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Jasmonates: Mechanisms and functions in abiotic stress tolerance of plants

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A B S T R A C T

Recent advancement in plant biology and innovative molecular and biochemical techniques has caused in the nearly exponential accumulation of our knowledge on hormonal signaling of plants under a variety of abiotic stress conditions. Jasmonates are naturally occurring plant oxylipins and important members of their family include methyl jasmonate, jasmonic acid, and jasmonyl-isolucine. These growth regulators are involved in several physiological and biochemical procedures in plant growth and development, such as seed development, leaf growth and, senescence. Jasmonates are also involved in plant defense mechanism against wounding by pathogens and insects attack. New reports indicate that jasmonates can modulate aspects of plant growth and resistance to different abiotic stresses such as drought, salinity, thermal stress, light stress, heavy metals, and flooding stress. In general, jasmonates can protect plants from the damaging effects of environmental stresses via. up-regulating the gene expression and regulating some physiological and biochemical responses. Jasmonates can maintain the integrity of plant cells under different abiotic stresses through enhancing antioxidant capacity (enzymatic and non-enzymatic) and synthesis of different osmoprotectants such as proline and glycine betaine. These growth regulators can also remobilize the photoassimilates to the vegetative sinks and improve plant growth under stressful conditions.

1. Introduction

Plants have different mechanisms for adaptation and resistance against the environmental stresses. Because they cannot avoid the stress full conditions, they have been equipped to different biochemical, physiological and molecular responses (Ghassemi-Golezani and Farhangi-Abriz, 2019). These responses contain modifications in gene expression, biosynthesis of special proteins and secondary metabolites, alterations in hormonal signaling and antioxidative activities. Gene expression at the molecular level is one of the main mechanisms in physiological processes, and phytohormones have a key role in this process (Khan et al., 2019). Phytohormones are a group of natural molecules, including auxins, gibberellins, cytokinin, abscisic acid, jasmonic acid, salicylic acid, ethylene and few others (Wani et al., 2016; Ghassemi-Golezani and Nikpour-Rashidabad, 2017). Hormone responses are important to the growth and development of plants. Also, their adjusting roles during growth and development, they play main roles in signal transduction pathways during reactions to biotic and abiotic stresses (Peleg and Blumwald, 2011).

Jasmonic acid (JA) and its metabolites are important plant phytohormones, that regulate plant responses to biotic and abiotic stresses and role in several features of growth and development (Siva et al., 2015; Dar et al., 2015). Jasmonates adjust growth and development not by simple pathway, but through multifarious interconnections between diverse signaling pathways. For example, usually, a broad interaction happens between JA and salicylic acid and/or abscisic acid in plant cells (Per et al., 2018). In plant cells, after biosynthesis through the octadecanoid pathway, JA can be joined to the different amino acids, such as isoleucine (Ile) to create Ile–JA or transformed to methyl jasmonate (Me–JA) or other similar components (Wasternack, 2014). The complex of Ile–JA is the active form of jasmonic acid. The biotic and abiotic stresses cause a drastic increase in JA levels in plant cells. In overall, jasmonates help the plants to alleviate the harmful effects of environmental stresses.

Many types of research have been conducted on the role of endogenous and exogenous JA and its metabolites in defense mechanisms against abiotic stresses. Reports frequently indicate changes in the content of numerous phytohormones in plant cells, which associate with modifications in the expression of specific genes involved in their biosynthesis and the mechanisms they control under normal and stressful conditions (Per et al., 2018). The JA was stated to take the main part in responses to the different environmental stresses such as drought, salinity, and heavy metal toxicity (Lehmann et al., 1995; Ghassemi-Golezani and Farhangi-Abriz, 2018 a). Foliar application of

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JA under the salt stress, improved the salt stress tolerance in rice seedlings (Kang et al., 2005). Treatment with JA also leads to a reduction in sodium accumulation in soybean roots and leaves. This superior effect shows the involvement of JA in ion homeostasis based on the increased H^+-ATPase activity of tonoplast and decreased root growth of plants (Ghassemi-Golezani and Farhangi-Abriz, 2018 a). The positive correlation between the freezing tolerance and JA level in plant cell was reported by Hu et al. (2013).

Since environmental stresses are considered as one of the probable dangers of plant production, the present review attempts mainly to improve our knowledge about the possible effects and mechanisms of JA on abiotic stress tolerance of plants.

2. Synthesis and molecular structure

Jasmonates family include methyl jasmonate, jasmonic acid, and jasmonyl-isoleucine. Jasmonic acid was identified by Demole et al.,) 1962) in the essential oil of jasmine plants. Thereafter, various physiological and biochemical effects of jasmonic acid on plant growth and development, such as promotion of senescence and root growth inhibition, were recognized (Parthier et al., 1992). The pathway of jasmonic acid biosynthesis was clarified by Vick and Zimmerman (1983). Vick and Zimmerman (1983) indicated that jasmonic acid is a linolenic acid (LA)-derived cyclopentanone compound, which originates from polyunsaturated fatty acids such as linolenic acid and linoleic acid and is synthesized by lipoxygenase pathway, by allene oxide synthase and lipoxygenase enzymes in the cell peroxisomes (Feussner and Wasternack, 2002). In the oxylipin biosynthesis (Fig. 1), only 13-hydroperoxide from α-linolenic acid can be utilized by the allene oxide synthase branch for jasmonic acid production. Jasmonic acid biosynthesis launch with linolenic acid as the substrate is stated to as the Vick and Zimmermann pathway, which was considered the main basis of jasmonic acid production in plants. However, there are some other ways as the alternative routes of jasmonic acid biosynthesis in plants such as synthesis from linoleic acid and hexadecatrienoic acid.

In plants, the jasmonate molecule containing two chiral centers placed at 3 and 7 numbers of structural carbons, exposed four possible isomers, with an R or S absolute configuration. The jasmonate isomers containing (3R, 7S) and (3S, 7R), have their side chains in a cis location, and known as (+) and (−) 7 iso jasmonic acid or (+) and (−) epi-jasmonic acid. The enantiomers (3R, 7R) and (3S, 7S) jasmonic acid or (−) jasmonic acid and (+) jasmonic acid, have their side chains in the trans configuration. Usually, the cis orientation is less constant and will modify to the more stable trans formation (Delker et al., 2006). Different structures of jasmonic acid isomers are shown in Fig. 2.

Early studies showed that exogenous jasmonic acid can stimulate senescence and action as a plant growth regulator. It was found that jasmonic acid alters gene expression under environmental stresses and could cause the physiological changes in plant cells. These results imply a role for jasmonate in plant defense that has been confirmed (Creelman and Mullet, 1995; Wasternack and Parthier, 1997).

