carbon, thereby ensuring that both the plants and the fungi continue to benefit from this association. To accomplish this regulation, extensive transcriptional programming and cellular rearrangements are needed in the plants, along with continuous signalling and exchange between the plants and the fungi (Maclean et al. 2017). Later phases of arbuscular mycorrhizal interactions are controlled by a variety of factors, together with nutrient exchange and phytohormone activity (Gutjahr 2014; Lanfranco et al. 2018). Analysis of arbuscular mycorrhizal symbiont regulation by phytohormones has revealed a complex pattern of modifications in hormonal content or altered responses to hormones in mycorrhizal plants and reciprocal effects of hormones on the symbiotic interaction (Pons et al. 2020). Phytohormones are known to be important signalling regulators, which participate in all physiological processes in plants, including interactions between the plants and microorganisms (Liao et al. 2018). There is growing evidence of the important roles played by various phytohormones—such as strigolactones, gibberellic acid, auxins, abscisic acid and brassinosteroids—which have been identified as positive controls of arbuscular mycorrhiza symbionts.

As phytohormone signalling in arbuscular mycorrhizal growth is a new research area, many novel findings related to phytohormone regulation and potential interactions during establishment of arbuscular mycorrhizal symbiosis have been published in recent years (Liao et al. 2018). DELLA proteins are a small cluster of GRAS transcriptional controls, which have been found to act as a central node in numerous signalling pathways, including hormonal crosstalk during nodulation and arbuscular mycorrhizal colonization.

9.3.2.1 Phytohormones Produced by Arbuscular Mycorrhizal Fungi

This chapter mainly discusses the following key aspects of the contributions of phytohormones to arbuscular mycorrhizal symbiosis: investigation of plant mutants affected by phytohormone synthesis or perception, and exogenous hormone treatment of mycorrhizal plants (Pons et al. 2020). Studies of phytohormone perception mutants have focused on the effects of phytohormones on plants. Both exogenous treatment and phytohormone deficiency lead to modified hormonal content in colonized roots, which can affect either or both of the symbiosis partners. Despite this, and because phytohormones are commonly perceived as plant signals, the reported outcomes of these studies have usually concentrated only on the effects on plants (Liao et al. 2018). Similarly, hormonal content changes measured in mycorrhizal plants are usually attributed to hormonal metabolism changes in plant cells. This interpretation overlooks the potential influence of the fungi on the hormonal pool. However, many microbes can produce phytohormones, and this could be the case with arbuscular mycorrhizal (AM) fungi (Kudoyarova et al. 2019). Among the soil microbes associated with plants, fungi and PGPRs have been found to produce several phytohormones (such as abscisic acid, auxin, gibberellic acid and cytokinins) that can have growth-promoting effects (Hamayun et al. 2010; Kang et al. 2012; Spaepen et al. 2014; Kudoyarova et al. 2019). In the fungal kingdom, phytohormone production has been documented in both symbionts (such as mycorrhizal fungi) and pathogens (Chanclud and Morel 2016).

Ethylene is commonly produced by fungal species and in certain cases, the biosynthesis pathways have been described (Splivallo et al. 2009). Ethylene-forming enzyme (EFE), characterized in *Penicillium digitatum* and *Fusarium oxysporum*, produces ethylene via two simultaneous reactions using L-arginine and 2-oxoglutarate as co-substrates (Pons et al. 2020). Both pathways differ from the major one used for ethylene production in plants, which is a methionine- and light-independent pathway involving ACC synthase and amino-cyclopropane-carboxylate oxidase (ACO).

Considering that numerous plant-associated microbes produce phytohormones, it is possible that arbuscular mycorrhizal fungi do so too, given that they have evolved together with their host plants for more than 400 million years (Pons et al. 2020). This possibility is not easy to study experimentally, because these fungi are obligate biotrophs that can be isolated and cultured only for short periods, limiting the availability of biological material for such study (Liao et al. 2018). There is indirect evidence from previous studies that phytohormones may be present in some mycorrhizal fungi. Enzyme-linked immunosorbent assay (ELISA) tests have shown that the spores and hyphal sheaths of *Rhizophagus* species may contain aglycone and glycosylated abscisic acid, and indirect bioassays have indicated the presence of gibberellin and cytokinin-like molecules (Pons et al. 2020). Genes encoding CLAVATA3/Embryo Surrounding Region-Related (CLE) peptide hormone, which positively modulates the symbiosis process, have been identified in arbuscular mycorrhizal fungal genomes (Le Marquer et al. 2019).

