Role of Phytohormone Signaling During Stress

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Abstract

Plant hormones are among the most important plant components regulating different plant functions, which can equip the plant to survive under stress conditions. There has been extensive research work regarding the effects of plant hormones on plant growth and development. The notable phytohormones include auxin, abscisic acid, ethylene, cytokinins, gibberellins, jasmonates, salicylic acid, brassinosteroids, and strigolactones. Role of phytohormones may be useful for the production of transgenic plants, which are tolerant to stress. Selected plant hormone biosynthesis, their role on plant growth under stress, signal transduction pathways, and interactions are reviewed.

Keywords

Auxins • ABA • Gibberellins • Jasmonates • Brassinosteroids

1 Introduction

Plant hormones are a group of biochemical products handling different functions in plant. Plant hormones include auxin, abscisic acid (ABA), ethylene, cytokinins, gibberellins, jasmonates, salicylic acid, brassinosteroids, and strigolactones. They can regulate plant growth and development under different conditions including stress (Table 17.1). There are different physiological alterations made by plant hormones at cellular and molecular level. At the time of hormonal activity plant genes are activated resulting in different morphological and physiological responses in plant (Table 17.1). Fluctuations in hormones can influence plant growth (Kagale et al. 2007; Jackson 2008; Hirayama and Shinozaki 2010).

The functions of plant hormones include: tissue organogenesis and development by affecting cell cycling, fruit ripening, controlling water behavior in plant by adjusting the stomata activity, and enhanced plant resistance to stress by activating different signaling pathways (Van der Knaap et al. 1999; Wang et al. 2007; Tuteja 2007).

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Table 17.1 Plant hormones and their activities

Hormone	Activities	Reference
Auxin	(1) Regulation of phototropism, (2) regulation of embryo and fruit development, (3) organogenesis, formation and differentiation of vascular bundle, (4) root growth and development, (5) apical formation and dominance	Han et al. (2009), Tomasz and Jiri (2006)
ABA	(1) Dormancy and development, (2) stomatal activity, (3) morphogenesis of embryo, (4) protein and lipid production, (5) senescence of different tissues, and (6) tolerance to pathogens	Tuteja (2007), Tripathi and Tuteja (2007)
Cytokinins	(1) Cell division and differentiation, (2) formation of membrane components, (3) carbon cycle in photosynthesis, (4) chlorophyll formation, (5) delaying leaf and chlorophyll senescence by decreasing the rate of protein and RNA degradation, (6) development of seed, (7) differentiation of vesicular bundle, (8) root and shoot growth, (9) balance of nutrients, and (10) stress resistance	Yordanov et al. (2000), Kulaeva and Prokoptseva (2004), Muller and Sheen (2007)
Ethylene	(1) Seed germination, (2) tissue senescence and abscission, and (3) tissue elongation under submerged conditions	Arteca and Arteca (2008)
Gibberellins	(1) Inducing plant systemic resistance, (2) seed germination, and (3) mediating plant response to environmental stresses	Ueguchi-Tanaka et al. (2005), Achard et al. (2006), Griffiths et al. (2006), Miransari and Smith (2009a, b)
Brassinosteroids	(1) Enhancing plant resistance to environmental stresses	Nunez et al. (2003), Vardhini and Rao (2003)
Jasmonates	(1) Enhancing plant resistance versus different environmental stresses and pathogen infection, (2) nodule morphogenesis	Wasternack (2007), Murray et al. (2007), Balbi and Devoto (2008), Hu et al. (2009)
Salicylic acid	Inducing plant systemic resistance	Lian et al. (2000), Sun et al. (2006), Chen et al. (2009)
Strigolactones	(1) Hyphal branching in AM fungi, (2) shoot branching in the host plant as well as the parasitic plant, *Striga*	Akiyama et al. (2005), López-Ráez et al. (2008), Miransari (2011)

Plant hormones regulate plant growth and development through a set of complex interaction between their signaling pathways. A signaling pathway is defined by a collection of elements, which eventually results in plant response to different parameters including stress (Schwartz and Baron 1999; Klipp and Liebermeister 2006). Research has indicated the importance of plant hormones during stress. During stress the activation of different signaling pathways mediated by different plant hormones and their interaction can enhance plant resistance to stress (Nakamura et al. 2006; Rolland et al. 2006; Truman et al. 2007). Accordingly, some of the most important findings regarding the effects of plant hormones through their signaling pathways on different stresses are presented.