3. *Physiological and biochemical effects of jasmonates*

For the first time, physiological and biochemical effects of jasmonates were reported in *Artemisia absinthium* (leaf senescence) and *Vicia faba* (growth inhibition) (Ueda and Kato, 1980; Dathe et al., 1981). This family of growth regulators has a wide range of effects on plant species, ranging from promotion to inhibition of physiological processes. Parthier (1991) reported that the effect showed on the plant may even be concentration dependent, such that some processes enthused at lower concentrations but inhibited at upper levels. For example, jasmonates at low concentrations inhibit the seed germination and seedling growth. However, in the higher levels stimulate the germination process. Plants treated with jasmonates made the smaller petioles than do control plants (Cipollini, 2005). Treatment of barley plants with JA (2.5×10^{-6} and 2.5×10^{-4} M) reduced the seedling growth. However, the lower concentration had no effect on the growth of seedlings (Popova and Vaklinova, 1988). The high concentration of jasmonates (upper than 50 mM) stimulates leaf senescence, this response contains a damage of chlorophyll and degradation of chloroplast proteins (Weidhase et al., 1987). Although jasmonates can induce ethylene biosynthesis by stimulating the activity of the ethylene making enzyme (Czapski and Saniewski, 1992). Czapski and Saniewski (1992) reported that the application of jasmonates stimulated the tomato fruit ripening by increasing ethylene biosynthesis.

Most of the plant growth regulators such as abscisic acid, gibberellins, and jasmonic acid, affect the rate of photosynthetic activities in

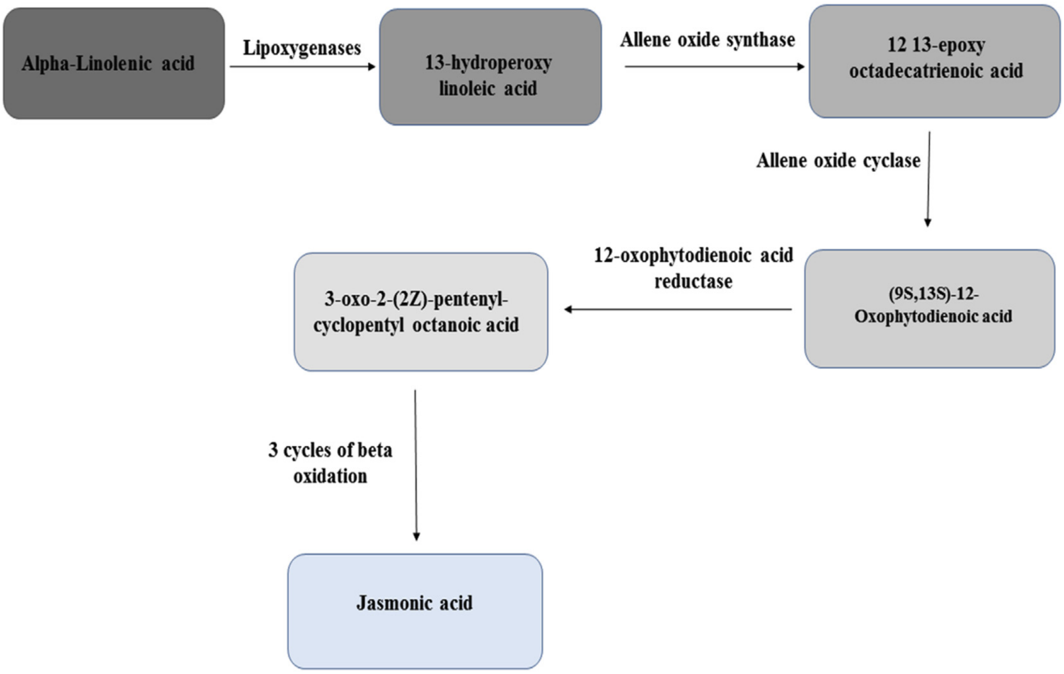
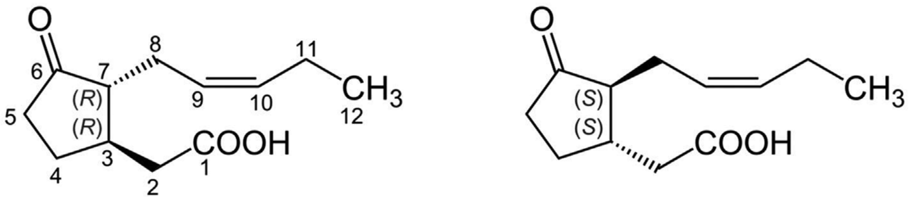
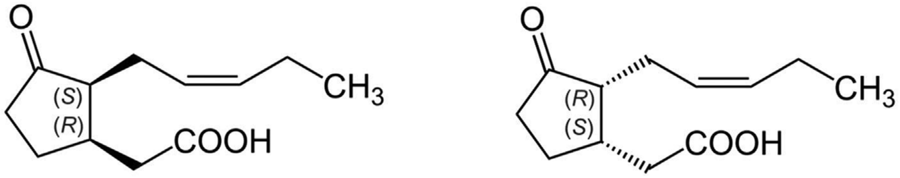


Fig. 1. The jasmonic acid biosynthesis pathway from the unsaturated fatty acids (Alpha-linolenic acid) in plant cells.



(3R, 7R)-Jasmonic acid
(-)-Jasmonic acid

(3S, 7S)-Jasmonic acid
(+)-Jasmonic acid



(3R, 7S)-Jasmonic acid
(+)-7-Iso-Jasmic acid
(+)-epi-jasmonic acid

(3S, 7R)-Jasmonic acid
(-)-7-Iso-Jasmonic acid
(-)-epi-Jasmonic acid

Fig. 2. Chemical structure in various isomers of jasmonic acid.

plants. Treatment of plants with jasmonates has numerous effects on photosynthetic activities, such as a breakdown in the biosynthesis of rubisco and inhibition of the Hill reaction (Weidhase et al., 1987; Popova and Vaklinova, 1988). The inhibition in the Hill reaction activity in response to the JA is associated with the change in chloroplast membrane stability. Foliar application of JA affects the PSI and PSII centers and enhanced the resistance to the environmental stresses (Maslenkova et al., 1990). Foliar application of JA in barley plants altered the chloroplast ultrastructure and reduced the number of thylakoids per granum (Popova et al., 2003). Gehring et al. (1997) reported that the jasmonates reduced the stomatal conductivity by an alkalization of the guard cell cytoplasm. Foliar application of jasmonates increased the anthocyanin accumulation in different plant leaves (Tamari et al., 1995; Saniewski et al., 2006). Heijari et al. (2005) reported that treatment of *Pinus sylvestris* L with methyl jasmonate reduced photosynthetic rate and growth.

