Plant Responses to Exogenous Salicylic and Jasmonic Acids Under Drought Stress

Kazem Ghassemi-Golezani and Salar Farhangi-Abriz

Abstract In a vast area of the farming lands in the world, drought stress is an important factor for limiting plant growth and productivity. Adjusting hormonal signaling of plants under drought stress is one of the main goals of plant physiologist to increase drought stress tolerance and productivity of plants. Salicylic (SA) and jasmonic acids (JA) are involved in plant defense mechanism against abiotic stress tolerance such as drought. These growth regulators considerably enhance antioxidative capacity (enzymatic and non-enzymatic) of plant cells, which largely reduce lipid peroxidation and maintain membrane integrity. Exogenous salicylic and jasmonic acids increase plant osmolytes such as proline and soluble carbohydrates in response to drought stress. The critical roles of these growth regulators in enhancing photosynthetic activities under drought stress have been confirmed. Moreover, salicylic and jasmonic acids can change the biosynthesis of secondary metabolites in drought subjected plants. In this chapter, the SA and JA mechanisms of actions in changing physiological and biochemical properties of plants favoring drought tolerance were discussed.

1 Introduction

Global plant production is affected by periodical drought stress. Drought is a long dry period, which happens in an area when it receives a below average precipitation (Ali et al. 2017; Farhangi-Abriz and Ghassemi-Golezani 2019). This stress has an extensive impact on physiological and biochemical aspects of plants. Various aspects of plant physiology such as photo-synthetical activities, source and sink relationships, hormonal signaling and plant growth are affected by drought stress (Li and Liu 2016; Anjum et al. 2017). Changes in hormonal signaling is one of the important responses in plant cells, which controls various aspects of plant growth and physiology under drought stress (Pandey et al. 2017). Plant hormones such as Salicylic acid (SA) and jasmonic acid (JA) are the natural groups of molecules, which have important roles

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in adjusting plant growth and reacting to environmental stresses such as drought and salinity (Ilyas et al. 2017; Ghassemi-Golezani and Farhangi-Abriz 2018).

SA is generally present in plants in the form of methylated, glycosylated, glucose-ester, and amino acid conjugates or in a free state (Zhang and Li 2019). This hormone can be detected in large amounts in plant leaves after pathogenic infection (Qi et al. 2018). SA controls different parameters of plant growth such as root and shoot growth and leaf expansion (Mimouni et al. 2016). Exogenous application of SA noticeably improves plant growth under drought (Sharma et al. 2017), salt (Farhangi-Abriz and Ghassemi-Golezani 2018), heat (Wassie et al. 2020) and heavy metal (Kohli et al. 2017) stresses. This growth regulator also increases antioxidative activities and osmolytes production of plants under adverse conditions such as drought (Rao et al. 2012). Endogenous SA is strongly correlated with enzymatic and non-enzymatic antioxidants and osmolytes under normal and stressful conditions (Farhangi-Abriz et al. 2020). The organic osmolytes in plant tissues, such as proline and soluble carbohydrates are increased in response to foliar application of SA (Moustafa-Farag et al. 2020). This treatment also enhances root development of plants under drought and consequently improves water uptake by plants (Hayat et al. 2010).

Jasmonates family include jasmonic acid, methyl jasmonate, and jasmonyl-isoleucine are involved in control of plant responses to different kinds of environmental stresses and play an important role in several aspects of growth and development (Farhangi-Abriz and Ghassemi-Golezani 2019; Ruan et al. 2019). Jasmonic acid adjusts growth and development of plants through diverse interconnections between various signaling molecules such as SA and abscisic acid (ABA) (Sasaki et al. 2001). Exogenous application of JA under drought stress improves drought tolerance in brassica species (Alam et al. 2014). Many reports show that exogenous JA increases antioxidative defense mechanisms in drought stressed plants (Alam et al. 2014). JA increases production of ABA which in turn controls stomata behavior and water status of plants under drought stress (Farhangi-Abriz and Ghassemi-Golezani 2019). de Ollas et al. (2013) found that accumulation of JA in root cells is required for ABA biosynthesis in rice plants. In this chapter, the responses of plants to SA and JA under drought stress are evaluated, in order to identify the possible mechanisms of SA and JA involvement in drought subjected plants. Some possible effects of SA and JA on changing plant response to drought stress are summarized in Fig. 1.

