

REVIEW

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Plant response to jasmonates: current developments and their role in changing environment

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Abstract

Jasmonates (JAs) are universally known lipid-derived phytohormones which regulate overall plant growth under both abiotic and biotic stresses. They are helpful in developing root and reproductive system in plants. Also, JA signaling triggers gene expression. They coordinate with other plant hormones under changing environmental conditions. JAs alone or sometimes in combination with other plant hormones ameliorate stress conditions. They also participate in upregulation of antioxidant metabolism, osmolyte synthesis, and metabolite accumulation. Pretreatment and/or exogenous application of JA exhibited multi-stress resilience under changing environment as well as other biotic stress conditions. The present review focuses on our current understanding of how plants respond to JAs' application under extremely low or high temperature, highly alkaline condition, or even when attacked by herbivorous insects/animals. As a consequence of injury, the plant produces defense molecules to protect itself from damage. Their major role and mechanism of action under heavy metal/metalloid-induced toxicity have also been discussed.

Keywords: Jasmonates, Hormones, Signaling, Plant growth and development

Background

Plants are exposed to a variety of abiotic and biotic stresses such as drought, salinity, acidity, flooding, cold, heat, metal, and metalloid-induced toxicity. These stresses adversely influence the growth and yield of plants (Husen et al. 2014; Getnet et al. 2015; Embiale et al. 2016; Bernal-Vicente et al. 2018; Yurchenko et al. 2018; Balfagón et al. 2018). Even though plant hormones are produced in very low amounts, they regulate many external and internal stimuli (Kazan 2015; Siddiqi and Husen 2017; Pandey et al. 2017; Husen et al. 2018, 2019; Pandey et al. 2017; Podlešáková et al. 2019). They play a vital role in saving the plant from stress and improve quality of crops (Kazan 2013; Santino et al. 2013; Colebrook et al. 2014; Husen et al. 2016, 2017, 2018; Hanaka et al. 2018).

Jasmonic acid (JA) and its cyclopentanone derivatives are produced by plants. They are collectively known as

jasmonates (JAs). These multifunctional hormones are involved in plant development and defense processes (Seo et al. 2001; Huang et al. 2017; Per et al. 2018). Besides developmental functions of plants, JAs activate plants against pathogens and environmental stresses (Pauwels et al. 2009; Seo et al. 2011). It has also been reported that JAs are signaling hormones induced under stress and respond quickly to them (Du et al. 2013). They are involved in plant development, reproduction (Wasternack 2007; Browse 2009) floral development, growth inhibition, fruit ripening, tendril coiling, potato tuberization, trichome formation, and fungi arbuscular micorrhizal association (Browse 2005; Balbi and Devoto 2008; Reinbothe et al. 2009; Yoshida et al. 2009). JA also acts as a regulator of leaf and root morphogenesis in soybean (Xue and Zhang 2007) and control plant fertility. It has been found that *Arabidopsis* mutants deficient in JA synthesis are male sterile (Ishiguro et al. 2001; Park et al. 2002; von Malek et al. 2002). JA also controls overall development related to expression of numerous genes in stamen tissue (Song et al. 2011).

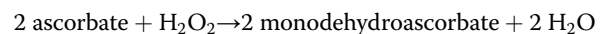
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Per et al. (2018) have reported specific role of JA under abiotic stress. However, Kazan (2015) has reviewed the diverse roles of JA and ethylene in abiotic stress tolerance. JA and ethylene regulate root development and anthocyanin accumulation which may be associated with abiotic stress tolerance. Biotic stress in plants is caused by viruses, bacteria, fungi, nematodes, parasites, and insects/pests. In order to protect themselves, plants develop a mechanism in defense. Such responses are mediated by JA, salicylic acid (SA), brassinosteroids, ethylene, polyamines, and abscisic acid (ABA) acting as primary signals in regulation of plant defense. For instance, defense response against biotrophic pathogens is mediated by SA (Durrant and Dong 2004) while JA and ethylene mediate responses against necrotrophs (Glazebrook 2005). However, attack by pathogens and mode of defense by plants may vary from species to species. JAs have also been examined for secondary metabolite production. Ren and Dai (2012) have reported that JA involved in the signaling pathway for fungal (AL12 - *Gilmaniella* sp.) endophyte-induced volatile oil from *Atractylodes lancea* plantlets exhibits antimicrobial activity. Secondary metabolites (terpenes, flavonoides, and alkaloids) present in the oil are supposed to be involved in plant responses to biotic and abiotic stresses (Rodriguez et al. 2009; Mucciarelli et al. 2007; Wang et al. 2010). Plants produce JA in defense during infection or any treatment. Other signaling molecules have also been found to be associated with secondary metabolism (Yuan et al. 2001; Nojiri et al. 1996; Gao et al. 2012). For instance, SA activates defense-related genes, which, in turn encode pathogenesis related proteins (Van and Van 1999). Kunkel and Brooks (2002) have shown that fungal elicitor caused increase in JA production, secondary metabolites biosynthetic gene expression, and metabolite accumulation in many plants. Ren and Dai (2012) have found that when endophytic fungus was inoculated in *A. lancea*, it triggered JA biosynthesis which increased quantity of oil in the plant. Besides, JA, NO, H₂O₂, and SA are also known to mediate the signaling pathway in *A. lancea* plantlets (Wang et al. 2011a). However, JA may act as downstream signal of NO while H₂O₂ acts as intermediate factor between JA and NO. It has been observed that H₂O₂, SA, and JA may work together in fungus-induced volatile oil synthesis in *A. lancea* plantlets. However, it has been reported previously (Wang et al. 2011b) that NO mediates volatile oil accumulation induced by fungus via SA- and H₂O₂-dependent pathways. JA and SA are equally important signaling molecules in plant defense responses. When the biosynthesis of one component such as JA is suppressed by some inhibitor, accumulation of SA is enhanced and vice versa. Thus, JA works as a downstream signaling molecule in NO and H₂O₂ mediates volatile oil accumulation induced by entophytic fungus. JA synthesis occurs through