Jasmonates stimulated the accumulation of proteins in different plant species (JA-induced proteins). These proteins, mainly belong to the thylakoid-bounded polypeptides and help to the plants in environmental stress tolerance (Maslenkova et al., 1992). Treatment of plants with jasmonates alters the proteome profile of plants. For example, foliar application of methyl jasmonate downregulates the protein synthesis in barley leaves (Reinbothe et al., 1993). Reinbothe et al. (1994) stated that jasmonates induced the JA-induced protein 60 and inactivated the synthesis of the ribosome in barley plants. However, it is important to remind that jasmonates did not expose the similar effects in all plants.

Jasmonates are produced by conjunction with amino acid isoleucine and perceived by a co-receptor complex of the Jasmonate ZIM-domain (JAZ) repressor proteins. JAZ proteins control JA-responsive gene transcription by hindering DNA-binding transcription factors. According to the Yan et al. (2009) and Thireault et al. (2015) there are 13 kinds of JAZ proteins in *Arabidopsis thaliana*. These proteins are necessary for the interface with coronatine insensitive 1 and different transcription factors. Chini et al. (2007) reported that the jasmonate insensitive 3 is a primary repressor of gene expression in the JAs signaling. Jasmonate insensitive 3 and other JAZ proteins have been reported to interact with F-box protein coronatine insensitive 1. Coronatine is a 3D-mimic, and therefore is an agonist of JA-isoleucine that can stimulate the JA pathway by binding to the coronatine insensitive-JAZ co-receptor multifaceted. F-box proteins such as coronatine insensitive 1 have different roles in plant response to the environmental stresses, for example coronatine insensitive 1 controls signal transduction processes in shade avoided plants (Goossens et al., 2016).

The Jasmonic acid pathway is activated through *COI1* leading to the degradation of JAZ repressor proteins. JAZ repressors repress *MYC2* and activates target gens against the environmental conditions. Different JA-responsive genes have been recognized (Table 1) that are obviously upregulated, leading to the synthesis of JA-induced proteins. Devoto et al. (2005) reported that activation of *COI1* gene regulated the stress response in *Arabidopsis thaliana*. JA can activate the *COI1* and decrease the harmful effects of environmental stresses such as wound. *AtMYB44* is the other jasmonate responsive gene in Arabidopsis plants which has a regulatory effect on abscisic acid production. Kim et al. (2009 b) showed that the Overexpression of *AtJMT* caused a large enhancement in abscisic acid and jasmonates concentrations in *Oryza sativa* tissues. The *AtJMT* is a jasmonate responsive gene with a high reactivity to endogenous content of jasmonates. The *OsWRKY13* is the other jasmonate responsive gene in *Oryza sativa* which has a positive effect on pathogenic defense mechanisms in this plant (Qiu et al., 2007). Some reports suggest that jasmonates modify the expression of proteinase inhibitor genes in plant cells (Wager, 2012; Boex-Fontvieille et al., 2016). However, this mechanism is more likely to be observed in biotic stressed plants. Andresen et al. (1992) and Lehmann et al. (1995) reported that treatment of barley plants with JA or upon the endogenous increase of JA enhanced some of the JA-induced proteins such as 23-kD protein. This protein is commonly visible after the elevation of jasmonate levels in plant cells. Ghassemi-Golezani and Farhangi-Abriz (2018 a) reported that the foliar application of JA increased the H^+-ATPase activity of tonoplast and ATP content in root cells of soybean plants.

4. The roles of jasmonates under abiotic stress

The roles of jasmonates in environmental stress tolerance of plants have been widely reported (Riemann et al., 2015; Ahmad et al., 2016; Farhangi-Abriz and Ghassemi-Golezani, 2018). JA can increase the tolerance of plants to diverse environmental stresses such as drought (Wasternack, 2014), salinity (Farhangi-Abriz and Ghassemi-Golezani, 2018), thermal stress (Sharma and Laxmi, 2016), heavy metals (Dar et al., 2015). Foliar application of jasmonates could be useful in improving stress tolerance in different plants. In this manuscript, the possible mechanisms of jasmonates in increasing environmental stress tolerance of plant are briefly discussed. Possible mechanisms of

Table 1
Some of the physiological responses of plants to jasmonate-responsive genes.

Plant species	Gene name	Response	References
Arabidopsis thaliana	*dad1*	Activation of this gene produced the phospholipase A1 and consequently reduced the filament elongation and postponed anther dehiscence	Ishiguro et al. (2001)
Arabidopsis thaliana	*Cev1*	This gene activates the cellulose synthase CeS3A in plant cells and cause to constitutive expression of vegetative storage proteins	Ellis et al. (2002)
Arabidopsis thaliana	*Ore9*/max2	This gene by increasing F-box proteins delayed the leaf senescence and enhanced the shoot branching	Domagalska and Leyser (2011)
Arabidopsis thaliana	*Jam1*	Upregulation of this gene increased the anthocyanin production and resistance to herbivores	Nakata et al. (2013)
Arabidopsis thaliana	*Jam2 and 3*	Increasing the defense responses such as anthocyanin production and root growth inhibition	Sasaki-Sekimoto et al. (2013)
Arabidopsis thaliana	*Jav1*	Improving tolerance to the herbivores and pathogens, but, infrangible development	Hu et al. (2013 b)
Arabidopsis thaliana	*Aim1*	Increasing the synthesis of multifunctional proteins and abnormal inflorescence meristem	Richmond and Bleecker (1999)
Arabidopsis thaliana	*Atvsp*	This gene activates some of the defense response mechanisms in plant cells	Van Wees et al. (1999)
Arabidopsis thaliana	*NPR1*	Decreases the jasmonate biosynthesis and adjust the salicylic acid production in plant cells	Mao et al. (2007)
Arabidopsis thaliana	*ERF1*	This gene activates the ethylene and jasmonate pathways in plant defense mechanisms	Lorenzo et al. (2003)
Arabidopsis thaliana	*COI1*	The *COI1* plays a critical role in the wound and JA signaling	Devoto et al. (2005)
Arabidopsis thaliana	*AtMYB44*	Activation of this gene induces the anthocyanin production and improvement of ABA-mediated responses	Jung et al. (2010)
Arabidopsis thaliana	*ORA59*	This gene has an important role in pathogen and disease tolerance in plants	Pré et al. (2008)
Nicotiana tabacum	*NtODC1*	Activates the G-box and TGACG-motif elements in plant cells	Xu et al. (2004)
Nicotiana tabacum	*JERF1*	*JERF1* activates the expression of GCC box-containing genes such as *GLA, osmotin, Prb-1b* and *CHN50* in plant cells. These genes have important roles in the enhancement of biotic and abiotic stress tolerance in plants.	Zhang et al. (2004)
Oryza sativa	*AtJMT*	Overexpression of this gene causes a large reduction in grain yield through increased abscisic acid and jasmonates concentrations in panicles.	Kim et al. (2009 b)
Oryza sativa	*OsWRKY13*	Overexpression of *OsWRKY13* can improve rice tolerance to biotic stresses such as, fungal blast and bacterial blight at both the seedling and adult stages, and shows no influence on the fertility.	Qiu et al. (2007)