2 The Roles of Salicylic and Jasmonic Acids in Drought Sressed Plants

2.1 *Oxidative Stress Tolerance*

Reactive oxygen species (ROS), such as hydrogen peroxide, superoxide anion, hydroxyl radicals and singlet oxygen are generated at low levels in plant organelles, especially in peroxisomes, mitochondria, chloroplasts, plasma membrane and

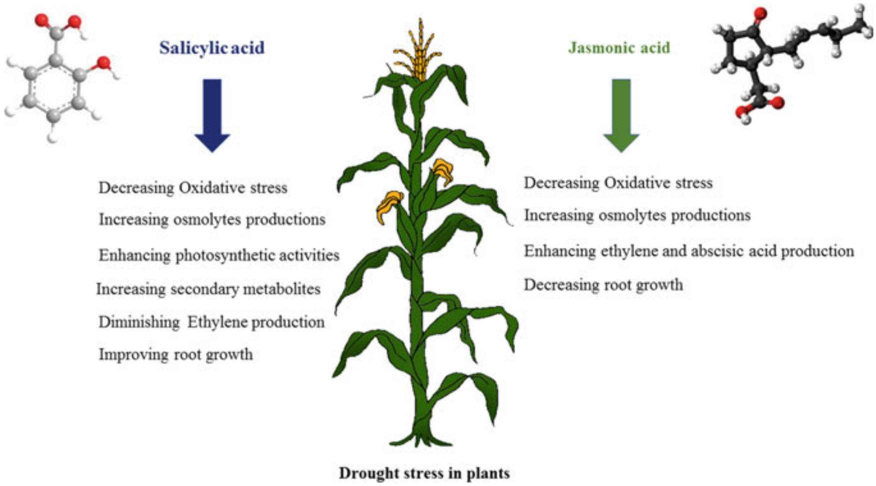

Fig. 1 Some important impacts of salicylic and jasmonic acids on plant response to drought stress

apoplast under normal water availability. However, generation of ROS is stimulated by drought condition (Kar 2011; Choudhury et al. 2017). Higher levels of ROSs act as noxious substances which can damage different molecules such as proteins, lipids and nucleotides (Banerjee and Roychoudhury 2018). Once the plant confront drought, the initial physiological response will be stomatal closure to evade water losses due to transpiration, but this response will have some harmful effects on photosynthesis and electron transportation system with limited CO2 fixation, altered photosynthetic activities and higher rate of photorespiration (Chaves et al. 2002; Osakabe et al. 2014). Plants have different antioxidative defense systems to control or detoxify ROSs in their cells. Different enzymatic (such as superoxide dismutase, catalase, peroxidases) and non-enzymatic antioxidant systems (such as proline, flavonoids, carotenoids, ascorbate, glutathione and α-tocopherol) have the capacity to scavenge ROSs in plant cells (Osakabe et al. 2014). Antioxidants and stress hormones are produced in a high amount under drought stress. According to available reports, there was a strong correlation between endogenous concentrations of stress hormones such as SA and JA with antioxidative activities in plant cells (Farhangi-Abriz et al. 2020).

The interaction of SA with ROSs was initially reported by Chen et al. (1993). Subsequent investigations revealed that SA activates different stress tolerance genes and transcription factors such as *TGA* factors from *bZip* family, bind to *cis*-elements containing *TGA* box and *WRKY* transcription factors, which control most of the antioxidative activities in plant cells (Singh et al. 2002; Johnson et al. 2003). It is confirmed that plants increase SA accumulation after being exposed to drought stress (Okuma et al. 2014). *ICS1* and *ICS2* are the two *Arabidopsis* genes coding for isochorismate, which is the key enzyme in adjusting SA biosynthesis. Environmental stresses such as drought upregulate *ICS1* and *ICS2* genes and consequently enhance

SA concentration in plant cells (Herrera-Vásquez et al. 2015). SA-deficient transgenic rice has lower antioxidant capacity and higher ROS levels (Yang et al. 2004). Durner and Klessig (1996) showed that SA detoxifies hydroxyl radicals and thus protects plants against catalase inactivation by hydrogen peroxide.