oxylipin biosynthesis pathway (Wasternack 2007; Gfeller et al. 2010) during herbivore attack. The effects of methyl jasmonate (MJ), JA, and *cis*-jasmone on anthocyanins and procyanidins have been studied (Horbowicz et al. 2009). JAs either as in the form of solution or vapor has been applied (Horbowicz et al. 2009). JA stimulated the anthocyanin accumulation when applied as solution but when used as vapor, it decreased the accumulation in *Fagopyrum esculentum* hypocotyls. JA solution had negligible effect on biosynthesis of anthocyanins in buckwheat seedlings. MJ works by moving in both phloem and xylem perhaps due to a difference in biochemical behavior (Zhang and Baldwin 1997). In another experiment, 21-day-old melon (*Cucumis melo*) cells treated with JA at very low concentration (0.5, 5.0, and 10 μmol) were checked for defense-related factors like antioxidant enzymes, ascorbate metabolism, and phenolic compounds. It was found that JA induced primary and secondary metabolism in melon cells (Nafie et al. 2011) by producing bioactive molecules in defense. Melon cells exhibited enhanced oxidative enzyme activities and ascorbic acid, coumarin, and p-coumaric amounts without growth retardation. Induced intracellular JA functions as signal transducer acting upstream to H₂O₂ and regulate the antioxidant activity of catalase (CAT), peroxidase (POD), and synthesis of five isozymes and ascorbic POD detoxifying enzymes. It is certain that the production of secondary metabolites in melon cells is activated by JA and induces melon resistance. CAT activity was increased by 24% at 10 μmol JA. JA application stimulates many responses in plants including synthesis of hormones, gene expression, crop production, and defense against biotic/abiotic stress (Ahmad et al. 2016). JA increased the POD activity up to 137% after 24 h. The enzyme activity revealed the presence of five POD isoforms. Ascorbate peroxidase (APX), ascorbic oxidase, and glutathione reductase (GR) also increased. APX helps in detoxification of H₂O₂ according to the reaction given below:



Hamberg and Gardner (1992) have reported that hydroxylated JA derivatives are more useful and regulate tuber formation in potato, but the process is also controlled by light, temperature, and gibberellic acid (Lin et al. 2013). It means that JAs control tuber formation indirectly through crosstalk with GA signaling (Wasternack and Hause 2013). Reactive oxygen species (ROS) is generated under stress, causing damage to plants by oxidation of lipids, proteins, and nucleic acid (Gille and Singler 1995; Gill and Tuteja 2010). JA and MJ also increase antioxidant activity in raspberry fruit (Ghasemnezhad and Javaherdashti 2008). JAs also increase resistance of plants against pests in field pots of tomato (Thaler et al. 2001). They also provide resistance to edible plants and vegetables against fungi and nematodes

(Schmelz et al. 2002; Soriano et al. 2004). MJ and *cis*-jasmonone (James 2005) have also been shown to repel herbivores in plants. Effect of different concentrations of JA on the growth of flower, height, and weight of marigold plant has been reported. JA increases the dry weight of flower, plant height, and 1000 seed weight (Ataei et al. 2013). Height and weight increased with increasing concentration of JA and attained maximum at a concentration of 150 μ M JA. The number of flowers also increased but carotenoids decreased with increasing concentration of JA above 75 μ M. JA regulates photosynthesis but MJ and JA together increase plant resistance to infection by green mold (Rohwer and Erwin 2008). Sasaki-Sekimoto et al. (2005) have demonstrated that ozone exposure caused induction of numerous genes involved in antioxidant metabolism in the wild type. But, in JA-deficient *Arabidopsis* 12-oxophytodieneoate reductase 3 (*opr3*) mutants, the induction of antioxidant genes was stopped. *Arabidopsis opr3* mutants were found to be more sensitive due to ozone exposure in comparison to wild type. It has been suggested that the coordinated activation of the metabolic pathways mediated by JAs provides resistance to under stress conditions.