2 Auxins

Auxin is among the most important plant hormones affecting plant growth and development. Auxin can modulate plant growth by affecting the process of phototropism in plant (Darwin 1880; Tomasz and Jiri 2006). In addition, auxin can regulate the development of embryo and fruit, organogenesis, formation and differentiation of vascular bundle, root growth and development, and apical formation and dominance (Han et al. 2009). The place of auxin synthesis is stem tip and young leaf, and it is then translocated to the site of action (Ljung et al. 2001).

Among the most important functions of auxin in plant is the formation of lateral roots

(Han et al. 2009), which is of special significance to plant growth under different conditions including stress. For example, root growth under compaction is adversely affected, decreasing plant growth as a result of reduction in the uptake of water and nutrients (Miransari et al. 2007, 2008, 2009a, b). Therefore, role of auxin under such conditions can be important in the alleviation of stress by stimulating root growth.

The expression of different auxin-responsive genes indicates that there is a cross-talk between auxin and signaling pathways (Jain and Khurana 2009). Auxin can rapidly induce the accumulation of a significant number of transcript factors related to different plant genes under different conditions including stress. Such plant genes include *Aux/IAA*, *GH3*, and small auxin-up RNA (*SAUR*) genes (Guilfoyle 1999). Molecular genetics and biochemical research have suggested that the *Aux/IAA* genes are related to auxin signaling (Leyser 2002; Woodward and Bartel 2005). These genes can activate the proteins, which can suppress the transcriptional activities regulated by auxin (Tiwari et al. 2004; Woodward and Bartel 2005).

The *GH3* genes are responsible for the production of enzymes, which produce amino acid-related products by adenylation of indole 3-acetic acid and hence inhibit the production of extra-free auxin resulting in auxin homeostasis (Staswick et al. 2005). The *GH3* genes can also turn the produced amino acid-related products into salicylic acid and jasmonates (Staswick et al. 2002). The *SAUR* genes can result in the production of proteins, which may influence cell elongation regulated by auxin (Hagen and Guilfoyle 2002).

Auxin signaling pathway is related to the expression of different genes, which are mostly induced by two transcriptional factors including auxin response factors (ARFs) and the Aux/IAA repressors. The auxin response promoter elements in the responsive auxin genes are bound by ARFs. Reduction of auxin concentration to the amounts less than the threshold level results in the combined activation of ARFs and Aux/IAA repressors and hence the inhibition of the responsive genes. However, high concentration of auxin would adversely affect the Aux/IAA repressors and hence restores the activity of such responsive genes (Han et al. 2009; Jain and Khurana 2009; Ghanashyam and Jain 2009).

3 Abscisic Acid

There are a wide range of functions controlled and affected by ABA in plant including seed dormancy and development, stomatal activity, morphogenesis of embryo, protein and lipid production, senescence of different tissues, and tolerance to pathogens (Tuteja 2007; Tripathi and Tuteja 2007). Different stresses result in cell desiccation and osmotic imbalance and hence there may be similar signaling pathways and genes, expressed during the stress (Tuteja 2007).

Stresses such as drought and salinity result in the production of ABA in the roots and its eventual translocation to the shoots affecting stomata activities and cellular growth. In addition, ABA can also be produced in plant leaf and translocated to the other parts of plant (Wilkinson and Davies 2002; Chaves et al. 2009). The other parameter controlling ABA localization is the xylem/apoplastic pH. For example, when plant is subjected to drought stress the higher xylem/apoplastic pH prohibits the movement of ABA from the xylem/apoplastic to the symplastic space resulting in the enhancement of ABA concentration in the guard cells. Different stresses including drought, light, salinity, and nitrate can increase xylem sap pH and hence affect stomata activities (Jia and Davies 2007). ABA can also influence plant growth under stress by affecting gene expression. Furthermore, under drought and high light stress, the production of sugars and their translocation in the xylem can affect stomata response to ABA (Wilkinson and Davies 2002).

