

How does jasmonic acid improve drought tolerance? Mechanisms and future prospects

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Abstract

Drought stress poses a significant challenge to agriculture sustainability across the globe. Drought stress negatively affects the plant growth and productivity and the intensity of this serious abiotic stress is continuously increasing which is a serious threat across the globe. Different measures are being used to mitigate the adverse impacts of drought stress. Among these measures, the application of exogenous osmolytes and growth hormones is considered an important way to mitigate the adverse impacts of drought. Recently, jasmonic acid (JA) has emerged as an excellent growth hormone to improve drought tolerance owing to its involvement in different plant physiological and biochemical processes. Jasmonic acid improves membrane stability plant water relations, nutrient uptake, osmolyte accumulation, and antioxidant activities that can counter the toxic effects of drought. It also contributes to signaling pathways, i.e., genes network, stress-responsive proteins, signaling intermediates, and enzymes that protect the plants from the toxic effects of drought. Further, JA also protects and maintains the integrity of plant cells by up-regulating the antioxidant defense system and increasing osmolyte accumulation. In this review, we have documented the protective role of JA under drought stress. The various mechanisms of JA in inducing drought tolerance are discussed and different research gaps are also identified. This review will help the readers to learn more about the role of JA to mitigate the toxic effects of drought and it will provide new knowledge to develop the drought tolerance in plants.

Keywords: antioxidants; drought; jasmonates; plant hormones; stress signaling

Introduction

Climate change is leading to global warming which is causing drought events across the globe. Drought stress is a serious abiotic stress and can cause yield losses of more than 50% or even crop failures (Abdullah *et*

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al., 2015). The intensity of drought stress is continuously increasing which is posing a threat to crop productivity and global food security (Ma *et al.*, 2018). The field crops are facing the negative effects of climate change and drought stress particularly in arid and semi-arid regions (El-Sanatawy *et al.*, 2021; Megahed *et al.*, 2022; Ramirez-Builes *et al.*, 2024). The intensity of drought stress and increasing temperature are predicted to be more frequent and worse in the future. Therefore, it is expected that the intensity of drought stress will be increased in arid and semi-arid regions which will reduce the global food supply in the future (Salman *et al.*, 2021).

Drought stress negatively affects plant growth, development, photosynthesis, yield, and quality (Ma *et al.*, 2018). Drought stress also decreases chlorophyll synthesis, damages the photosynthetic apparatus, and causes a reduction in assimilate production (Shao *et al.*, 2022; Nguyen *et al.*, 2024). Drought stress reduces cell turgor and water content, and it also limits transpiration rate and leaf gas exchange (Desoky *et al.*, 2021; Kamara *et al.*, 2021; Mansour *et al.*, 2021). Further, drought-induced oxidative stress also increases reactive oxygen species production (ROS) that damages the cellular membranes, proteins, and lipids and triggers oxidative stress (Hassan *et al.*, 2020; Mannan *et al.*, 2022; Selem *et al.*, 2022). Drought stress also causes the degradation of chlorophyll and it disturbs the nutrient and water uptake and causes the inactivation of enzymes therefore, leads to a significant reduction in plant growth (Sakran *et al.*, 2022; Mannan *et al.*, 2022; Fan *et al.*, 2024).

Drought stress also negatively affects the plant growth and yield traits. For instance, drought stress reduces seed germination, and seedling growth which leads to a reduction in final stand establishment (Desoky *et al.*, 2021; Mageed *et al.*, 2021; Li *et al.*, 2024). Besides this drought stress also reduces the plant height, and yield traits and it also negatively affects the final quality (Rad *et al.*, 2012; Jamshidi *et al.*, 2015). However, plants possess an excellent enzymatic and non-enzymatic antioxidant defense system that can protect plants from the worst effects of oxidative stress (Habibullah *et al.*, 2021; El-Hady *et al.*, 2022). Besides this, plants also accumulate various osmolytes that also protect them from the toxic effects of drought stress. However, in some plants, endogenous antioxidants is not excellent enough to cope with the toxic effects of drought stress. Therefore, in context, the plant needs exogenous application of various materials to improve its antioxidant activities to tolerate drought stress (El-Sanatawy *et al.*, 2021; ElShamey *et al.*, 2021; Wu *et al.*, 2024).