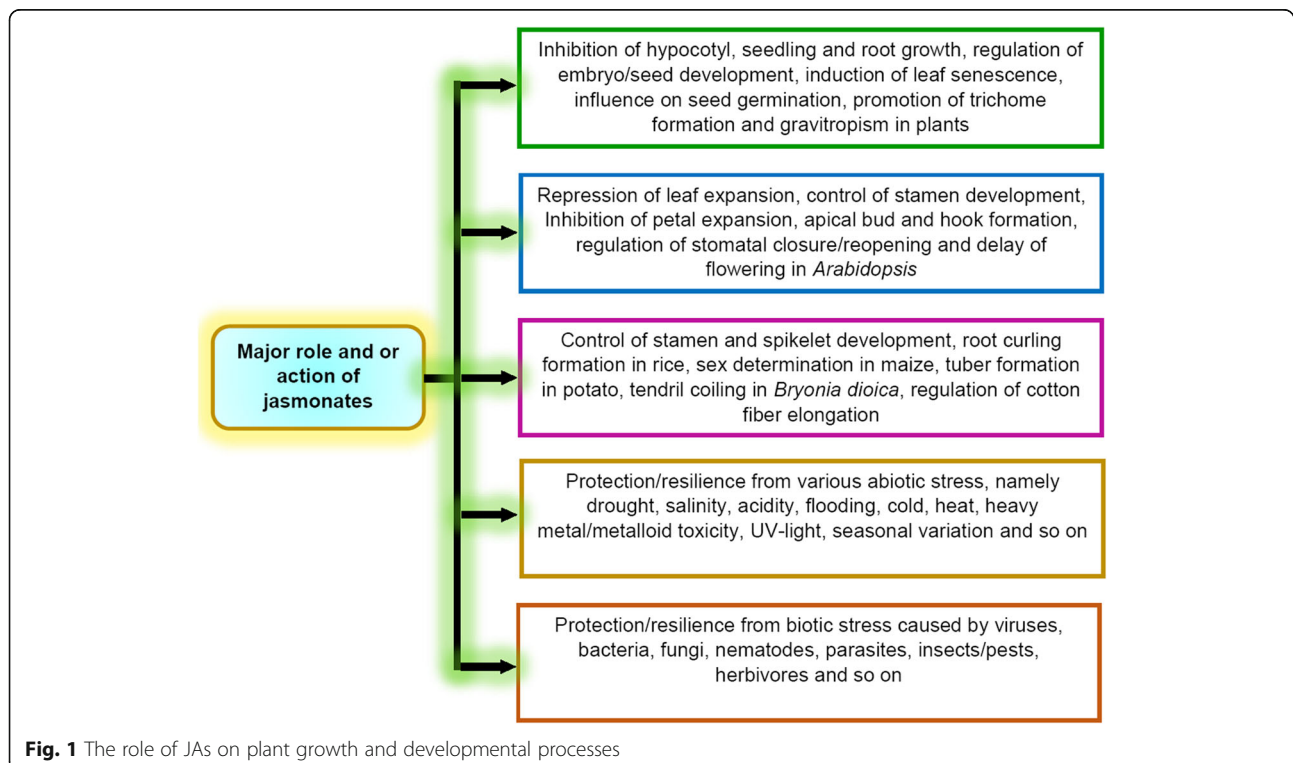
Although, cancer preventive effect of some vegetables such as broccoli, cauliflower, or cabbage is known (van Poppel et al. 1999), the chemical responsible for it has recently been explored (Farooqi et al. 2012). JAs have been found to be active against several human cancer cell lines (Cohen and Flescher 2009). The activity is due

to interference of JAs with energy metabolism mitochondrial perturbation and production of ROS leading to cell death. JA, MJ, and *cis*-jasmonone are highly effective in cancer therapy. Extract from *Viscum album*, *Jasminum*, *Chloranthus*, *Cymbidium*, *Rosmarinus*, and *Lonicera* plants contain fairly large quantity of JA and MJ. Activity mediated by JA/MJ is given by its induction of biosynthesis of glucosinolates in cruciferous vegetables. Treatment of cauliflower by MJ before harvesting increased glucosinolate up to 5-fold and increased marker enzymes of anticancer bioactivity (Ku et al. 2013).

In this review, we have discussed the current status of the application of JAs in plants and their response under changing environmental conditions. Moreover, a summary of major role of JAs on various plant growth and developmental processes is presented in Fig. 1.

Biosynthesis of JA

Most fascinating and interesting role of JA includes plant stress responses, signaling, and metabolic pathways. Several processes such as seed germination, root growth, flower development, and tuber formation have been shown to be regulated by JA/JA-Ile (*N*-jasmonoyl-L-isoleucine). JA/JA-Ile are involved in metabolic function, signaling, and interaction with other hormones (Katsir et al. 2008; Kombrink 2012; Pieterse et al. 2012). Fatty acid substrate of JA biosynthesis is α -linolenic acid (Ahmad and Jhon 2005; Cervilla et al. 2007) which is released from galactolipids of chloroplast membranes.