Chaves and Oliveira (2004) indicated that under stress the production of soluble sugars, which can also act as signal molecules in plant, is altered. In addition, such sugar molecules can also be interactive with plant hormones (Rolland et al. 2006). It has been indicated that nitrous oxide is also a signal molecule influencing the effects of plant hormones and other signal

molecules in response to environmental parameters by enhancing the sensitivity of plant cells to such signal molecules. In addition, nitrous oxide can also influence ABA effects on the activity of stomata (Neill et al. 2003).

Under water stress the amount of ABA increases (Kulkarni et al. 2000; Liu et al. 2005). ABA can primarily control water transpiration from the leaf and then can alleviate the stress and enhance plant tolerance by activating the expression of different stress genes (Bray 2004; Zhang et al. 2006). Genes, which are expressed under drought stress, include functional and regulatory ones. Functional genes can perform some specific functions related to the alleviation of stress by inducing different transporters including detoxifying enzymes, enzymes related to the production of osmolyte, and different proteases. However, regulatory genes including transcription factors, phosphatases and protein kinases, and the ones related to the production of ABA, can regulate the activity of functional genes (Aroca et al. 2007).

With respect to the functions mentioned for ABA, it is the most important plant signal activated during stress (Zhang et al. 2006). Interestingly and similarly, the soil fungi, arbuscular mycorrhiza (AM), can alleviate drought stress in their host plants. AM fungi can establish symbiosis with their host plant and enhance its water and nutrient uptake by its extensive hyphal network in exchange for carbon. Mycorrhizal plants are able to regulate their ABA level more efficiently (Auge 2001; Aroca et al. 2007).

The *nced* genes, which are expressed in plant under drought stress (Wan and Li 2006), are induced by ABA, if available at a minimum amount (Cohen et al. 1999). The effects of small RNA pathways on ABA were evaluated by Zhang et al. (2008) using mutants. They found that adverse effects on small RNA pathways can increase the production of ABA indicating that there is a link between small RNA pathways and signaling pathways resulting in the production of ABA in plant cells.

Under submerged conditions there is some kind of interesting interactions between different plant hormones. The accumulated amounts of ethylene down regulate the production of ABA through inhibiting the expression of 9-*cis*-epoxycarotenoid dioxygenase and by turning ABA into pahseic acid. The 9-*cis*-epoxycarotenoid dioxygenase are among the genes, responsible for the production of ABA through the pathway of carotenoid cleavage dioxygenases (Kende et al. 1998; Benschop et al. 2005). Prevented production of endogenous ABA results in the activation of the enzyme, gibberellin 3-oxidase, which catalyses the pathway related to the production of gibberellins (Benschop et al. 2006), and in submerged rice the production of gibberellins by the internodes (Kende et al. 1998). Down regulation of gibberellins-related genes can induce the elongation of rice roots under submerged conditions. The activities of such genes include the loosening of the cell wall, cell cycle, and starch turnover (Van der Knaap et al. 1999, 2000).

4   Cytokinins

The plant hormone cytokinins can regulate the following important functions in plant: (1) cell division and differentiation, (2) formation of membrane components, (3) carbon cycle in photosynthesis, (4) chlorophyll formation, (5) delaying leaf and chlorophyll senescence by decreasing the rate of protein and RNA degradation, which is related to the controlling effects of hormone on the production of protease and activity of RNase, (6) development of seed, (7) differentiation of vesicular bundle, (8) root and shoot growth, (9) balance of nutrients, and (10) stress resistance (Yordanov et al. 2000; Muller and Sheen 2007). The receptors perceiving cytokinins were found in the cellular membrane. Cytokinins are able to act multifunctionally by affecting different physiological processes in plant and controlling stresses (Kulaeva and Prokoptseva 2004).

Under nonstressed or stressed conditions, decreased level of cytokinins result in leaf senescence (Naqvi 1995). Exogenous application of cytokinins delays the process of leaf senescence (Okamoto et al. 2010). The process of leaf senescence can also be delayed by regulating the

related genes pathways, which are under the influence of cytokinins level in plant (Naqvi 1995). The gene, which is responsible for the production of cytokinins is *ipt*, which produces the enzyme isopentyl transferase, promoting the formation of isopentenyladenosine-5′-monophosphate (McGraw 1987). The *ipt* genes are expressed at low levels under controlled and drought-stress conditions, being highly specific in the cellular tissue (Vyroubalova et al. 2009).