Therefore, it is mandatory to develop the appropriate measures to mitigate the adverse impacts of drought stress on plants to ensure better crop productivity and global food security. The application of growth hormones is considered an effective measure to mitigate the adverse impacts of drought stress on plants. Jasmonic acid (JA) is an important hormone that can play an important role in improving drought tolerance in plants. Jasmonic acid regulates stomata movements which helps to reduce water loss and thus ensures plant survival under drought stress (Savchenko *et al.*, 2014; Meier *et al.*, 2024). The jasmonic application could promote leaf senescence, minimize water loss, and promote plant survival under drought stress (Ge *et al.*, 2010). Jasmonic acid also improves chlorophyll synthesis it maintains leaf water status, improves water and nutrient uptake, and ensures better plant growth under drought stress (Fu *et al.*, 2017; Wang *et al.*, 2024). Further, jasmonic acid also improves antioxidant activities, and osmolyte accumulation that improves membrane stability protects the plants from the toxic effects of oxidative damage and ensures plant survival under drought stress (Mohamed *et al.*, 2017). Additionally, jasmonic acid also improves the accumulation of sugar, phenolics, and flavonoids that enhance the capacity of plants against drought stress (Mohamed *et al.*, 2017). Therefore, in present review discussed the toxic effects of drought stress on plants and various mechanisms through which jasmonic acid can mitigate the adverse impacts of drought stress in plants. In addition, this manuscript also identified the various research gaps that must be fulfilled to ensure better crop productivity using jasmonic acid under drought stress.

Plant responses to drought stress

Drought stress is a serious abiotic stress that negatively affects plant growth and development and leads to a serious decrease in final productivity. Drought stress decreases plant height, and leaf production, and causes leaf wilting, and it also causes leaf senescence. Drought stress reduces plant height due to less cell expansion and less assimilates production (Li *et al.*, 2020; Anjum *et al.*, 2017; Misra *et al.*, 2020; Patmi *et al.*, 2020). Leaf is an important organ for transpiration and assimilates production and they are also a dominant indicator in response to drought stress.

Water shortage decreases the leaf area which reduces the transpiration (Werner *et al.*, 1999) which directly affects the photosynthesis and yield in plants. The decrease in leaf area under drought stress could be attributed to a reduction in leaf turgor, an increase in canopy temperature, and a reduction in net photo-assimilate production (Taiz *et al.*, 2015). Besides this drought stress also reduces the cell turgor which negatively affects photosynthesis and reduces the leaf area (Misra *et al.*, 2020). In addition, drought stress also causes leaf rolling in plants due to loss of upper epidermis and turgor pressure (Willick *et al.*, 2018). Plant roots play an important role under drought stress as they directly absorb the water from the soil (Lobet *et al.*, 2018; Jiang *et al.*, 2024). The plant root system like root hairs, root branches, and the density of roots could be significantly affected by water deficiency. Drought stress reduces root elongation and causes thinning of roots and it also accelerates root death (Xiao *et al.*, 2020).

Drought stress also induces stomata closing, reduces cell turgor pressure tissue water contents and uptake of nutrients, and results in a reduction in plant growth (Tarafdar *et al.*, 2022). Drought stress also disrupts the plant's physiological activities, reduces chlorophyll contents, and damages the photosynthetic apparatus which negatively affects the plant's photosynthetic efficiency (Demidchik, 2018; Tang *et al.*, 2023). The drought-induced stomata closing negatively affects the synthesis of chlorophyll, gas exchange, nutrients, and water uptake negatively affects plant growth and development (Fahad *et al.*, 2017; Muhammad *et al.*, 2021).

The closing of stomata reduces use of carbon dioxide (CO₂) which negatively affects the plant's photosynthetic activity and has a great impact on photosynthesis (Flexas *et al.*, 2004). Further, stomata closing also reduces transpiration which limits the uptake of water and nutrients and causes a reduction in nutrient concentration in plant plants and plant growth (Rivas *et al.*, 2016). The drought-mediated reduction in water uptake reduces the leaf relative water contents (RWC) which negatively affects plant physiological functioning under drought stress (Hartmann *et al.*, 2013; Alghabari *et al.*, 2015). Chloroplast is an important organelle for photosynthesis, nonetheless, drought stress deteriorates the chloroplast structure which adversely affects the synthesis of chlorophyll (Sun *et al.*, 2013; Nezhadahmadi *et al.*, 2013).

Water deficit conditions also increase ROS production which negatively affects plant physiological and metabolic functioning (Oğuz *et al.*, 2022). These ROS also damage the proteins, lipids, and membranes and cause oxidative damage to plants. Nonetheless, plants possess an excellent antioxidant system to tolerate the toxic effects of drought stress (Hossain *et al.*, 2013). Further, plants send either positive or negative signals between the roots and shoots to adapt to environmental conditions (Roblero *et al.*, 2020; Hassan *et al.*, 2021). Besides this, they also produce different hormones (abscisic acid (ABA), auxin, cytokinins, ethylene, and gibberellins) and osmolytes (proline and sugars) that protect the plants from the toxic effects of drought and improve their performance under drought conditions (Wang *et al.*, 2020). This osmolyte protects the plants from the toxic effect of drought maintains the water flow, and prevents the production of ROS (Padmavathi and Rao, 2013; Mwadzingeni *et al.*, 2016). Additionally, plants also increase the synthesis of different sugars like mannitol, sucrose, and trehalose under drought stress which also provides them protection against ROS (Zhang *et al.*, 2020).