Phospholipase 1 is responsible for generation of the JA substrate. Wound- and pathogen-induced biosynthesis of JA is faster (Yang et al. 2007) where unidentified lipases may be involved (Ellinger et al. 2010). Acids and enzymes are released upon stress as a defense signal (Jung et al. 2009; Zoeller et al. 2012). Ca^{2+} -dependent protein kinases are negative regulators in wound and herbivore-induced JA accumulation (Yang et al. 2012). A wound-induced protein kinase (WIPK) is quickly activated around the wound inducing JA biosynthesis (Wu et al. 2007). Per et al. (2018) have recently reviewed the biosynthesis of JA. The mechanism underlying the synthesis and signaling pathway has been discussed (Fig. 2). First step in the biosynthesis of JA involves oxidation of phospholipid α -linolenic acid, in the presence of phospholipases to 12-oxophytodienoic acid (Bannenberg et al. 2009). After a chain of oxidation reactions in the presence of various enzymes, JA and its derivatives are produced (Kombrink 2012; Wasternack and Hause 2013).

Role of JA under changing environment

Plants under adverse environmental conditions regulate their developmental and physiological processes. Such conditions are often correlated with global warming (climate abnormalities) which directly or indirectly lead to the concurrence of a number of stresses. They also influence plant growth and productivity. JA is a proven

endogenous regulator of stress responses and overall plant growth and productivity.

Role of JA under salinity stress

Salt stress in plants is caused mainly owing to high Na^+ and Cl^- ion concentrations in the soil. Na^+ retained in the woody roots and Cl^- accumulated in shoots caused severe damage to plants (Moya et al. 2003). Salt stress decreases the dry weight of root/shoots and root length, but there is a simultaneous decrease in K^+ , Ca^{2+} , and Mg^{2+} concentration in shoots of plant (Munns and Termaat 1986; Yeo and Flowers 1986). Kang et al. (2005) have investigated the effect of salt stress and recovery by applying JAs to two different rice (*Oryza sativa*) cultivars, Dongjinchalbyeo (DJC, salt tolerant), and Dongjinbyeo (DJ, salt sensitive). Salt stress significantly decreased the root length of plants even at very low NaCl concentration (20 mM) with a simultaneous increase in the ABA concentration. ABA concentration in the salt tolerant variety of rice increased with increasing NaCl concentration while in salt sensitive cultivar, ABA sharply decreased in all parts of rice plants. JA was found to decrease in both the salt sensitive (DJ) and salt tolerant (DJC) rice cultivars. Post application in stressed plants with 30- μ M JA and 24 and 4 h after NaCl treatment, removed salt inhibition on dry mass production more effectively than prior application of JA, before salt stress. Uptake of Na decreased with a consequent increase in Ca, Mg levels, and a little increase in K by JA application. Salt-