Cytokinins are able to protect the process of photosynthesis in plants under stress. The related mechanism includes the interaction of cytokinins with receptor proteins resulting in the production of the signal pathway. Consequently, the genes are expressed and produce mRNAs, photosynthesis-related proteins, the enzyme ribulose bisphosphate carboxylase/oxygenase, electrons, and carbon (Chernyadev 2009; Bianco et al. 2009).

It is likely to enhance plant tolerance to drought by genetically modifying the plant using the *ipt* gene regulated by the related promoter, which delays the process of leaf senescence. In addition, the rate of photosynthesis and production of antioxidant enzymes increase under such genetic modification. It must be mentioned that there is a kind of regulatory interactions between leaf transpiration and leaf photosynthesis while the leaf senescence takes place in the plant (Rivero et al. 2007, 2009).

While leaf senescence can increase plant tolerance to drought stress by significantly reducing the rate of leaf transpiration, the presence of old leaf in plant can contribute to the enhanced photosynthesis process in plant (Chaves et al. 2003; Rivero et al. 2007, 2009). Under stresses such as drought while the production and transport of cytokinins are prohibited, its degradation is encouraged resulting in a decrease in plant growth as well as plant-reduced tolerance to stress (Yang et al. 2002; Kudoyarova et al. 2006).

The two-component pathways related to cytokinins regulation may affect ABA activity and can alleviate the effects of osmotic stress. The three histidine kinases as cytokinins receptors can adversely regulate ABA activity, as well as the stress. Accordingly, it can be mentioned that during the stress control in plant, there is a cross-talk between cytokinin, ABA, and the osmotic stress indicating that cytokinin pathway and metabolism is of particular importance to plant growth and development, especially under stress (Tran et al. 2009).

5   Ethylene

Ethylene is a gaseous plant hormone with important functioning in plant. Although ethylene is among plant hormones with the simplest structures, it can regulate some of the most important functioning in plant including seed germination, tissue senescence, and abscission (Arteca and Arteca 2008). There are some complex pathways and signaling related to ethylene, stimulated by other plant hormones and parameters such as plant growth, pathogens, and sugars (Abeles et al. 2004; Stepanova and Alonso 2005).

There is a set of interactions between ethylene and ethylene receptors in the plasma membrane indicating the pathway of ethylene signaling, although such a pathway is adversely affected by the ethylene receptors. The membrane receptors are two-component histidine protein kinases (Mount and Chang 2002). The degradation of ethylene receptors after ethylene binding can further increase ethylene sensitivity, determined by the presence of a novel protein. The degradation of transcription factors in the nucleus is also controlled (Kendrick and Chang 2008).

In the recent years the signaling pathway of ethylene is among the most known pathways. The important transcription factor is ETHYLENE INSENSITIVE3 (EIN3). However, what has to be yet investigated is the biochemical mechanism by which the ethylene receptor signaling is performed (Kendrick and Chang 2008). A key process in the functioning of ethylene is the degradation of proteins, which control both ethylene biosynthesis and ethylene perceiving by the receptors. The other important component related to ethylene signaling is the degradation of EIN3 by the proteins EIN-BINDING F-BOXES (McClellan and Chang 2008).

Importantly, the elevated production of ethylene under stress adversely affects plant growth and development. If there is any way by which the degradation of ethylene is performed, the stress of ethylene on plant growth and development can be controlled. Plant growth promoting rhizobacteria (PGPR) have the ability to produce the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which can degrade the precursor for ethylene production by the ACC oxidase pathway. There has been extensive research work regarding such alleviating effects of ACC-deaminase on plant growth and development under stress, especially by professor Glick and his research team (Glick et al. 2007; Yang et al. 2008; Jalili et al. 2009).

The other important functioning regarding ethylene is its important role under submerged condition, which is considered stressful to most plant species. Under submerged conditions, the plant must own some unique abilities to be able to grow under such conditions. Increased rate of adventitious roots as well as formation of new leaf and hence increased photosynthesis under submerged conditions is among such abilities regulated by ethylene. Ethylene concentration can increase up to 100 times higher in plants under submerged compared with nonsubmerged conditions resulting in tissue elongation. Such kind of elongation is a result of processes, which would loosen the cell wall, extend and divide the cell, and is also under the influence of ethylene interaction with other plant hormones (Jackson 2008).