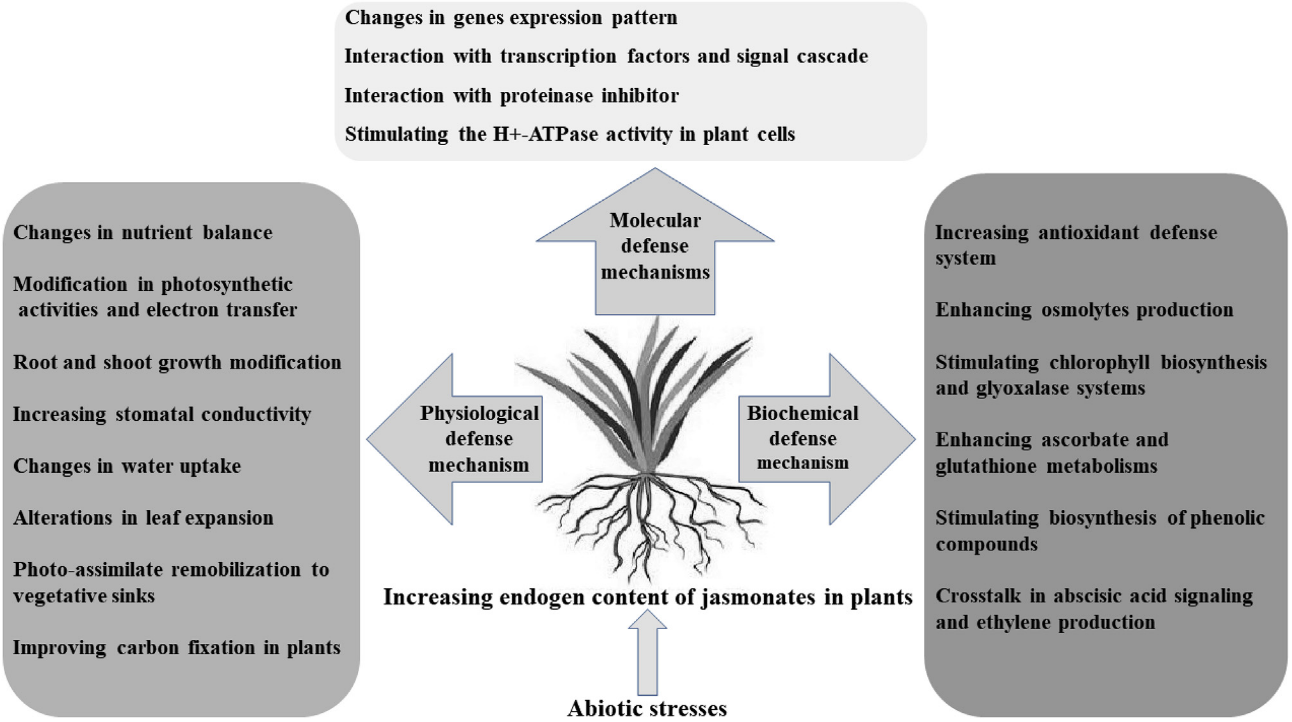


Fig. 3. Summary of jasmonates mechanisms in increasing abiotic stress tolerance in plants.

jasmonates in abiotic stress tolerance are shown in Fig. 3.

4.1. Drought

Among the stress factors, drought is the most important factor responsible for the disruption of yearly agricultural production (Pandey et al., 2017). Drought stress modifies the normal growth balance and result in a series of morphological, physiological, biochemical and molecular changes in plants and hence affects their growth and productivity (Pandey et al., 2017). This environmental stress also causes a reduction in cell water potential and turgor, which elevates inter-or intracellular solute concentrations and other harmful effects on plant growth (Todaka et al., 2015). Compared to the several studies on the role of jasmonic acid in the response to biotic stresses, relatively less has been known about its role under abiotic stresses such as drought. Previous studies displayed that drought increases jasmonic acid level in leaves and roots of some plants (Kiribuchi et al., 2005). Overexpression of jasmonic acid carboxyl methyl transferase gene (AtJMT) in rice showed an increased level of jasmonic acid under drought condition and indicated that plants can produce jasmonic acid during drought stress (Kim et al., 2009 a). These results showed that jasmonic acid production and signaling are the important adaptation mechanism of

Table 2
Mechanisms of jasmonates in alleviation of drought injuries in different plant species.

Plant species	Mechanisms	References
Glycine max	Application of methyl-jasmonate increased the antioxidant activities such as superoxide dismutase, peroxidase, and catalase and consequently reduced the membrane lipid peroxidation in soybean leaves.	Anjum et al. (2011)
Brassica oleracea	Application of methyl-jasmonate improved the tolerance of water stress through enhanced the synthesis of chlorophyll and net photosynthetic rate.	Wu et al. (2012)
Cicer arietinum	Jasmonates stimulated the early signaling in chickpea root and by molecular modification, improved the drought stress tolerance in this plant.	De Domenico et al. (2012)
Oryza sativa	Jasmonates stimulated the biosynthesis of some special proteins such as OsbHLH148 and increased the drought stress tolerance in *Oryza sativa*.	Seo et al. (2011)
Oryza sativa	Jasmonates increased the abscisic acid content in plant tissues and improved the drought stress tolerance.	Kim et al. (2009)
Zea mays	Pretreatment of seeds with methyl-jasmonate increased the ion uptake and antioxidative activities in maize plants under water stress.	Abdelgawad et al. (2014)
Brassica napus	Application of jasmonic acid stimulated the antioxidative activities, chlorophyll biosynthesis and glyoxalase systems under water stress.	Alam et al. (2014)
Agropyron cristatum	Jasmonic acid enhanced the ascorbate and glutathione metabolisms in plant tissues and induced the water stress tolerance	Shan and Liang (2010)
Triticum aestivum	Exogenous jasmonic acid enhanced the nitric oxide production and antioxidative systems such as ascorbate-glutathione cycle under water stress.	Shan et al. (2015)
Arabidopsis thaliana	Jasmonic acid increased the abscisic acid content in plant tissues and induced the abscisic acid-dependent response such as proline accumulation under water stress.	de Ollas et al. (2015)
Thymus vulgaris	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)
Triticum aestivum	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)
Oryza sativa	Priming with methyl jasmonate reduced the negative effects of water stress in rice seedlings by improving photosynthetic activities and photochemical efficiency of PSII (Fv/Fm).	Sheteiwy et al. (2018)

plants to drought stress. Some of these mechanisms are shown in Table 2.