Jasmonic acid is a key play to improve drought tolerance

Jasmonic acid is considered an effective way to improve drought tolerance. In given below section we provided comprehensive details on the role of jasmonic acid in mitigating drought stress in plants.

Jasmonic acid improves seedling growth and maintains water uptake and plant water relations under drought stress

Drought stress significantly reduces seed germination owing to the non-availability of water. However, during drought application of jasmonic acid has been reported to improve seed germination (Ghafari and Tadayon, 2019). Drought stress also increases the seedling growth, root, and shoot fresh dry mass (Table 1), and ensures better plant performance (Ghafari and Tadayon, 2019). For instance, in a study it was reported that drought stress decreased seed germination by more than 26%, however, the application of jasmonic acid improved the seed germination by 27% and enhanced the water potential by 60% owing to an increase in accumulation soluble sugars and proline accumulation (Noshin Ilyas *et al.*, 2017). In a study Anjum and his colleagues found that exogenous application of jasmonic acid improves the plant height, (5.4%), leaves per plant (2.75%), peduncle length (2.73%), and spike length (2.25%) of wheat over the control (Anjum *et al.*, 2019).

Table 1. The role of jasmonic acid in improving the plant growth, and physiological traits under drought stress

Plant type	Stress condition	Dose and type of JA	Protective Role	References
<i>Foeniculum vulgare</i>	40% FC	50 μ M MeJA	JA enhanced water use efficiency, grain yield and oil production	Parmoon <i>et al.</i> (2022)
<i>Oryza sativa</i>	Drought was imposed at heading stage (-40 kPa)	100 μ mol L ⁻¹ MeJA	JA enhanced growth, yield, physiochemical properties, yield and quality	Meng <i>et al.</i> (2023)
<i>Impatiens walleriana</i>	Drought stress (5% and 15% FC)	50 μ M MeJA	JA improved chlorophyll contents, growth and photosynthesis	Đurić <i>et al.</i> (2023)
<i>Chenopodium quinoa</i>	60% field capacity	Jasmonic acid (0, 1 and 2 mg L ⁻¹)	JA improved yield, growth, photosynthesis and chlorophyll synthesis	Keshtkar <i>et al.</i> (2022)
<i>Hordeum vulgare L.</i>	Drought was induced by skipping irrigation at the anthesis stage for two weeks	JA 50 and 100 μ mol L ⁻¹	JA application improved barley growth and yield by improving physiological and morphological traits	Nasiri <i>et al.</i> (2023)
<i>Gossypium</i>	Drought stress was imposed by decreasing irrigation interval from 10 to 20 days	JA (0, 25, 50, and 100 mg L ⁻¹)	JA mitigated the negative effects of water deficit by enhancing photosynthesis, and reducing ROS production	Yosefi <i>et al.</i> (2018)
<i>Impatiens walleriana</i>	Water deficit conditions caused by PEG8000	MeJA (0, 5, 50, and 100 μ M)	MeJA boosted the plant growth, leaf water status, and chlorophyll contents	Đurić <i>et al.</i> (2023)
<i>Gossypium</i>	Drought stress was applied by skipping irrigation at 45, 65- and 75-days of crop	JA (100 mg L ⁻¹)	JA improved vegetative and reproductive development and increased photosynthesis, and leaf water status.	Muhammad <i>et al.</i> (2021)

Relative water content is the key indicator of plant leaf water status (Mohamed and Latif, 2017). Drought stress significantly reduces the leaf RWC in plants due to restricted water uptake (Anjum *et al.*, 2011a; Miranshahi and Sayyari, 2016). However, jasmonic acid possesses excellent potential and it can improve the RWC (Figure 1) under drought (Sadeghipour, 2018) and jasmonic acid-mediated increase in leaf RWC is well echoed in many crops (Mahmood *et al.*, 2012; Wu *et al.*, 2012; Alam *et al.*, 2014; Ahmad and Murali, 2015; Pazirandeh *et al.*, 2015; Mohamed and Latif, 2017; Sheteiwiy *et al.*, 2018). Jasmonic acid induces stomata closing and it also improves root hydraulic conductivity via calcium and ABA-dependent signaling pathways which improve the water uptake and ensures better leaf water status under drought stress (SanchezRomera *et al.*, 2014; Sadeghipour, 2018). Further, in soybean and barley plants it was reported that an exogenous supply of JA appreciably improved the tissue water status under drought stress which enhanced the overall performance of these plants (Pazirandeh *et al.*, 2015; Mohamed *et al.*, 2017). In another study conducted on cauliflower and soybean plants showed that drought stress significantly reduced the leaf RWC, however, exogenous application of jasmonic acid mitigated the drought-induced toxic effects and improved the leaf water status (Anjum *et al.*, 2011; Huiling *et al.*, 2012). In conclusion JA ensures better water uptake under drought which ensures better plant growth and development.