Under submerged, due to the efficiency of oxygen and high concentration of CO_2 the synthesis of ethylene can increase up to four times higher in the base of rice stem. The increased ethylene concentration is a result of higher biosynthesis of ethylene prerequisite 1-aminocyclopropane-1-carboxylic acid (ACC). Such alterations are accompanied with some other genetic processes including mRNA control on the activation of ACC oxidase genes. These activities would collectively result in the enhanced production of ethylene in rice under submerged conditions (Mekhedov and Kende 1996; Vriezen et al. 1999; Zhou et al. 2001).

6 Gibberellins

Gibberellins are plant hormones performing different functions in plant. The three enzymes of cyclases, monooxygenases, and dioxygenases catalyze the production of gibberellins, which are tetracyclic diterpenoids, from geranylgeranyl diphosphate (Sponsel and Hedden 2004). Gibberellins are able to enhance plant growth by degrading the negative growth regulators DELLA proteins (Ueguchi-Tanaka et al. 2005; Griffiths et al. 2006). Gibberellins can induce plant systemic resistance and result in seed germination. Fungi and bacteria are also able to produce gibberellins as secondary metabolites resulting in the signaling interaction with their host plant (MacMillan 2001; Miransari and Smith 2009a, b).

It has been recently indicated that *Arabidopsis* DELLA proteins, as negative regulator of gibberellins signaling, can influence plant systemic resistance by affecting jasmonates and salicylic acid signaling pathways (Navarro et al. 2008). The *Arabidopsis* mutant which does not have the DELLA genes is very susceptible to pathogenic fungi (Navarro et al. 2008). DELLA proteins are able to activate plant systemic resistance to pathogenic fungi by affecting the jasmonates/ethylene pathways. Accordingly, DELLA proteins can influence plant systemic resistance by affecting the combined response of salicylic acid, jasmonates, and ethylene pathways to the fungal infection.

It has also been indicated that the response of plant to the environmental stresses is also mediated by DELLA proteins affecting the combined response of plant hormonal pathways to the stress (Achard et al. 2006). Mutant, which do not have gibberellins receptors in their cellular membrane, accumulate higher rate of gibberellins enhancing plant response to pathogenic fungi relative to the wild types (Tanaka et al. 2006). In addition to fungi, viral infection can also affect gibberellins pathway in plant. For example, rice dwarf virus suppressed the expression of the enzyme *ent*-kaurene oxidase, which results in the production of gibberellins in rice plants (Zhu et al. 2005).

7 Brassinosteroids

Brassinosteroids are plant hormones found in different parts of the plant including seed, pollen, flower, fruit, leaf, vesicular bundle, root, and shoot. Such steroidal compounds can be found in association with sugars and fatty acids. So far about 70 different plant brassinosteroids have been recognized and isolated, affecting plant growth and development (Sasse 2003; Yu et al. 2008). Under biotic (pathogen infection) and abiotic stresses the level of brassinosteroids in plant may increase. However, the related mechanisms are not known yet (Krishna 2003).

Different stresses such as salinity, drought, heavy metals, high or low temperature, etc., usually result in the similar cellular pathways and responses including the regulation of antioxidants, production of stress protein, and increased concentration of solutes altering the production of hormones in plant (Smirnoff 1995; Sajedi et al. 2011). There is a cross-talk between different hormones affecting plant growth and development. Under stress, the production of kinase protein in plant and the related responses by plant hormones is altered resulting in the induction of signals related to the production of reactive oxygen species, which is of high significance in the alleviation of stress. In addition, there is also some sort of interaction between different plant hormones under stress. For example, among the mechanisms by which brassinosteroids can affect plant response to stress is the production of jasmonates (Mussig et al. 2000; Schaller et al. 2000; Miller et al. 2010).

Under stress the production of reactive oxygen species can adversely affect cellular growth and development (Sajedi et al. 2011). The role of brassinosteroids in different plant physiological mechanisms, which results in the regulation of plant growth and development, has been indicated. However, there is not much known about the controlling effects of brassinosteroids on oxidative stress.

Under stress, use of exogenous brassinosteroids results in the modification of antioxidant enzymes including gluthatione peroxidase, ascorbate peroxidase, superoxide dismutase, and catalase as well as the non-enzymatic antioxidants including gluthatione, cartenoids, tocopherols, ascorbic acid, etc. (Nunez et al. 2003; Vardhini and Rao 2003). In sorghum (*Sorghum vulagre* L.) subjected to osmotic stress while brassinosteroids increased the activity of catalase, they decreased the activities of ascorbic acid oxidase and peroxidase (Vardhini and Rao 2003).