Exogenous application of plant growth regulators such as the jasmonic acid is one of the useful strategies to alleviate the harmful effects of drought on plants. There were many reports from different researchers, who are indicated that exogenous application of jasmonic acid could be useful for crop production under drought stress via stimulating anti-oxidant enzymes activities. Abdelgawad et al. (2014) reported that exogenous jasmonic acid under drought stress, increased antioxidant enzymes and alleviated oxidative stress in maize plants. Moreover, Kumari et al. (2006) indicated that jasmonic acid reduced lipid peroxidation in peanut seedlings under drought stress via decreasing oxidative stress by increasing antioxidant enzymes activities. Alam et al. (2014) found that foliar spray of jasmonic acid increased the activity of some important antioxidant enzymes such as glutathione peroxidase, ascorbate peroxidase, and catalase activities in Brassica species, thereby inhibited reactive oxygen species (ROS) generation under drought stress. It is not clear yet that how jasmonic acid acts to modify the antioxidant systems. It is possible that jasmonic acid influences enzyme activities through changes in gene transcription, translation or post-transcriptional modifications. However, the organ-specific nature of this hormone suggests that the effects of jasmonic acid are tightly controlled and responsible for directing specific sub-cellular changes in metabolism (Comparot et al., 2002).

Jasmonic acid could also adjust water potential in plant cells, which has a useful effect on alleviating drought stress in plants (Anjum et al., 2011; Shan et al., 2015). This mechanism can be described with genes up-regulating by jasmonic acid, some of which have a key role in drought adaptation in plants via stimulating the synthesis of secondary metabolites, cell wall formation, encoding stress protective and defense proteins and solutes such as proline (Abdelgawad et al., 2014). Bandurska et al. (2003) defined that exogenous application of jasmonic acid on barley genotypes improved biosynthesis of proline under drought stress. Moreover, jasmonic acid improved osmotic adjustments in plant cells via the accumulation of other osmo-regulators such as soluble carbohydrates and proteins (Abdelgawad et al., 2014). This increment of soluble carbohydrates due to jasmonic acid treatment is attributed to enhancing invertase activity in treated plants. Jasmonic acid also regulated ascorbate and glutathione metabolism in *Agropyron cristatum* leaves under water stress (Shan and Liang, 2010).

The other important effect of jasmonic acid under drought stress is the stimulation of the synthesis of other growth regulators. Exogenous jasmonic acid induces abscisic acid (ABA) synthesis in plants, because the synthesis of jasmonic acid and ABA have a crosstalk with each other (Creelman and Mullet, 1995). Onkokesung et al. (2011) defined that jasmonic acid signaling can have a starter effect on ethylene synthesis in different plants. Moreover, jasmonic acid signaling has a synergistic effect on some other growth regulators such as polyamines. Application of jasmonic acid increased spermidine content in barley genotypes, saving their cell membranes from peroxidation, because polyamines have a key role in the activation of antioxidant enzymes (Bandurska et al., 2003).

Foliar spray of jasmonic acid alleviated oxidative stress and other harmful effects of drought stress on plants, but inhibited root growth, leaf expansion and chlorophyll synthesis in some crops under drought and normal conditions. Liu and Avramova (2016) reported that priming with jasmonic acid improved drought stress tolerance by stimulating specific dehydration stress responsive gene expression in Arabidopsis plants. Decreasing leaf expansion due to jasmonic acid treatment is related to the epinastic effect of this growth regulator. Moreover, jasmonic acid stimulated leaf senescence, microtubule degradation and chlorophyllase activity in some plants (Sembdner and Parthier, 1993; Hassanein et al., 2009).

4.2. Salt stress

Salinization and alkalization are known to influence more than 10% of the world's arable land which hinders crop productivity (Parihar et al., 2015). Saline lands have high levels of sodium (Na^+) and chloride (Cl^-) content and consequently exert hazard abiotic stress on crops. About 20% of agricultural lands (Munns and Tester, 2008) are currently affected by salt toxicity. Usage of saline water with high EC and TDS for irrigation and the addition of chemical fertilizers to the soils are the main issues responsible for increasing soil salinity (Munns and Tester, 2008). Soil and water salinity causes trouble in the delivery of nutrients, membrane permeability, metabolism of carbon and nitrogen and reduction of chlorophyll synthesis, leading to the increment of toxic ions and respiration rate (Ahmad et al., 2013; Kumar et al., 2018). Severe salinity results in the production of reactive oxygen species (ROS) in plants, which causes oxidative stress that damages the

DNA, proteins, and peptides, deactivate enzymes and enhance lipid peroxidation (Farhangi-Abriz and Torabian, 2017).

The endogenous jasmonic acid content increases in response to salt stress have been implicated in leaves of *Iris hexagona* (Wang et al., 2001). There is growing indication that jasmonates mitigate the harmful effects of salt stress in plants. Jasmonic acid alleviated salt inhibition of biomass production in rice (Kang et al., 2005) and reduced the inhibitory effects of salt toxicity on the rate of carbon fixation and protein synthesis in *Pisum sativum* (Velitchkova and Fedina, 1998). Foliar spray of jasmonic acid successfully lowered salt toxicity symptoms in soybean seedlings (Yoon et al., 2009). Jasmonic acid induced the enzyme cationic peroxidase, pathogenesis associated proteins like PR-1 and PR-10 and salt-stressed responsive proteins in roots of rice seedlings (Moons et al., 1997).

Foliar application of jasmonic acid under salt stress, improved physiological performance of safflower via increasing chlorophyll content, relative water content, the maximum quantum yield of photosystem II (Fv/Fm), plant biomass and grain yield (Ghassemi-Golezani and Hosseinzadeh-Mahootchi, 2015). Also, exogenous application of jasmonic acid increased antioxidant enzymes activity, reduced lipid peroxidation and also improved the potassium content of plants under salt stress (Faghih et al., 2017; Farhangi-Abriz and Ghassemi-Golezani, 2018). Farhangi-Abriz and Ghassemi-Golezani (2016) reported that jasmonic acid decreased protein percentage in soybean seeds via inhabitation nitrogen absorption with the roots, however, the sulphur content of leaves, improved by jasmonic acid. Treatment of plants with jasmonic acid enriched the seeds with sulphur containing amino acids such as methionine and aromatic amino acids include phenyl-alanine and tyrosine by stimulating the shikimate pathway (Tzin and Galili, 2010). Recently Ghassemi-Golezani and Farhangi-Abriz (2018 b) found that foliar application of jasmonic acid under salt stress, significantly enhances the percentages of total oil, linoleic and linolenic acids production from oleic acid via increasing the activity of lipoxygenase. This alters the profile of soybean oil and improves unsaturated index (UI) of oil. In another study Ghassemi-Golezani and Farhangi-Abriz (2018 a) showed that foliar application of JA stimulated the H^+-ATPase activity in root tonoplast and reduced the sodium uptake by soybean plants. Treatment of *Pisum sativum* plants with MeJA reduced the salt toxicity and recovered the carbon fixation and Fv/Fm (Velitchkova and Fedina, 1998). Priming with JA partially hardened barley plant to subsequent salt stress (Walia et al., 2007). This positive effect was accompanied by decreased sodium accumulation and maintenance of more adequate levels of nutrients. Seed pretreatment by JA enhanced salt tolerance of soybean plants by improving the accumulation of osmo-protectants (Sheteawi, 2007). Azooz et al. (2015) reported that priming with 50 µm jasmonic acid induced salt tolerance in Hassawi okra seedlings. Harpreet et al. (2013) stated that priming with jasmonic acid increased the sugar accumulation and improved the salinity tolerance in rapeseed plants. Some of the JA mechanisms in alleviating salt toxicity in different plants are presented in Table 3.