9.3.2.2 Enhancement of Plant Development by Arbuscular Mycorrhizal Fungi Under Stress Conditions

As microbial symbionts, arbuscular mycorrhizal fungi play important roles in the plant micro-ecosystem. They are found on plant organs and inhabit internal plant tissues in natural and managed ecosystems (Card et al. 2016). Arbuscular mycorrhizal fungi help their host plants to thrive in stressful conditions via complex processes in both the plants and the fungal species, increasing photosynthesis, other gas exchange–related processes and water uptake. Numerous reports have described how fungal symbiosis improves plant resistance to a variety of stresses, such as extreme temperatures, disease, drought, salinity and metal contamination (Begum et al. 2019).

Drought stress has various impacts on plant health, such as deficiency of water supply to the roots, a reduction in the transpiration rate and stimulation of oxidative stress (Impa et al. 2012; Hasanuzzaman et al. 2013). It also has deleterious impacts on plant development and growth by affecting enzyme activity, nutrient assimilation and ion uptake (Ahanger and Agarwal 2017; Ahanger et al. 2017). However, there is strong evidence that arbuscular mycorrhizal fungi reduce drought stress in various crops, including wheat, soybean, barley, strawberry, maize and onion (Mena-Violante et al. 2006; Ruiz-Lozano et al. 2016; Yooyongwech et al. 2016; Moradtalab et al. 2019). Plant tolerance of drought may be mainly due to the large volume of soil that is accessible to the roots via the extended hyphae of the fungi (Gianinazzi et al. 2010; Orfanoudakis et al. 2010; Zhang et al. 2017). This symbiotic consortium is known to modulate diverse physio-biochemical processes in plants, such as enhanced osmotic adjustment, stomatal management through control of abscisic acid metabolism and increases in proline and glutathione levels (Kubikova et al. 2001; Ruiz-Sánchez et al. 2010; Yooyongwech et al. 2013; Rani 2016). Onion (*Allium sativum*) plants inoculated with arbuscular mycorrhizal fungi demonstrated better development and growth traits, including a higher leaf area index and greater fresh and dry biomass, under salinity stress conditions (Borde et al. 2010).

The strong impacts of arbuscular mycorrhizal fungi on plant development under intensely stressful conditions are most likely due to the efficiency of these fungi in optimizing morphological and physiological processes, thereby increasing the plant biomass and uptake of vital nutrients such as P, Zn and Cu, and decreasing the toxic effects of metals on the host plants (Kanwal et al. 2015; Miransari 2017).

Root colonization with arbuscular mycorrhizal fungi increases plant resistance to soilborne pathogenic fungi (Wang et al. 2018). Arbuscular mycorrhizal fungi provide resistance to blackleg disease in *Solanum tuberosum* (potato), which is caused by the pathogenic bacterial strain *Pectobacterium carotovora* subsp. *atrosepticum* (Bagy et al. 2019), and bioprotective effects that help plants withstand both viral diseases and soilborne fungal pathogens that cause wilting or root rot. Arbuscular mycorrhizal symbiosis also stimulates host plant resistance to chewing insects, shoot pathogens and nematodes. Various mechanisms such as regulation of plant tolerance, manipulation of induced systemic resistance and altered vector pressure are involved in these interactions (Hao et al. 2019).

9.3.3 Ectomycorrhizal Fungi Associated with Plants

Ectomycorrhizal fungi belonging to the Basidiomycota and Ascomycota are the major symbionts of many plants in numerous ecosystems worldwide (Smith and

Read 2008; Tedersoo 2017). They clearly affect mineral nutrient uptake in their host plants (angiosperms, shrubs and gymnosperms) and play roles in essential forest ecosystem processes such as nutrient cycling, carbon sequestration and breakdown of organic substances. They also help their host plants to tolerate abiotic stresses (Read and Perez-Moreno 2003; Clemmensen et al. 2015; Shah et al. 2016; Mello and Balestrini 2018).

Most ectomycorrhizal plants are completely dependent on their mycorrhizal symbiosis and cannot complete their life cycle without this root association (Vlk et al. 2020). Stimulation of root growth and development during ectomycorrhizal fungus formation depends partially on changes in plant metabolism or susceptibility to phytohormones, which are the chief regulators of plant responses to growth, development and environmental factors (Garcia et al. 2015). Various ectomycorrhizal fungi, including basidiomycetes and ascomycetes, can produce phytohormones such as auxins, ethylene, jasmonate and gibberellic acid, thereby improving the entire nutritional condition of the plants in response to numerous different factors (Guerrero-Galán et al. 2019).

The expansion of the nutrient exchange surface provided through the mycelia of ectomycorrhizal fungi is a crucial factor in increased absorption of mineral nutrients and water by the host plants because the hyphae are potentially able to penetrate nearby soil pores (Bogeat-Triboulot et al. 2004; Lehto and Zwiazek 2011). An additional beneficial influence is improvement of the soil texture by the mycelia, facilitating plant root formation (Rillig and Mummey 2006). All of these influences boost growth, development and biomass accumulation by mycorrhizal plants, making them stronger and better adapted to challenging environments than nonmycorrhizal plants (Smith and Read 2008).