Exogenous application of SA is a practical way to increase SA concentration in plant cells (Farhangi-Abriz et al. 2020). Many reports showed that SA could be absorb by plant leaves, even in normal or stressful conditions (Nassef 2017; Ghassemi-Golezani et al. 2018a). Foliar application of SA increases antioxidative activities of plants under drought stress. Singh and Usha (2003) stated that irrespective of intensity of drought stress and SA concentration (1–3 mM), SA treated plants had the highest level of superoxide dismutase activity compared to untreated plants. In a pot experiment, Saruhan et al. (2012) investigated the role of SA in increasing antioxidative activities of different maize cultivars (*Zea mays* L.). The results of this study showed that SA treatment noticeably increased superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase and monodehydroascorbate reductase activities. Similar reports are available in tomato (Hayat et al. 2008), wheat (Sedaghat et al. 2017), barley (Torun 2019) and cotton (Hussain et al. 2020).

Kadioglu et al. (2011) reported that foliar application of SA significantly improved endogenous content of SA in *Ctenanthe setosa* plants and consequently improved the non-enzymatic antioxidants such as ascorbate, glutathione, α-tocopherol, and carotenoid contents under drought stress. In a field experiment, Ghassemi-Golezani et al. (2019) evaluated the possible effects of SA on promoting water stress tolerance of rapeseed and found that foliar spray of SA (1 mM) significantly enhanced peroxidase, catalase, superoxide dismutase, and ascorbate peroxidase activities, but reduced hydrogen peroxide generation under drought stress. These increments in antioxidative activities noticeably improved membrane integrity of plant cells under water deficit. In another field experiment, the drought-subjected ajowan (c*arum copticum* L.) plants produced more non-enzymatic compounds such as carotenoids and anthocyanins in response to foliar application of SA (Ghassemi et al. 2019).

JA is another stress hormone that has some important roles on decreasing oxidative stress of plants under different environmental conditions such as drought (Alam et al. 2014) and salt stress (Farhangi-Abriz and Ghassemi-Golezani 2018). Compared to research works showing a positive impact of jasmonic acid in response to pathogen attacks, less has been known about its' role on plants under abiotic stresses such as drought. Previous researches confirmed that water stress increases jasmonic acid production in leaves and roots of plants (Kiribuchi et al. 2005). Overexpression of some key genes in jasmonic acid biosynthesis pathway such as jasmonic acid carboxyl methyl transferase gene (*AtJMT*) in rice showed an increased level of jasmonic acid under drought condition (Kim et al. 2009a). Increasing endogenous content of JA has a positive effect on rising antioxidative activities in plant cells (Farhangi-Abriz et al. 2020). The JA may affect enzyme activities through changes in gene transcription and translation. The organ-specific nature of JA shows that the effects of this hormone are responsible for directing specific cellular and sub-cellular modifications in metabolism (Comparot et al. 2002).

Many reports showed positive effects of JA application on rising antioxidative activities in different plant species under water deficit (Farhangi-Abriz and Ghassemi-Golezani 2019). According to Alam et al. (2014) jasmonic acid stimulates the glyoxalase systems in plant cells and enhances antioxidative activities under drought stress. These researchers also found that foliar application of JA increases the activities of some important antioxidant enzymes such as ascorbate peroxidase, glutathione peroxidase, and catalase in *Brassica* species, leading to ROS detoxification under drought stress. Anjum et al. (2011) reported that foliar application of methyl-jasmonate enhances the superoxide dismutase, peroxidase, and catalase activities in soybean leaves and consequently reduces membrane lipid peroxidation under water stress. Priming with JA was also helpful in rising antioxidative activities of seedlings under water limitation. Abdelgawad et al. (2014) found that pretreatment of maize seeds with methyl-jasmonate increases the antioxidative activities of seedlings under drought condition. Foliar application of JA not only improves activities of antioxidants, but also increases the production of non-enzymatic antioxidants such as ascorbate and glutathione molecules (Shan and Liang 2010). The positive impacts of JA on increasing ascorbate–glutathione cycle have been confirmed by Shan et al. (2015) in wheat plants. Foliar spray of jasmonic acid alleviated oxidative stress in *Thymus vulgaris* by increasing antioxidative activities (Alavi-Samani et al. 2015). Ghaffari et al. (2020) showed that foliar applications of jasmonic acid increases the catalase, and peroxidase activities and reduces lipid peroxidation in sugar beet. The antioxidant activities of SA and JA treated plants are summarized in Table 1.