4.3. *Heat stress*

Both of the high and low temperatures are hazardous for crops, and these abiotic stresses have an important role in decreasing crop productivity in agriculture. The enhancing brutality of the high temperature at global level presents an alarming risk to the farmers. As evident by massive yield losses in various food crops, the escalating adverse effects of heat stress are putting the global food as well as nutritional security at great risk. The estimates based on worldwide environment model analysis suggest that the tropical and subtropical areas of the world will be the most awful sufferer from the future tragedy of heat stress (Battisti and Naylor, 2009). According to a report in Africa, analysis of historical data covering more than 20000 maize trials proposed 1–2% yield losses under tropical and subtropical conditions, respectively, due to the rise of each one-degree temperature beyond 30 °C (Lobell et al., 2011). Under this situation, several pathways are activated by gene expression and consequently, some of the special proteins with low molecular weight (Heat shock proteins) are synthesized by plants (Suri and Dhindsa, 2008). The key mechanism of crops for heat tolerance is the production of heat shock proteins. This action is a preserved molecular protection mechanism in response to high temperatures and is detected in cells from numerous groups of plant species.

Jasmonic acid is a well-known long-distance growth regulator that facilitates protective responses and production of some secondary metabolites, phytohormones and heat shock proteins in plant cells (Creelman and Mullet, 1995). The role of jasmonic acid signaling in contributing to heat tolerance has been reported in Arabidopsis (Clarke et al., 2009). Hasanuzzaman et al. (2013) stated that the increase of jasmonic acid under heat stress is a great defense response of plants to this unfavorable condition. Foliar application of low doses of jasmonic acid preserved the cell feasibility in heat-stressed plants as verified by the leaf electro leakage assays (Kazan, 2015). Mueller-Uri et al. (1988) indicated that foliar application of jasmonic acid induced modification of gene expression in barley and improved the synthesis of some low weight proteins which are known as heat shock proteins. Some other scientists believed that jasmonic acid by modification of phenolic components in plant tissues, induced the synthesis of heat shock proteins and enhanced heat tolerance of plants (Saltveit, 2000). On the other hand, foliar spray of jasmonic acid by increasing abscisic acid content in plant cells can be helpful in decreasing the harmful effects of heat stress, because rising abscisic acid in plant cells, stimulates stomata closing and causing successful water-saving strategy under the stress (Creelman and Mullet, 1997; Lehmann et al., 1995; Acharya and Assmann, 2009). Moreover, exogenous application of jasmonic acid under environmental stress such as heat stress, adjusts water potential of plant cells, thereby preserving water content. Under the high temperature, transpiration rate of the leaves is rising. Jasmonic acid increases the water potential in plant cells by improving the synthesis of some Osmo-regulators, including proline and soluble carbohydrates (Bandurska et al., 2003). More researches are needed to improve our knowledge about the mechanisms of jasmonic acid in mitigation of injurious effects of heat stress on plants.

4.4. *Cold stress*

Among the environmental challenges, low-temperature stress is very critical for plant growth and development. Plants show an optimum rate of growth and development at an optimal temperature of their daily life period (Fitter and Hay, 2012). When the environmental temperature differs from optimal level, biochemical, physiological, and molecular changes happen within the plants. This is a defense mechanism of plants to maximize growth and development processes and to preserve the cellular and molecular homeostasis at an optimum level during the thermal stress condition (Fitter and Hay, 2012). Plants experience low-temperature stress (cold or chilling stress) at 0–15 °C. They respond to lower temperatures by wide reprogramming of gene expression, physiological and metabolic changes (Chinnusamy et al., 2007). In the last years, great attention has been paid to the roles of long-distance signal molecules such as jasmonates under the low-temperature stress (Lee et al., 2005).

Researchers indicated that a number of different stress phytohormones and plant stress regulators such as abscisic acid, jasmonates and ethylene can facilitate the low-temperature stress tolerance in plants (Wasternack, 2014; Kosova et al., 2012). It was found that in wheat plants jasmonic acid content enhanced after the cold stress (Kosova et al., 2012). Furthermore, the jasmonic acid content of leaves raised in *Pinus pinaster*, when the plants were exposed to cold and water stresses (Pedranzani et al., 2007). Moreover, the expression of LOX (one of the first enzymes in jasmonic acid biosynthetic pathway) in kiwi (*Actinidia delicosa*) and *Caragana jubata* was controlled positively during

Table 3
Mechanisms of jasmonates in alleviation of salt toxicity in different plant species.

Plant species	Mechanisms	References
Glycine max	Foliar sprays of jasmonic acid inhibit the sodium uptake and stimulate the H^+-ATPase activity of tonoplast, ATP synthesis, nutrient uptake and salt tolerance of soybean.	Ghassemi-Golezani and Farhangi-Abriz (2018)
Glycine max	Foliar application of jasmonic acid enhanced the synthesis of aromatic amino acids and sulphur uptake under salt stress.	Farhangi-Abriz and Ghassemi-Golezani (2016)
Glycine max	Jasmonic acid enhanced the antioxidative activities and osmolytes production in soybean leaves under salt stress.	Farhangi-Abriz and Ghassemi-Golezani (2018)
Triticum aestivum	Jasmonic acid decreased the reactive oxygen species generation and enhanced the antioxidant enzymes activities.	Qiu et al. (2014)
Matricaria chamomilla	Methyl-jasmonate stimulated the proline biosynthesis and catalase, peroxidase and ascorbate peroxidase activities under salt stress.	Salimi et al. (2016)
Solanum lycopersicum	Jasmonic acid increased the flavonoid, proline and glycine betaine synthesis, antioxidative activities and reduced the lipid peroxidation under sodium chloride toxicity	Ahmad et al. (2018)
Ocimum basilicum	Treatment of plants with methyl-jasmonate improved the antioxidative activities in leaf tissues under salt stress	Talebi et al. (2018)
Brassica napus	Exogenously applied methyl-jasmonate stimulated photosynthetic activities, antioxidant system, relative water content and soluble sugar content in *Brassica napus* leaves under salt stress	Ahmadi et al. (2018)
Arabidopsis thaliana	Jasmonic acid stimulated the synthesis of some proteins and this growth regulator has a key role in the alleviation of salt toxicity.	Zhang et al. (2017)
Fragaria × ananassa	Methyl-jasmonate improved the carbon fixation and reduced the sodium uptake by plants under salt stress.	Faghih et al. (2017)
Zea mays	Treatment of salt-stressed plants with the exogenous jasmonic acid improved the sodium exclusion by decreasing the sodium uptake at the root surface.	Shahzad et al. (2015)
Rosmarinus officinalis	Jasmonic acid increased the synthesis of chlorophyll and antioxidative activities under salinity.	Nahrjoo and Sedaghathoor (2018)