The evolutionary diversity of ectomycorrhizal fungi suggests that they may perform various different functional roles in the physiology of the host. Little is known about the precise mechanisms by which ectomycorrhizal fungi reduce the impact of salinity on their host plants (Guerrero-Galán et al. 2019).

9.3.3.1 Phytohormones Produced by Ectomycorrhizal Fungi

Auxins are phytohormones that facilitate root colonization in ectomycorrhizal plants (Vayssières et al. 2015). In addition, ectomycorrhizal fungi can induce plant ethylene and auxin signalling to encourage lateral root growth and root hair elongation (Ditengou et al. 2000; Reboutier et al. 2002; Felten et al. 2009; Splivallo et al. 2009; Vayssières et al. 2015).

Salicylic acid signalling plays a crucial role in plant defence mechanisms, acting as an antagonist of ethylene and jasmonate signalling (Glazebrook 2005; Spoel and Dong 2008; Pieterse et al. 2012). In addition, exogenous salicylic acid treatment does not influence fungal colonization.

Ultimately, the crosstalk between gibberellic acid and jasmonate signalling regulates plant responses (Hou et al. 2010; Wild et al. 2012; Yang et al. 2012; Song et al. 2014). Initial reports have suggested that exogenous gibberellic acid prevents hyphal development in various ectomycorrhizal species (Basso et al. 2020).

9.3.3.2 Enhancement of Plant Development by Ectomycorrhizal Fungi Under Stress Conditions

Ectomycorrhizal fungi form symbiotic associations with plant roots and help to promote growth and protect the plant from various biotic and abiotic stresses. The association with ectomycorrhizal fungus symbionts has been suggested to be a major factor in improved tolerance of woody plant species to salinity stress, decreasing sodium uptake by photosynthetic organs (Guerrero-Galán et al. 2019).

Plants are more sensitive to increased concentrations of heavy metals in the rhizosphere than microbes, but this may be at least partially due to evolutionary selection of tolerant fungi (Gadd 2007; Amir et al. 2014). Ectomycorrhizal fungi are able to alleviate stress caused by the presence of phytotoxic substances (Joner and Leyval 2003; Amir et al. 2014). The efficiency of ectomycorrhizal fungi in defending their host plants may be due to development of the hyphal sheath, which reduces direct contact between the roots and the elements stored in the soil.

Mycorrhizal fungi exhibit mechanisms that preserve the host's health under drought stress. Ectomycorrhizal fungi induces expression of plant aquaporins in drought conditions, which improve the host plants' drought tolerance via regulation of stomatal, root and shoot conductance, and thereby regulate transpiration in the host plants (Lehto and Zwiazek 2011). Because of their extensive mycelial biomass and development of rhizomorphs, ectomycorrhizal fungi are able to transport soil water more proficiently and access moisture in the substratum (Egerton-Warburton et al. 2003). Mycorrhizal plant seedlings tolerate drought stress better than nonmycorrhizal seedlings (Augé 2001; Lehto and Zwiazek 2011).

The extent to which ectomycorrhizal trees control their photosynthesis depends on the type of ectomycorrhiza they have. Waterlogging reduces the oxygen content of the soil. Numerous wetland trees have developed mechanisms for transporting oxygen to feeder roots.

9.4 Conclusion

Agricultural crops suffer various environmental stresses (biotic as well as abiotic ones), which adversely affect their productivity. Scientific methods and high-throughput technologies have made substantial contributions in addressing these concerns but have met with limited success. There is substantial evidence that application of exogenous phytohormones from microbial sources could be a crucial tool for enhancing plant tolerance of both biotic and abiotic stresses, furnish potential practical usages under realignment or highest environmental conditions. The beneficial impacts that microorganisms have on plants—such as plant growth stimulation, resistance of biotic stresses (pathogens) and tolerance of abiotic stresses—are due to the efficiency of the microorganisms in producing various phytohormones (including auxins, abscisic acid, cytokinins, gibberellic acid and salicylic acid) in plant tissues. Moreover, plant-associated microorganisms have the ability to regulate phytohormone levels and changes in plant tissues through biochemical processes that limit the damaging impacts of abiotic stresses, such as nutrient deficiency, drought, heavy metal contamination and salinity. The symbiotic alliance of host plants with microorganisms (particularly fungi), including ectomycorrhizal and arbuscular mycorrhizal fungi, provide distinct benefits for plant species. Genetic interplay between plant hormones for enhanced tolerance towards stress conditions presents substantial opportunities to help agricultural systems adapt to climate change and enhance agricultural production.

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