2.2 Osmotic Stress Tolerance

Water stress causes cell dehydration and changes cell metabolism. Production and accumulation of osmolytes such as proline, soluble carbohydrates, proteins and glycine betaine are the main changes in cell metabolism under drought (Kaur and Asthir 2017; Hussain et al. 2019). Drought-induced production and accumulation of osmolytes have been reported in various plant species. previous findings proved that production and accumulation of osmoprotectants can enhance drought tolerance of plants (Li et al. 2017; Shinde et al. 2018). Drought-induced limitation of water availability hinders cell expansion, cell division and growth of plants (Riboldi et al. 2016; Feng et al. 2016). Salehi-Lisar and Bakhshayeshan-Agdam (2016) reported that reduction of plant growth under drought stress is related to a decrement in cell water potential. Drought stress reduces some important plant-water related parameters such as relative water content, osmotic potential, leaf water potential, transpiration rate and pressure potential (Kirkham 2014). The other well-known mechanisms of osmolytes are detoxification of toxic compounds such as ROS, and protection of membrane and mitochondrial structures and photosynthetic system (Hayat et al. 2012). Furthermore, most of the osmolytes have signaling roles under drought stress. The concentration of natural osmoprotectants in cytoplasmic area can exceed 200 mM

Table 1 Salicylic acid and jasmonic acid impacts on antioxidative activities of different plant species under drought stress

Hormones	Plant species	Application method and dosage	Effects on plants	References
Salicylic acid	*Brassica napus* L	Foliar application—1 mM	Foliar sprays of salicylic acid increased the antioxidant enzymes activities such as peroxidase, catalase, superoxide dismutase, and ascorbate peroxidase and consequently reduced lipid peroxidation under drought stress	Ghassemi-Golezani et al. (2019)
Salicylic acid	*Oryza sativa*	Seed priming (0.5 and 1 mM)	Seed priming with salicylic acid noticeably improved seedling growth by increasing catalase, ascorbate peroxidase and guaiacol peroxidase activities under drought stress	Sohag et al. (2020)
Salicylic acid	*Brassica napus*	Foliar application—1.5 mM	Salicylic acid improves drought-stress tolerance by increasing the redox status and decreasing reactive oxygen species generation in *Brassica rapa*	Hien La et al. (2020)
Salicylic acid	*Phaseolus vulgaris*	Foliar application—1 mM	Foliar application of salicylic acid increased superoxide dismutase, catalase and ascorbate peroxidase activities, and reduced lipid peroxidation of plants under drought stress	Lopes et al. (2019)
Jasmonic acid	*Agropyron cristatum*	Protirement of plant—1 µM	Jasmonic acid enhanced the ascorbate and glutathione metabolisms in plant tissues and induced the water stress tolerance	Shan and Liang (2010)

(continued)

Table 1 (continued)

Hormones	Plant species	Application method and dosage	Effects on plants	References
Jasmonic acid	*Triticum aestivum*	Protirement of plant—10 μM	Exogenous jasmonic acid enhanced the nitric oxide production and antioxidative systems such as ascorbate–glutathione cycle under water stress	Shan et al. (2015)
Jasmonic acid	*Triticum aestivum*	Foliar application—100 μM	Jasmonic acid significantly enhanced antioxidative activities in wheat seedlings and improved drought stress tolerance	Abeed et al. (2020)
Jasmonic acid	*Thymus vulgaris*	Foliar application—200 μM	Foliar application of JA decreased the harmful effects of water stress on thymus plants by enhancing antioxidative activates and root growth	Alavi-Samani et al. (2015)

which is osmotically important in preserving cell turgor for water uptake under water stress condition (Sharma et al. 2019). Foliar application of SA and JA can enhance the drought stress tolerance of plants by increasing osmolytes production.