Under salinity stress, treating rice seedlings with brassinosteroids significantly enhanced the activity of catalase, superoxide dismutase, and glutathione reductase and slightly increased the activity of ascorbate peroxidase (Nunez et al. 2003). The fact that molecular oxygen is necessary for the production of brassinosteroids at different stages indicates that this hormone can mediate the effects of hypoxia on plant growth and development. Upreti and Murti (2004) indicated that brassinosteroids can increase root nodulation in *Phaseolus vulgaris* as well as ABA contents and cytokinin transzeatin riboside.

Brassinosteroids can also enhance root nodulation and crop yield under nonstressed and water-stressed conditions by affecting the content of cytokinin in the nodulated roots of *Phaseolus vulgaris*. Seedling growth of sorghum and sugar beet was increased by brassinosteroids under osmotic and water stress, respectively. Such alleviating effects were attributed to the enhanced level of acid invertase in the plant young leaf (Schilling et al. 1991). As a result of osmotic stress, the content of protein in three sorghum varieties decreased, which was completely restored and stimulated by brassinosteroids. The stress also increased the proline level (Vardhini and Rao 2003).

Use of brassinosteroids alleviated the stress of cadmium on the performance of chickpea (Hasan et al. 2008) and mustard (Hayat et al. 2007) and also the stresses of aluminum and nickel on the growth of mung bean (Ali et al. 2008) and mustard (Alam et al. 2007), respectively. Such alleviating effects may be attributed to the enhanced activities of antioxidant enzymes such as catalase, superoxidase, and peroxidase by brassinosteroids (Hasan et al. 2008).

In case of salinity stress, brassinosteroids alleviated the stress of salinity on rice (*Oryza sativa*),

seed germination, and seedling growth. The hormone was also able to restore plant chlorophylls and enhance the activity of nitrate reductase under salinity. Brassinosteroids increased the cellular growth of rice seedlings under suboptimal temperature (15°C) as well as the germination of rice and corn seeds (He et al. 1991; Fujii and Saka 2001). Although brassinosteroids and ABA may affect plant systemic resistance at the time of pathogen infection, the induction of plant systemic resistance is mostly related to the combining effects of signaling pathways induced by salicylic acid, jasmonic acid, and ethylene.

8   Jasmonates

Jasmonates are lipid plant hormones affecting plant systemic resistance as well as plant growth and development and elasticity by their signaling pathways. The lipase enzymes synthesize jasmonates as oxylipins (oxygenated fatty acids). The enzymes, which are located in the chloroplast membrane, result in the release of linolenic acid, which is then oxygenated by lipoxygenases and produces hydroperoxide derivatives (Wasternack 2007; Schaller and Stintzi 2009).

Jasmonates are able to affect gene expression in plant positively or negatively while interacting with other plant hormones including salicylic acid, auxin, ABA, and ethylene (Wasternack 2007). Jasmonates can enhance plant resistance versus different environmental stresses and pathogen infection. There is a high rate of positive or negative cross-talk and interactions between jasmonates and the other plant hormone salicylic acid determining the ultimate response of plant to stress (Wasternack 2007; Balbi and Devoto 2008).

Plant mutants lacking the ability to synthesize jasmonates have been used to investigate the signaling pathways, which result in the production of jasmonates (Devoto and Turner 2005; Lorenzo and Solano 2005; Schilmiller et al. 2007). Jasmonates can also mediate plant response to stress by affecting the production of reactive oxygen species, nitrous oxide (NO), influx of calcium as well as activation of nitrogen protein kinase (Hu et al. 2009).

The important role of jasmonates in nodule organogenesis has also been indicated by different researchers. Nodules are root organs developed during the symbiosis between the soil bacteria *Rhizobium* and their specific host plant from the leguminous family. Nodules are the place of rhizobium residence, for the fixation of atmospheric N by the production of rhizobium nitrogenase (Miransari and Smith 2007, 2008, 2009a, b). It has been recently indicated that for the onset of nodule development, the cytokinins signaling pathway is necessary (Murray et al. 2007).