low-temperature stress (Zhang et al., 2006; Bhardwaj et al., 2011). Earlier studies have been specified the role of jasmonates in relieving chilling damage by stimulating the production of proteinase inhibitors, cryo-protective agents, polyamines, lower activity of LOXs, ABA and antioxidants (Gonzalez-Aguilar et al., 2000; Cao et al., 2009; Zhao et al., 2013). The role of jasmonic acid in increasing the freezing tolerance has also been tested in rice seedlings. It has been stated that the jasmonic acid application in low dosage before chilling stress considerably enhances the survival ratio of chilled rice seedlings (Lee et al., 1997). It was also detected that jasmonic acid preserved the water status of chilled plants by inhibiting the stomatal opening and increasing hydrolytic conductivity (Acharya and Assmann, 2009).

4.5. Light stress

Plants have acquired diverse abilities to sense their environment and adapt their growth and development as required. The diverse utilization of solar light for photosynthetic activities as well as a signal to organize physiological responses to the environment is an excellent example of such ability. Light quality and quantity inputs are altered to developmental outputs predominantly through hormonal signaling pathways (Svyatyna and Riemann, 2012). In general, plant hormones play some important roles in converting photon inputs into productions that array plant growth and development. The relationship of light quality and biosynthesis of jasmonates has been reported by Moreno et al. (2009). One of the light depended developmental plant response is the shade avoidance syndrome (SAS). This response is generally adjusted by the plant growth regulators such as auxin, brassinosteroids, cytokinins, jasmonates and ethylene. Recent studies also implicate that the jasmonates have an important role in light-dependent responses, including SAS in plants. Some of the plants under the shade and dim light stress, alter their gene expression pattern by Jasmonate signals. Increasing jasmonate biosynthesis in plants enhances some secondary metabolites such as phenolic components under the shade stress (Li and Kubota, 2009). Accumulation of jasmonates in plant leaves also increases the thickness of leaves under the shade stress. The biochemical, morphological and molecular events related to sensing of jasmonate signals have recently been updated with the detection of a family of low weight proteins known as JAZ (Jasmonate Zim-Domain) proteins in Arabidopsis (Pauwels et al., 2010; Kazan and Manners, 2011). Some of these actions may be necessary for escaping pathogen attacks, because under the shade condition, pathogen and pest populations can quickly rise due to the increased humidity at the lower canopy.

Sunlight is an important motion and energy input for plant growth, but, excessive light intensity has the potential to harm the photosynthetic systems. Excessive light intensity also stimulates systemic light-responsive gene expression which supports the plant to acclimatize to excessive light intensity stress. Excessive sunlight intensity can enhance the endogenous content of jasmonates in plant cells by a positive feedback. Zinc-finger transcription factor (ZAT 10) can overexpress under excessive light intensity in Arabidopsis (Rossel et al., 2007). ZAT10, made by 12-oxo-phytodienoic acid, is an intermediate of JA biosynthesis (Taki et al., 2005). This result indicates that ZAT10 adjusting JA biosynthesis as part of a positive feedback circle through exposure to excessive light intensity. It is well-known that excessive light intensity has the potential to generate reactive oxygen species that oxidize polyunsaturated membrane fatty acids such as peroxidation of a-linolenic acid. Since jasmonate biosynthesis is controlled by substrate accessibility (Wasternack, 2014), it is reasonable to suppose that excessive light intensity can produce jasmonate precursors from chloroplast lipids by non-enzymatic reactions. A Previous report has also shown a light stress-mediated jasmonates biosynthesis in Arabidopsis plants via the fibrillins proteins (Youssef et al., 2010). These proteins are structural plastid proteins, which shows a positive reaction to excessive light intensity in plants. Expression of some jasmonate responsive genes such as VSP2 and LOX2 were reduced in jasmonate applied fibrillin RNAi plants (Youssef et al., 2010). In plant cells, anthocyanin is controlled by both light intensity and endogenous content of jasmonates (Devoto et al., 2005). An association between the light intensity and jasmonates signaling pathways was confirmed in previous works, proving that coronatine insensitive 1 was important for jasmonate-induced anthocyanin production in plant cells (Chen et al., 2007). This procedure requires the jasmonates and some light-responsive transcription factors such as PAP1 (MYB75), PAP2 (MYB90), bHLH and GL3 (GLABROUS3) (Shan et al., 2009), which regulate the phenylpropanoid metabolism in plant cells.

Ultraviolet-B (UV–B) radiation is another light dependent stress in plants. Most of the plant species, due to their eco-physiological nature are potentially very sensitive to Ultraviolet-B radiation, although the response varies among species and genotypes. This difference is completely dependent upon the biochemical, physiological and molecular responses of plant cells to implement the protective mechanisms against the UV-B radiation (Li et al., 1993). A light with a high level of UV-B radiation, is one of the main environmental factors in controlling plant

Table 4
Mechanisms of jasmonates in alleviation of heavy metal toxicity in different plant species.

Plant species	Heavy metal	Mechanisms	References
Glycine max	Nickel	Jasmonic acid enhanced the superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase activities, and reduced the reactive oxygen species generation in soybean plants. Also, this growth regulator stimulated the proline, glycine betaine, total protein, and total soluble sugar under nickel toxicity.	Sirhindi et al. (2016)
Solanum nigrum	Cadmium	Application of a low concentration of methyl-jasmonate considerably decreased the translocation and accumulation of cadmium in both the shoots and roots.	Yan et al. (2015)
Vicia faba	Cadmium	Jasmonic acid stimulated the antioxidative activities, proline and glycine betaine accumulation in plant tissues and biomass production under cadmium toxicity.	Ahmad et al. (2017)
Brassica juncea	Cadmium	Methyl-jasmonate protected the chloroplast structure against cadmium toxicity and increased the sulphur assimilation and glutathione production in *Brassica juncea*.	Per et al. (2016)
Glycine max	Nickel	Priming of soybean seeds with jasmonic acid significantly increased the growth of *Glycine* max under nickel toxicity. Jasmonic acid inhibited the nickel uptake and accumulation in plant tissues and reactive oxygen species generation.	Mir et al. (2018)
Glycine max	Nickel	Jasmonic acid enhanced the nickel toxicity in *Glycine* max by stimulating antioxidative activities, but this growth regulator did not change the photosynthetic pigments.	Sirhindi et al. (2015)
Brassica napus	Cadmium	Jasmonic acid reduced the cadmium uptake and increased the gas exchange capacity and photosynthetic pigments in leaves. Also, this growth regulator reduced the membrane damage and malondialdehyde content and increased the nutrient uptake.	Ali et al. (2018)
Vaccinium corymbosum	Aluminum	Low doses of methyl-jasmonate enhanced the content of phenolic compounds and antioxidative activities under aluminum toxicity.	Ulloa-Inostroza et al. (2017)
Phaseolus coccineus	Copper	Application of methyl-jasmonate stimulated the antioxidative activities in *Phaseolus coccineus*. Also, this growth regulator modified the organic acid production in *Phaseolus coccineus* under copper toxicity.	Hanaka et al. (2016)
Brassica napus	Arsenic	Methyl-jasmonate reduced the arsenic-induced oxidative damage and stimulated the ascorbate-glutathione cycle in *Brassica napus* plants.	Farooq et al. (2018)