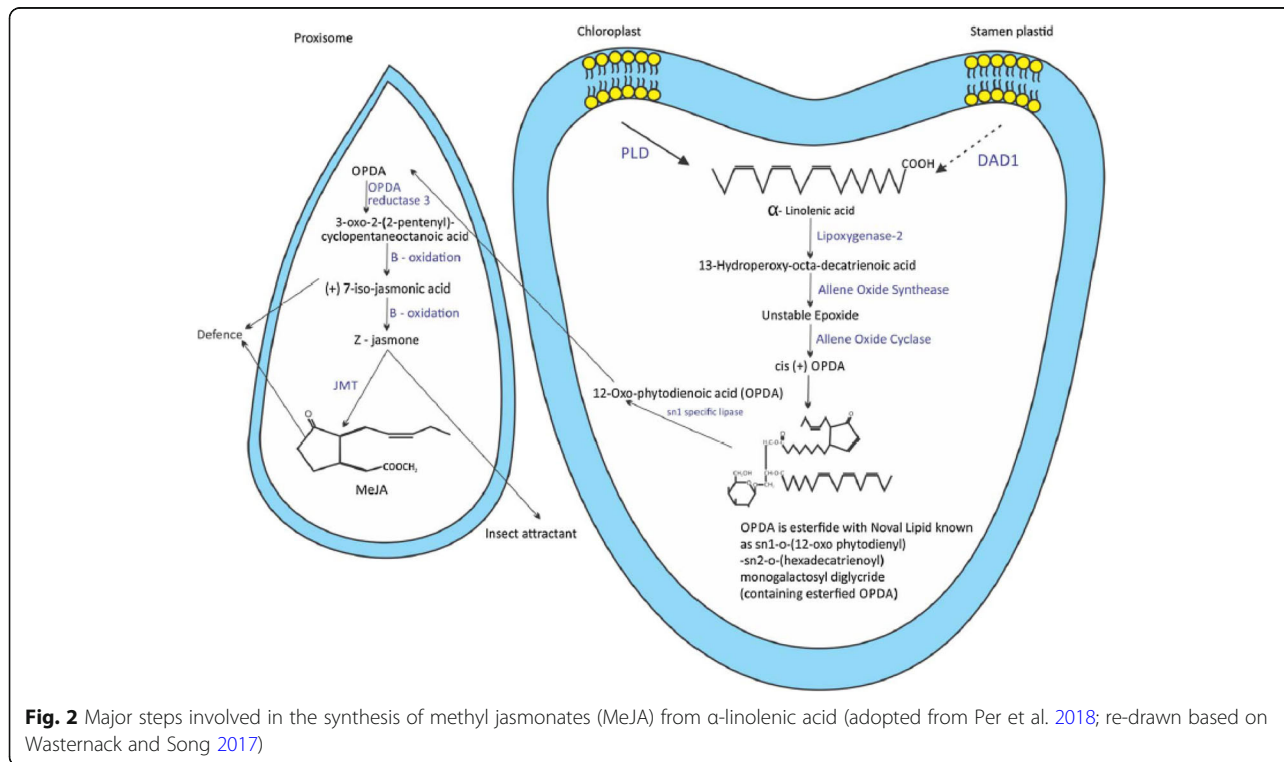


Fig. 2 Major steps involved in the synthesis of methyl jasmonates (MeJA) from α -linolenic acid (adopted from Per et al. 2018; re-drawn based on Wasternack and Song 2017)

sensitive cultivar accumulated more Na^+ than salt tolerant cultivar plants in the roots and shoots after NaCl treatment. Taken together, JA improved recovery of salt-stressed rice seedlings. Walia et al. (2006) have reported that the induction of JA-responsive genes in barley was considered as a crucial aspect under salinity. They (Walia et al. 2007) have further reported that three JA-regulated genes activate arginine decarboxylase and apoplasmic invertase which were probably involved in salinity tolerance mediated by JA. It has been reported that leaves accumulate ABA at high level under salt stress (Hurkman and Tanaka 1996; Moons et al. 1997). ABA accumulation is very sensitive to dehydration of leaf tissue. It also helps in triggering gene expression upon wounding and pathogenic infection (Moons et al. 1997). ABA causes stomatal closure (during dehydration/water stress) preventing loss of water through transpiration under water stress imposed by high NaCl concentration (Zeevaart and Creelman 1988). When JA is applied under stressed condition of plants, the conditions are reversed.

Yoon et al. (2009) have studied the influence of NaCl stress on soybean and reduction in stress by MeJA application under hydroponic condition. A very low concentration was applied to soybean seedlings under NaCl stress. It induced appreciable reduction in plant growth, endogenous bioactive gibberellin (GA), photosynthesis, and transpiration rate with a consequent increase in endogenous ABA and proline contents. Salt stress has been shown to reduce the biomass of tomato (Kaya et al. 2001), pea (Ahmad and Jhon 2005), and rice (Yeo et al. 1999) even though shoot dry weight is more sensitive to salinity than root dry weight (Essa 2002). However, the effect of salt stress was insignificant on root dry weight of soybean. MJ application induced ABA production in soybean stressed plant as a defense mechanism.

Most edible plants and vegetables exhibit limited growth and development in highly saline soil. High salinity has been reported to cause reduction in growth, lipid peroxidation, and H_2O_2 accumulation (Charparzadeh et al. 2004). It has also been reported that with increasing concentration of NaCl soluble proteins, sugars and total free amino acids including proline were progressively accumulated in alfalfa (Antoline and Sauchez-Dais 1992). JAs may act as modulator by suppressing the stress responses of plants (Popova et al. 1995). Sheteawi (2007) has investigated the possible ameliorative effect of JA and ascorbin (ascorbic acid + citric acid, 2:1) on NaCl stressed soybean. He noted that JA mitigated the inhibitory effect of NaCl on the growth parameters of soybean. Foliar spray or seed soaked in JA showed better growth. Fresh growth (174%) and dry weight of the plant (129%) were increased when soybean plant stressed with NaCl was sprayed with ascorbin (Khan et al. 2003). However, plants salinized with 100 mM NaCl showed stunted growth even when sprayed with ascorbin or JA perhaps due to high salinity beyond tolerance limit of plant

(Cherki et al. 2002). Ascorbin or JA in salt-stressed plants act as antioxidant and protect them from damaging by salinity. They also increased the N, P, and K level in soybean and enhanced accumulation of non-toxic metabolites such as proteins, sugars, and proline.