SA is an important signal molecule participating in defensive responses to abiotic stress (Khan et al. 2015). This hormone can enhance biosynthesis of osmolytes such as proline, glycine betaine and sugars under osmotic stress. Previous works have demonstrated that SA is involved in stimulating synthesis of proline under drought stress (Lee et al. 2019; de Andrade et al. 2020). Misra and Saxena (2009) reported that the activity of proline biosynthetic enzymes viz. γ-glutamyl kinase and pyrroline-5-carboxylate were enhanced in 0.5 mM SA-treated *Lens esculenta* plants. Three years later, Misra and Misra (2012) stated that SA reduces the activity of proline oxidase and consequently prevents proline degradation, which was later supported by Khan and Khan (2013) in wheat plants. Enhancing proline biosynthesis by SA is related to better nitrogen assimilation and photosynthetic activities (Sharma et al. 2019). SA stimulates glycine betaine synthesis in the range of 0.5–2.5 mM in plants exposed to various kinds of abiotic stresses such as drought and salinity (Sharma et al. 2019). Aldesuquy et al. (2012) reported that foliar application SA (0.05 M) in two cultivars of wheat (resistant Sakha 93 and sensitive Sakha 94) had a meaningful impact on rising growth and metabolism of drought stressed wheat cultivars by enhancing glycine and proline biosynthesis. Kareem et al. (2017) showed that foliar application of SA (1.44 and 2.88 mM) stimulates proline and glycine betaine biosynthesis. and enhances drought tolerance of wheat plants. Similar report is available for *Helianthus annuus* plants under drought stress (Hussain et al. 2009).

Soluble carbohydrates as important osmolytes in plant cells could be increased by SA treatment under drought stress (Fayez and Bazaid 2014). SA enhances soluble sugars in plant leaves by diminishing polysaccharide hydrolyzing enzymes (Khodary 2004). According to Sharma et al. (2019), soluble carbohydrates act as membrane stabilizers, ROS scavengers and Osmoprotectants under abiotic stresses. Beside the proline, glycine betaine and carbohydrates, free amino acids have imperative participation in regulating osmotic homeostasis in plant cells. Yadav et al. (2005) and Sankar et al. (2007) reported that SA enhances amino acids production in *Sorghum bicolor* and *Abelmoschus esculentus* and improves plant growth under water deficit condition. In another report, Abdallah et al. (2016) showed similar increment of amino acid content in quinoa plants in response to different concentrations of SA application (i.e., 200 and 400 mg L^{-1}) under drought stress. These researchers suggested that the elevation of amino acid biosynthesis in response to SA might be related to enhanced protein degradation.

The JA has a significant role in osmotic adjustment of plant cells. Foliar application of JA improves osmotic adjustment of plants via increasing the production of osmolytes such as proline and soluble carbohydrates (Farhangi-Abriz and Ghassemi-Golezani 2019). Shan et al. (2015) and Anjum et al. (2011) identified the helpful impacts of JA in reducing drought stress through the production of osmolytes such as proline. Endogenous JA up-regulates various important genes playing critical roles in water stress adaptation by stimulating different encoding stress responsive proteins and osmolytes such as proline (Per et al. 2018).

JA-induced increment of proline contents in drought stressed plants has been reported in wheat (Ilyas et al. 2017), barley (Bandurska et al. 2003) and rapeseed (Alam et al. 2014) plants. Increasing proline content is a good sign of drought tolerance in plants due to its role in the activation of Kreb's cycle and renewal of chlorophylls (Ashraf and Foolad 2007). Foliar application of JA also increases the production and accumulation of organic acids of Kreb's cycle such as citrate and malate, that enhance resistance to environmental stresses such as drought. In a study, foliar application of JA increased the GB content in pear leaves and consequently improved overall plant growth under water stress (Gao et al. 2004). Ilyas et al. (2017) found that exogenously applied jasmonic acid under water stress modulated the drought induced harmful effects through increasing the level of soluble carbohydrates in wheat plants. Soluble carbohydrates act as osmolytes and osmoprotectants and improve relative water content of plants under abiotic stress. Similarly, Farhangi-Abriz and Ghassemi-Golezani (2018) reported that foliar application of JA modulates the salt induced osmotic stress in soybean plants through increased contents of glycine betaine, soluble sugars as well as proline. The impacts of SA and JA on rising osmolytes of plants are summarized in Table 2.