The other plant hormones including auxin, ABA, ethylene, gibberellins, and brassinosteroids are also required for nodule development (Oldroyd et al. 2001; Ferguson et al. 2005; van Noorden et al. 2006). However, more research must be performed to indicate the other important details regarding the complex effects of hormonal signaling pathways on nodule organogenesis.

It has also been indicated that jasmonates can also influence nodule formation. For example, the antagonistic effects of jasmonates on the process of nodulation in *Medicago truncatula* and *Lotus japonicus* have been indicated (Sun et al. 2006; Nakagawa and Kawaguchi 2006). There is also some kind of positive and negative interactions between jasmonates and salicylic acid during the process of nodule formation (Sun et al. 2006). Jasmonates are able to alleviate the stress of salinity on barley growth. In plants treated with jasmonates, lower amounts of Na^+ were found in plant shoot. Such alleviating effects were attributed to the performance of the following three genes including apoplastic invertase, arginine decarboxylase, and Rubisco, regulated by jasmonates (Tuteja and Sopory 2008).

9   Salicylic Acid

Salicylic acid is also another important plant hormone affecting plant systemic resistance to pathogen infection (Lian et al. 2000). During the activation of plant systemic resistance, transcriptional factors are activated and transcriptional

repressors are inhibited (Dong 2001). It can adversely affect gene expression when affected by the stress hormone jasmonates. Borsani et al. (2001) indicated that salicylic acid can affect the production of reactive oxygen species as a result of osmotic stress by NaCl in *Arabidopsis* seedlings. According to Ndamukong et al. (2007), glutaredoxin is the protein regulating the pathways related to salicylic signaling. It has been indicated that the adverse effects of salicylic acid on pathogen growth in plants is by the suppressing effects of salicylic acid on the auxin signaling pathway (Wang et al. 2007). There are also positive and negative interactions between salicylic acid and jasmonates during the process of nodule organogenesis (Sun et al. 2006).

There are two different pathways by which salicylic acid is synthesized. The cinnamate pathway in which cinnamate is synthesized from the phenylalanine ammonia lyase (PAL) resulting in the production of salicylic acid. Silencing the PAL genes inhibits the production of salicylic acid in plant and inhibiting the activity of PAL genes chemically reduces the production of salicylic acid in plant. Salicylic acid is also produced in the isochorismate pathway catalyzed by isochorismate synthase (Chen et al. 2009).

In brief, it can be stated that plant parameters such as salicylic acid can enhance plant systemic resistance to stresses such as pathogen invasion by the following mechanisms: (1) expression of PAL genes, (2) expression of priming genes, (3) activation of pathways resulting in phytoalexin production, (4) deposition of callose, (5) oxidative burst, (6) phenolic compounds deposition, and (7) deposition of hydroxycinnamoyltyramine products (Goellner and Conrath 2008).

10   Strigolactones

Strigolactones are new classes of plant hormones produced from carotenoids, probably by carotenoid cleavage deoxygenase or 9-*cis* epoxycarotenoid deoxygenase. They affect the process of symbiosis between the soil fungi AM and the host plant as hyphal branching factors, shoot branching, and seed germination of parasitic weeds such as *Striga*. Their production by plants roots is significantly enhanced by phosphate starvation (Akiyama et al. 2005; López-Ráez et al. 2008; Miransari 2011).

During the process of symbiotic association between AM fungi and the host plant, an extensive network of hypha is developed, substantially increasing the uptake of water and nutrients by the host plant (Smith and Read 2008). Among different nutrients, phosphorous is more affected by AM fungi symbiosis with the host plant. Interestingly, strigolactones are more produced under phosphate starvation, which mediate the activation of strigolactones producing genes (López-Ráez and Bouwmeester 2008). However, other than P starvation, there is no any other details regarding the effects of strigolactones on stresses affecting plant growth.

11   Conclusion and Future Perspectives

Some of the most important details regarding the production of plant hormones, their signal pathways under different conditions including stress and the interactions between plant hormones were reviewed. Accordingly, plant hormones are among the most important plant components which can make the plant survive under different conditions including stress. Under stress plant hormones mediate plant genes, which can alleviate the stress by the production of stress proteins. There are yet more details that must be known regarding the functions of plant hormones under different conditions including stress. Elucidation of such details may result in the production of transgenic plants, which are more tolerant under stress.

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