In an experiment foliar application of JA was done on wheat seedlings for 3 days and subsequently subjected to NaCl solution (Qiun et al. 2014). Salinity thus produced decreased plant height, root length, shoot and dry weight, chlorophyll b, and carotenoid. The superoxide dismutase (SOD), POD, CAT, and APX activities were decreased under salt stress in wheat seedlings. Exogenous JA coupled with NaCl treated wheat seedlings showed significantly increased level of SOD, POD, CAT, and APX activities. Expression level of SOD, POD, CAT, and APX genes was significantly upregulated in wheat seedlings under salinity stress even when seedlings were not pre-treated with JA. It has been noted that exogenous JA treatment neutralize NaCl-induced oxidative stress which is reflected by a decrease in MDA and H_2O_2 concentration and the production rate of peroxide radical. Thus, JA helps in scavenging free radicals preventing lipid peroxidation by excess ROS produced during salinity stress. SOD acts as an antioxidant in plant cells, and its activity is increased in wheat seedlings treated with exogenous JA (Qiun et al. 2014). Exogenous JA also enhances APX, CAT, and POD activities in wheat seedlings (Qiun et al. 2014) similar to that observed by Noriega et al. (2011) in the case of soybean under cadmium stress. Enhancement in activity of above enzymes in soybean and wheat is a consequence of defensive mechanism under salt and drought stress (Anjum et al. 2011). Thus, exogenous JA application in wheat seedlings can enhance their tolerance to salt stress which is indicated by decreasing concentration of MDA and H_2O_2 , etc. During salinity stress, forced uptake of Na^+ ions into cytoplasm acts as a signal, triggering salinity adaptation (Ismail et al. 2014). Sodium ion concentration also increases during drought condition similar to that produced during salinity.

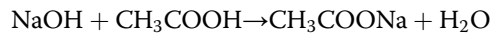
High $[\text{Na}^+] \rightarrow$ cytoplasm signal triggering salinity adaptation

Alkalinity and salinity stresses are synonymously used though in terms of pH they are different except that sodium ion concentration is identical for a given concentration of NaCl and NaOH (Wang et al. 2011a, 2011b). The alkaline sodium stress is therefore worse than saline stress because the soil becomes highly basic as shown below:



The OH^- ions actually precipitate the essential nutrients and trace elements in the soil preventing their absorption by plants (Li et al. 2009). However, organic acids may

neutralize a small fraction of OH⁻ ions in the soil according to the following equation.



JA at this stage sends adaptation signals such as stomatal closure to prevent loss of water by transpiration. ABA helps in closing and opening of stomata during drought and high salinity since it is accumulated in plants under stress. Closing/opening of stomata depends on the ionic concentration of Na and Ca ions and the osmotic pressure. JA contents also increase in maize root cells under drought conditions (Xin et al. 1997). Exogenous application of JA and MJ increases antioxidative activity of plants under water stress (Bandurska et al. 2003) because it enhances the activity of antioxidative enzymes (Nafie et al. 2011). However, JA under normal conditions can enhance the growth and yield but this process under saline and drought condition is delayed. Kim et al. (2009a) have studied the influence of JA on endogenous gibberellin acid and ABA in salt-stressed chard plant. They have shown the effect of JA application before and after the stress produced by NaCl. Endogenous ABA content was increased by JA treatment (75%). Similar result has also been reported by Wang et al. (2001). Exogenous application of MJ significantly mitigates salinity stress symptoms in soybean seedling (Yoon et al. 2009). Ahmad et al. (2018) have reported that the exogenous application of JA and NO alleviated NaCl toxicity in tomato by controlling the antioxidant metabolism, osmolyte synthesis, and metabolite accumulation. Mir et al. (2018) have also suggested that the pretreatment of maize seedlings with JA mitigated the toxic effects of excessive Na₂CO₃ on plant growth and photosynthesis. Yuan et al. (2018) have also reported that the exogenous application MJ alleviates the reduced growth of *Limonium bicolor* under salt stress. They have shown that the exposure of 300-mM NaCl inhibited seedling growth, while adverse effects of NaCl was mitigated by the exogenous application of 0.03-mM MeJA, resulting in a biomass close to the control plants. In a very recent study, Liu et al. (2019) have reported that a moss jasmonate ZIM-domain gene acts as a repressor, mediates JA-ABA synergistic crosstalk, and enhances plant growth under salt stress. However, for better understanding, the molecular mechanism of the interaction between ABA signaling and JA signaling is still need more investigation.