Table 2 Salicylic acid and jasmonic acid impacts on osmolytes production in different plant species under drought stress

Hormones	Plant species	Application method and dosage	Effects on plants	References
Salicylic acid	*Brassica rapa*	Foliar application—1.5 mM	Salicylic acid increased proline and drought stress tolerance of plants by up-regulating the expression of genes encoding pyrroline-5-carboxylate synthase (*P5CSA* and *P5CSB*) and down-regulating the expression of the gene encoding proline dehydrogenase (*PDH*) compared to non-SA pretreated plants	Hien La et al. (2020)
Salicylic acid	*Zea mays*	Root pretreatment—10 µM	Salicylic acid increased the biosynthesis of proline, soluble sugar and soluble protein contents under drought stress	Shan and Wang (2017)
Salicylic acid	*Triticum aestivum*	Seed priming—10 Mm	Seed priming with salicylic acid noticeably reduced drought stress effects on wheat plants by rising proline and soluble sugar contents in plant tissues	Ilyas et al. (2017)
Salicylic acid	*Zea mays*	Seed priming—2 mM	Salicylic acid increased the biosynthesis of proline, soluble sugar and total carbohydrate in maize seedlings and consequently improved water content of plants under drought stress	Tayyab et al. (2020)
Jasmonic acid	*Triticum aestivum*	Seed priming—100 µM	Seed priming with jasmonic acid increased the germination percentage, proline, and soluble carbohydrate accumulation and shoot growth of wheat plants under water stress	Ilyas et al. (2017)

(continued)

Table 2 (continued)

Hormones	Plant species	Application method and dosage	Effects on plants	References
Jasmonic acid	*Triticum aestivum*	Foliar application—100 μM	Jasmonic acid improved total osmotic potential of plant cells by rising the contents of osmoregulatory component such as soluble carbohydrates, soluble proteins and proline under drought stress	Abeed et al. (2020)
Jasmonic acid	*Fragaria* × *ananassaDuch*	Root treatment—0.05 mM	Jasmonic acid improved water stress tolerance of strawberry plants by increasing proline and protein contents	Yosefi et al. (2020)
Jasmonic acid	*Pyrus communis* L.	Foliar application—50 mM	Jasmonic acid increased betaine accumulation in pear leaves and enhanced drought stress tolerance of plants	Gao et al. (2004)

2.3 Photosynthetic Activities

Crops are exposed to water stress when there is not adequate water accessible, or the water present cannot be taken up by the plants. Water stress diminishes photosynthetic activities for some reasons: (1) stomatal closure decreases the carbon fixation in leaves, and (2) water shortage damages the cell membrane and inhibits electron transportation systems (Lavergne et al. 2020). Some stress tolerance hormones such as SA and JA can have positive impacts on improving photosynthetic activities of plants under water deficit. Singh and Usha (2003) reported that foliar application of SA (1–3 mM) enhances total chlorophyll content of wheat seedlings under water stress. These researchers, also showed that SA improves carboxylase activity of Rubisco enzyme in stressed plants. High values of leaf chlorophyll in response to SA could be related to preserving chlorophyll structure from degradation by antioxidative enzymes. Moreover, SA enhances chlorophyll stability index by elevating nitrogen metabolism in plant cells (Farhangi-Abriz and Ghassemi-Golezani 2016). Hayat et al. (2008) stated that SA increases net photosynthetic rate of tomato plants under water stress by enhancing internal CO_2 concentration, stomatal conductance, transpiration and photosynthetic rates. According to these researchers, the beneficial effect of SA on increasing photosynthetic activities of tomato leaves could be related to high activities of some important enzymes such as carbonic anhydrase. The increment of carbonic anhydrase activity by SA treatment has been also reported in lemongrass (Idrees et al. 2010). Tang et al. (2017) exanimated the possible effects of

SA on gas exchange, pigment contents and chlorophyll fluorescence in water stressed soybean plants. The results showed that SA significantly improves gas exchange rate, chlorophyll content and chlorophyll fluorescence parameters of soybean leaves under water stress. This report revealed that SA-induced increment of PSII efficiency (ΦPSII) under water stress is related to strengthening photochemical quenching. SA not only improves photosynthetic activities in C3 plants, but also enhances photosynthetic performance in C4 plants. Idrees et al. (2010) reported a positive effect of SA on promoting the phosphoenolpyruvate carboxylase activities in lemongrass under drought stress. Similar impacts of SA application are shown in maize plants under cadmium toxicity (Krantev et al. 2008).