physiology and phenology. Jordan et al. (2002) stated that UV-B radiation with up-regulation and down-regulation of gene expression in plant cells, alter their life events such as growth and flowering. Ultraviolet B photons with the high level of energy cause the release of the signal-transduction pathway by damaging the cell membrane and activating the lipases enzyme and the stress-inducible genes (Hidema et al., 2000), which might be the initial signal that activates the octadecanoid pathway. Hence, the response to UV-B radiation may be controlled by jasmonates derived from linolenic acid through the octadecanoid pathway. Galis et al. (2006) reported that under UV-B radiation jasmonate enhances the production of some phenylpropanoid components such as polyamines, and this effect was mediated by a methyl jasmonate-inducible transcription factor in *Nicotiana tabacum*. Some studies showed that a plant's endogenous jasmonic acid content increases under light stress (Haga and Iino, 2004; Riemann et al., 2007). However, little attention was paid to the influence of exogenous jasmonic acid on plant UV-B resistance. As far as we know, only Zhang and Ervin (2005) and Fedina et al. (2009) reported that exogenous jasmonic acid methyl ester could offset the effects of UV-B radiation by increasing the antioxidant defense, proline synthesis and improving photosynthetic activities of barley seedlings (Fedina et al., 2009).

4.6. Heavy metal stress

Heavy metal ions play an essential role in various metabolic processes, making them important in trace element quantities for the metabolism, growth and development. Heavy metals are only able to exert any stimulatory or inhibitory effect on plants if they are present in a form available to the plants. Heavy metal stress has a strong and quick reduction in plant growth, enhanced leaf senescence and inhibition of the photosynthetic process (Maksymiec, 2007). Xiang and Oliver (1998) stated that cadmium and copper toxicity in soil increased the jasmonates content in *Arabidopsis thaliana* plants. This improvement in jasmonate synthesis is related to enhancing lipoxygenase activity in this situation (Tamás et al., 2009). Heijari et al. (2008) found that low doses of exogenous methyl jasmonate decreased the harmful effects of aluminum toxicity by increasing non-enzymatic antioxidants such as phenolic compounds and enzymatic antioxidants such as superoxide dismutase. Future studies by Spollansky et al. (2000) and Xue et al. (2008) indicated that in *Brugmansia candida* and *Cassia tora*, foliar application of methyl jasmonate significantly improved the plant's tolerance to the aluminum toxicity via stimulating lignin accumulation in the cell wall, decreasing oxidative stress and increasing peroxidase activity. Foliar spray of jasmonates under the cadmium toxicity, caused mitigation of cadmium damages by the decrease of lipid peroxidation, reactive oxygen species generation and rise in activities of antioxidant enzymes in soybean leaves (Keramat et al., 2009). Application of jasmonic acid at low dosage is effective in protecting plants from copper toxicity by adjusting photo-synthetic pigments (Poonam et al., 2013). Aftab et al. (2011) showed that application of methyl jasmonate considerably reduced the boron toxicity in *Artemisia annua* plants by enhancing antioxidant activities. Farooq et al. (2016) indicated that jasmonate application excellently alleviated the harmful effects of arsenic stress on canola plants and improved the biomass and chlorophyll fluorescence and decreased the lipid peroxidation and reactive oxygen species generation. Poonam et al. (2013) reported that jasmonic acid priming improved the copper toxicity in *Cajanus cajan* (L.) Millsp. seedlings by improving chlorophyll biosynthesis and antioxidative activities. Some of the JA mechanisms on reducing harmful effects of heavy metals are shown in Table 4.

4.7. Flooding stress

In nature, water is essential for plant growth, but extra water caused by flooding can lead to adverse effects on plant growth. Plants have different adaptive mechanisms such as adventitious root development, aerenchyma development and control of shoot growth, to overcome the oxygen absence under waterlogging (Sachs, 2008). Flooding is defined as a situation in which only plant roots are exposed to excess water, which restricts gas dispersal in the rhizosphere (Armstrong et al., 1994; Setter and Waters, 2003). Oxygen dispersion in water is about 10,000 times slower than in the atmosphere (Armstrong et al., 1994); thus, oxygen absence is caused by submergence or waterlogging may damage the crops (Colmer and Voesenek, 2009).

The crosstalk between the jasmonates and ethylene production is essential for root and aerenchyma formation and development under waterlogging. Ethylene is involved in aerenchyma formation, which was first identified in 1933 (Zimmerman and Hitchcock, 1933). Since then, it has been well established that ethylene has a positive effect on aerenchyma development (Verstraeten et al., 2014). In fact, flooding-induced ethylene accumulation is responsible for aerenchyma formation (Vidoz et al., 2010). Foliar application of jasmonates increases the ethylene production (Hudgins and Franceschi, 2004). So, jasmonic acid could enhance the ethylene production, which is useful under flood stress. Application of jasmonates under flooding stress considerably decreased the harmful effects of this stress and stimulated the growth of soybean plants by changing the proteome profile (Kamal and Komatsu, 2016).

5. Conclusions

Jasmonates improve stress tolerance of plants by molecular and physiological changes occurring under adverse environmental conditions. Most of these superior effects of jasmonates are related to molecular and physiological alteration by down or up-regulation of gene expression. In general, most of the researchers who have studied the effects of jasmonates on plants under abiotic stresses, reported that these growth regulators reduce the generation of reactive oxygen species by enhancing antioxidants activities in various plants. Jasmonates also alter the synthesis of other growth regulators such as abscisic acid and ethylene by adjusting interior signal transduction under harsh environment. Both of these hormones are involved in the rising stress tolerance of plants under different abiotic stress conditions. Future works could be focused on molecular levels of these physiological alterations by jasmonates under various environmental conditions, in order to improve our knowledge about the mechanisms of these growth regulators signaling in different plant species.

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