Role of JA under drought stress

Stomatal closure in plants limits the transpiration to retain water under drought conditions. ABA interacts with other plant hormones like JA and NO to stimulate stomatal closure. Stress-induced production of JA interacts

with ABA-mediate stomatal closure by stimulating the influx of extracellular Ca²⁺ or/and by activating H₂O₂/NO signaling (Harrison 2012). Many JA-associated signaling genes are regulatory drought stress (Huang et al. 2008). Stomatal aperture of *Arabidopsis* leaves has been found to be drastically reduced when treated with MJ for 10 min (Munemasa et al. 2007). It has been hypothesized that both ABA and MJ interact in guard cells and induce the formation of ROS and NO. Kim et al. (2009b) have shown that drought stress induces 19-fold increase in MJ level and 1.4-fold increase in ABA levels. These hormones affect the grain yield and their own biosynthesis. The plant hormone ABA, as a stress signal, also increases during water stress. ABA can also induce the expression of antioxidant gene encoding APX and GR in seedlings (Jiang and Zhang 2002; Hu et al. 2007). JA is helpful in regulating plant response under water scarcity (Liu et al. 2005). Water deficiency also cause damage to growing leaves due to induced osmotic effect which, in turn causes proline accumulation. It could be reversed after desalination (Nandwal et al. 2000). It has been practically demonstrated that under water scarcity induced by PEG 6000 in *Agropyron cristatum*, JA level, the transcript level, and activities of ascorbate peroxidase (APX), GR, monodehydroascorbate reductase, dehydroascorbate reductase (DHAR), L-galactono-1,4-lactone dehydrogenase, and γ-glutamylcysteine synthetase and ascorbic acid, glutathione, total ascorbate, and total glutathione were increased (Shan and Liang 2010). MJ treated *Allium sativum* L. under drought stress showed increase in shoot, root, and bulb growth (Bideshki and Arvin (2013). Total chlorophyll, anthocyanins, membrane permeability, root length, and growth were also significant. However, a combination of indole 3-butyric acid (IBA) and MJ is more effective for growth promotion under normal condition. However, IBA alone is ineffective under stress, although MJ enhances both the growth and yield.

Role of JA under heavy metal/metalloid induce toxicity

Although many metal ions are essential nutrients some are toxic to both plants and animals (Hou et al. 2007; Asgher et al. 2015; Iqbal et al. 2015). Excess of essential metals or even metalloid induce toxicity in plants, which may result into oxidative stress leading to physiological changes (Dhankar and Solanki 2011). JA application, however, enhanced accumulation of osmolytes while carotenoids enhanced antioxidant enzyme concentration which prevented the plants from damage by excess metal ions (Poonam et al. 2013). Pigeon pea exposed to JA showed accumulation of proteins (and total chlorophyll, carotenoids) and reduced the effect of copper (II) on the growth of seedlings. Excess cadmium produces ROS, H₂O₂, and superoxide radicals which cause oxidative damage in plants (Gallego et al. 2012). However, MJ application

reduces this damage by about 30% in soybean and *A. thaliana* (Maksymiec et al. 2005). Excess boron in the soil may be absorbed by plants and can cause visible damage such as leaf burn, decreased fruit size (Paull et al. 1992; Nable et al. 1997) besides ROS production in wheat, (Gunes et al. 2007) barley (Inal et al. 2009), and tomato (Cervilla et al. 2007). Foliar spray of MJ alleviated the above symptoms significantly by stimulating the antioxidant production with a consequent reduction in lipid peroxidation. Heavy metal stress is also alleviated by activating the antioxidant system (Yan et al. 2013). MJ strengthened tolerance in *A. thaliana* plants against copper and cadmium stress through accumulation of chelating ligands which form complex with metal ions and prevent their availability to plant. Singh and Shah (2014) reported that under cadmium stressed *O. sativa*, application of MJ exhibited remarkable changes in activity of CAT, SOD, and GR paralleled with increased glutathione pools. MJ application at 0.1 μM concentration increased plant dry weight, leaf chlorophyll content, CAT, and APX activity in Cd-treated *Capsicum frutescens* (Yan et al. 2013). Yan et al. (2015) also reported that MJ at 1.0 and 10 μM concentrations decreased uptake of Cd and increased APX activity in *Avicennia marina*. In another study, Chen et al. (2014) showed that exogenous application of MJ in *Kandelia obovata* also maintained endogenous level of JA, controlled stomatal closure, reduced transpiration rate, prevented the uptake of Cd, and reduced photosynthetic damage. Ahmad et al. (2017) have also suggested that JA mitigates the deleterious effects of Cd stress in *Vicia faba* by preventing the accumulation of Cd, H_2O_2 , and MDA and by increasing proline, glycine betaine, SOD, CAT, APX, and GR activities which reduced the oxidative stress. Recently, Farooq et al. (2018) have also reported that exogenous application of MJ to *Brassica napus* plants alleviated the arsenic-induced oxidative stress and improved overall plant growth and photosynthesis.