Foliar treatments of jasmonic acid and methyl-jasmonates are useful strategies for alleviating the harmful effects of drought on plant photosynthesis. Some researchers indicated that exogenous treatment of jasmonic acid could be useful for increasing photosynthetic activities in different plant species. Wu et al. (2012) reported that application of methyl-jasmonate improved drought tolerance of *Brassica oleracea* through enhancing the synthesis of chlorophyll and net photosynthetic rate. Sheteiwy et al. (2018) stated that Priming with methyl jasmonate reduces the negative effects of water stress in rice seedlings by improving photosynthetic activities and photochemical efficiency of PSII (Fv/Fm). Ma et al. (2014) investigated the photosynthetic responses of wheat to combined effects of water stress and exogenous methyl jasmonate and found that 0.25 μM MeJA increases the photosynthesis under water stress mainly through improving the water status and antioxidant capacity of wheat plants. Moreover, they showed that exogenous MeJA induces stomatal closure, that maintains water status and delays plant senescence under drought stress. Mahabub Alam et al. (2014) showed that application of 0.5 mM JA on *Brassica* species seedlings increases the biosynthesis of chlorophyll under water stress. A similar report is available for soybean (Mohamed and Latif 2017). In another study, Abbaspour and Rezaei (2014) found that foliar application of JA enhances hill reaction in *Dracocephalum moldavica* plants under water limitation.

2.4 Biosynthesis of Secondary Metabolites

SA as an endogenous signaling molecule plays an important role in plant defense mechanisms (Ahmad et al. 2019). This phytohormone has been used as a potential enhancer of some secondary metabolites such as alkaloids (Pitta-Alvarez et al. 2000), glucosinolates (Kiddle et al. 1994) and anthraquinones (Bulgakov et al. 2002). SA has also some positive roles in biosynthesis of terpenoids such as sesquiterpenoids (Aftab et al. 2010), diterpenoids (Wang et al. 2007) and triterpenoids (Shabani et al. 2009). Production and accumulation of secondary metabolites has an important role on rising water stress tolerance of plants. Foliar application of SA stimulated the biosynthesis of secondary metabolites such as phenolic compounds in plant leaves (Ali et al. 2007). Latif et al. (2016) showed that the accumulation of total soluble and cell wall-bound compounds and total soluble proteins in *Zea mays* plants were increased in response to foliar application of SA under water stress. Since SA is a plant produced phenolic compound, it can enhance phenolic compounds and also can produce new polyphenols (Yao and Tian 2005). Ghassemi-Golezani et al. (2018b) reported that foliar application of SA noticeably enhanced phenolic compounds such as thymol and carvacrol in ajowan (*Carum copticum* L.) plants under drought stress. These researchers also showed that foliar application of SA increased essential oil production of ajowan under drought stress.

JA is a signal molecule with great ability in changing biosynthesis of secondary metabolites in plant cells. JA by enhancing *ORCA* gene expression in plant cells enhances alkaloid metabolism in plant cells (Memelink et al. 2001). Exogenous application of JA on drought stressed *Agropyron cristatum* plants considerably enhanced ascorbate and glutathione metabolism and consequently improved water stress tolerance of plants (Shan and Liang 2010). Alavi-Samani et al. (2015) found that foliar treatment of JA under drought stress significantly increased carvacrol and thymol contents in the oils of two thyme species (*Thymus vulgaris* and *T. daenensis*), but reduced the essential oil yield and amount of γ-terpinene in the oil. These researchers indicated that foliar application of JA reduces the negative effects of water stress on thymol amount in *T. daenensis*, and γ-terpinene content in *T. vuglaris*. Farhangi-Abriz and Ghassemi-Golezani (2019) reported that exogenous JA enhances phenolic components of plants under water stress and consequently increases antioxidative activities and water stress tolerance of plants.

2.5 Plant Growth and Productivity

Improving crop production under unfavorable conditions is one of the main goals of agricultural scientists (Farooq et al. 2012). Changing hormonal signaling of plants is a practical strategy for enhancing plant growth and productivity under normal and stressful conditions (Bari and Jones 2009). SA changes various aspects of plant growth and development such as root and shoot growth, flowering time and grain production. This natural regulator increases root growth of plants by stimulating cell growth and division (Hayat and Ahmad 2007). In a study carried out in 2018, foliar application of SA in chickpea plants significantly increased the size of the root and improved water status of plants under drought stress (Khan et al. 2018). Quiroga et al. (2018) reported that exogenous SA noticeably improved aquaporins and root hydraulic properties in drought stressed maize plants. Foliar application of SA also manipulated the root proteome of plants and consequently increased plant adaptation to drought (Sharma et al. 2017). In a recent study, Pasternak et al. (2019) showed that salicylic acid affects root meristem patterning via auxin distribution in a concentration-dependent manner. These researchers stated that a wide range of SA concentrations activated auxin synthesis, but the effect of SA on auxin transport was rate dependent. SA-induced auxin production and accumulation were led to the formation of more layers of columella initials and extra layers of epidermis, cortex, and endodermis cells.