Role of JA under cold and heat stress

Cold stress (chilling and freezing) affect crop productivity because many crops are sensitive and intolerant to low temperature. Acute temperature variation damages the plants (Schwartz et al. 2006). Usually, chilling and freezing stress lead to chlorosis, necrosis, membrane damage, changes in cytoplasm viscosity, and changes in enzyme activities (Ruelland and Zachowski 2010) leading to death of plants. Plants are therefore forced to adaptation to cold stress, and they have evolved many tolerance mechanisms to survive under adverse environmental conditions (Shinozaki et al. 2003). Experiment on *Arabidopsis thaliana* belonging to Brassicaceae family showed variation in JA and other hormones under chilling and freezing conditions (Kolaksazov et al. 2013). All tolerant and non-tolerant plants showed very high level of JA at normal temperature of 22 °C. After chilling stress at

4 °C, the tolerant plants did not show considerable change in JA relative to 10-fold reduction in non-tolerant plants. Upon exposure to frost (below 0 °C), JA content drastically dropped in tolerant plants while the non-tolerant plants had nearly the same level of JA. It indicates that in *A. thaliana*, JA may be the principal jasmonate mediator of the cold stress.

MJ can reduce the negative effect of chilling injury in crop plants. For instance, JA induces accumulation of resveratrol in *Vitis vinifera* which is a healthy compound for human consumption (Verpoorte et al. 2000). It also induces the formation of many compounds of pharmaceutical interest and antioxidants such as flavonoids and vitamins (Martin et al. 2013). MJ reduces chilling injury in *Cucurbita pepo* through its regulation of ABA and polyamine levels (Wang and Buta 1994). MJ delays the onset of chilling injury symptoms in *C. pepo*. MJ-treated plants/fruits showed an increase in ABA level upon exposure to 5 °C which indicates that it may stimulate ABA synthesis at chilling temperatures. However, the treated and untreated samples had identical increase in putrescine level with a simultaneous decrease in spermidine and spermine contents. MJ and AA have similar effects in reducing chilling injury (Parthier et al. 1992). MJ can also enhance the accumulation of ABA in the exocarp tissue of Zucchini squash (Wang and Buta 1994). Perhaps MJ causes an alteration in tissue metabolism followed by an increased synthesis in ABA at chilling temperatures. MJ may act as second messenger of plants to transduce signals and facilitate the expression of defense genes in response to various stresses (Farmer et al. 1992; Gundlach et al. 1992; Reinbothe et al. 1993).

Like cold stress, heat stress also affects plant growth and development. Plants generally develop tolerance against these extreme variations in temperature. Heat stress leads to undesirable changes in plant growth at cellular level impairing cell homeostasis (Bokszczanin et al. 2013). Usually, high temperature forces a plant to synthesize heat shock proteins (HSPs) which prevent denaturation and assist refolding of damaged proteins (Boston et al. 1996). Clarke et al. (2009) have reported that JAs produce thermo tolerance in plants. Exogenous application of low dose of MJ has been shown to maintain the cell viability by controlling electrolyte leakage in heat stressed *A. thaliana* plants (Clarke et al. 2009). Nevertheless, expression of JA inducible gene *PDF1.2* was observed after heat stress exposure. Further, Clarke et al. (2009) have reported the proof of involvement of JA in thermotolerance from mutant analysis of SA and JA signaling mutants (*coi1-1*, *opr3*, and *jar1-1cpr5-1*). In another study, Du et al. (2013) have reported that several genes are involved in JA biosynthesis and signaling were induced by drought and cold treatment, but these genes were suppressed by heat stress in rice plants.

It was found that the endogenous JA level was increased under drought/cold stresses, but JA level was decreased under heat stress. The role of HSP90 and HSP70 in JACOR responses in HSP90 RNAi lines showing reduction in transcript levels of JA in *A. thaliana* has also been reported (Zhang et al. 2015). In a recent study, Hou et al. (2018) concluded that lipoxygenase positively contributed to high temperature response and exogenous MJ or SA stimuli. However, exogenous MJ or SA plays a promoting role on its corresponding endogenous phytohormone accumulation in *Gracilariopsis lemaneiformis* (red alga).

Conclusion

Jasmonic acid and its methyl ester play a significant role in plant growth and developmental processes under changing environmental as well as other biotic stresses. It has been established that JAs are emerging players in alleviating the deleterious effects under adverse conditions. They induce resistance against many biotic stresses. In plant systems, they regulate gene expression which controls overall plant growth, antioxidant metabolism, osmolyte synthesis, metabolite accumulation, and physiological parameters. Thus, these findings are useful in the development of resilient plants by genetic engineering/manipulation of JA biosynthesis. These hormones are produced only under abnormal conditions such as heat, cold, or salinity to protect the plant and induce resistance against pests and insects. Moreover, under changing environmental condition, JAs' networking and their crosstalk with other plant hormones needs further investigation.

Abbreviations

ABA: Abscisic acid; APX: Ascorbate peroxidase; CAT: Catalase; GA: Gibberellic acid; GR: Glutathione reductase; H₂O₂: Hydrogen peroxide; IBA: Indole 3-butyric acid; JA: Jasmonic acid; JA-Ile: N-jasmonoyl-L-isoleucine; JAs: Jasmonates; MJ: Methyl jasmonate; NaCl: Sodium chloride; NO: Nitric oxide; POD: Peroxidase; ROS: Reactive oxygen species; SA: Salicylic acid; WIPK: Wound-induced protein kinase

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