Flowering process is so important for successful grain production under normal or drought conditions. The effect of SA on the flowering process of plants was assessed since it is a parameter closely related to the productivity (Martínez et al. 2004). The SA treatment enhanced number of flowers in various kind of plant species (Martínez et al. 2004; Wada et al. 2010). Yildirim and Dursun (2008) showed that foliar application of SA increased the tomato yield. Sharafizad et al. (2012) reported that the highest grain yield of wheat was obtained with application of 0.07 mM SA. It is believed that increasing crop yield might be due to delayed senescence of plant leaves and flowers in response to exogenous SA (Imran et al. 2007) that will automatically help the plant in extending the duration of photosynthetically active sites and also prevent the premature loss of bulbs and flowers. Plants treated with salicylic acid in the field or greenhouse conditions had higher shoot growth and grain yield under drought. These responses could be related to the physiological and biochemical modifications in SA treated plants. For example, SA inhibited ABA and ethylene biosynthesis in plants and improved shoot growth (Meguro and Sato 2014; Li et al. 2019). Ullah et al. (2018) found that foliar application of SA significantly improved rapeseed growth and productivity under drought stress. Similar reports are available in maize (Rao et al. 2012), rice (Sohag et al. 2020), tomato (Hayat et al. 2008), ajowan (Ghassemi-Golezani et al. 2018b) and rapeseed (Ghassemi-Golezani et al. 2019) plants.

JA is an important natural plant growth regulator, which regulates a wide variety of physiological and developmental responses. This hormone has been shown to enhance stomatal closure, abscisic acid and ethylene synthesis, respiration, and carotenoid and anthocyanin formation in plants. JA is in charge for the activation of a number of defensive mechanisms against different biotic and abiotic stresses (Wang et al. 2020). This phytohormone significantly changes plant growth and productivity under normal and stressful conditions such as salt and drought stresses (Raza et al. 2020). Although there are various reports that show positive effects of JA on rising plant growth and productivity under various conditions (Anjum et al. 2011, 2016; Javadipour et al. 2019), some of the JA impacts on plant growth and productivity are negative. The JA treatment reduces growth of explants in tissue culture, and seed germination, chlorophyll synthesis and photosynthesis rate in plants (Creelman and Mullet 1997). Staswick (2009) showed that JA decreases plant growth by decreasing auxin production in plant cells. Investigations by Adams and Turner (2010) showed that inhibition of root growth of plants in response to JA treatment is related to increasing ethylene production in this organ. These researchers reported that COI1 as a jasmonate receptor in plant roots is responsible for ethylene production in plant cells. Ghassemi-Golezani and Farhangi-Abriz (2018) reported that foliar application of JA under osmotic stress caused by salinity decreases root growth of soybean plants. However, the inhibition of root growth in JA treated plants did not significantly affect the grain yield, compared to untreated plants. The JA treatment may also reduce the expansion of leaves and cotyledons (Ananieva et al. 2007). This hormone inhibits leaf expansion by reducing cell division and the activity of the mitotic cyclin CycB1;2, but the cell size is not changed by this hormone (Swiątek et al. 2004). Foliar application of JA reduces cotyledon expansion in plants by increasing ABA concentration in shoot tissues (Aleman et al. 2016). In a study by Kim et al. (2009b), jasmonates reduced grain yield by mediating stress signals to alter spikelet development in rice. Similarly, Kraus and Stout (2019) reported that seed pretreatment with jasmonates induces resistance to biotic stress, but reduces plant growth in rice.

3 Conclusions and Future Perspectives

The SA and JA as natural regulators can stimulate various defense mechanisms of plants under drought stress. These growth regulators considerably enhance antioxidants activities and osmolytes production in plant cells and consequently improve drought tolerance in plants. SA in comparison with JA has reliable results on improving crop growth and productivity under drought stress. However, JA shows various impacts on growth and productivity of drought subjected plants, depending on species. Future investigations could be focused on the impacts of different natural regulators on plant growth and productivity under normal and stressful conditions.

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