Jasmonic acid maintains membrane stability under drought stress

The production of ROS is significantly increases under drought stress which damages the membranes and reduces membrane stability and increases electrolyte leakage. The exogenous application of jasmonic acid can reduce this increase in ROS production which can protect the membranes from toxic effects of drought stress Martinez *et al.* (2018). Malondialdehyde (MDA) is an important indicator of membrane and its concentration is increased under drought stress which reduces the membrane stability (Martinez *et al.*, 2018). Different authors found that exogenous application of jasmonic acid can reduce the MDA production under drought can protect the membranes from toxic effects of drought (Mir *et al.*, 2018). In another study, Ghaffari *et al.* (2020) found that drought stress decreases the membrane stability by 39% as compared to control. However, jasmonic acid application (10 μ M) increased membrane stability by 23% (Ghaffari *et al.*, 2020). Likewise, different authors also found a decrease in the membrane by 75% under drought stress, however, JA application (0.001 and 1 μ M) mitigated the adverse impacts of drought and improved the membrane under water deficit conditions (Kaur *et al.*, 2013; Ghaffari *et al.*, 2020).

Further, Noshin Ilyas *et al.* (2017) reported a significant decrease in the membrane stability under drought stress. These authors treated the seeds with JA and salicylic and studied their effect on membrane stability under drought stress. They found that the membrane stability of wheat plants was decreased by 25% under drought stress. They also found that JA and SA increased membrane stability 10% and 6% under well-water conditions while JA and SA increased membrane stability by 9% and 4% respectively under drought conditions (Noshin Ilyas *et al.*, 2017). (Noshin Ilyas *et al.*, 2017). Further, Tayyab *et al.* (2020) found that the membrane stability of maize growing under drought was decreased by 58% while exogenous application of MEJA and SA significantly increased membrane stability by 106% under drought stress (Tayyab *et al.*, 2020). To sum up JA mitigates MDA and ROS production which protect the cellular membranes prevent the loss of important osmolyte and reduced EL.

Jasmonic acid improves nutrient uptake and maintains nutrient homeostasis under drought stress

Drought stress disturbs nutrient uptake and nutrient homeostasis and leads to a serious reduction in plant growth. For instance, in a study, it was found that 65% field capacity caused a little increase in P and K nutrients while 45% decreased the potassium (K), phosphorus (P), and nitrogen (N) concentrations. However, pre-soaked plants with MeJA showed an appreciable increase in N, P, and K uptake under normal and water

stress conditions (Abdelgawad *et al.*, 2014). Further, in another study, it was found that drought stress reduced nitrogen uptake, total sugars, and carbohydrates and it enhanced antioxidant activities and proline synthesis (GontiaMishra *et al.*, 2016). However, exogenous JA application mitigated the drought-induced toxic effects by increasing N uptake. In another study, it was reported that the application of JA (10 ppm) under drought stress significantly increased the levels of carbohydrates, total sugars, and macronutrients except P (Abd-El-All and Ali, 2019). Additionally, in a study conducted by Amanifsar (2019) showed that JA markedly increased the N and P concentration by 77.8% and 64.3% in plants growing under drought stress (Amanifar *et al.*, 2019). Thus, JA improves nutrient uptake and maintain nutrient homeostasis which ensures better plant performance under drought conditions.

Jasmonic acid protects photosynthetic apparatus and improves photosynthesis under drought stress

Drought stress is the main cause of the reduction of chlorophyll content owing to the increase in the activity of chlorophyll degrading enzyme (chlorophyllase) (Mohamed and Latif, 2017; Sheteiwiy *et al.*, 2018). In a study, Sadeghipour (2018) noted a severe reduction in chlorophyll synthesis due to drought stress, however, this reduction was reversed by the application of JA. This role of MeJA in improving the chlorophyll contents under drought stress is well reported in cauliflower (Wu *et al.*, 2012), maize (Abdelgawad *et al.*, 2014), *Brassica* (Alam *et al.*, 2014), and soybean (Mohamed and Latif, 2017). This effect of JA in increasing the photosynthetic pigments could be related to enhanced nutrient and water absorption (Kovac and Ravinkar, 1994).

In a study, maize seeds were presoaked with JA and then subjected to different WFC (65% and 45%). The results showed that 56% field capacity decreased the chlorophyll a, chlorophyll b, and carotenoid contents. However, exogenous JA significantly improved the concentration of aforesaid photosynthetic pigments under drought stress as compared to control (Abdelgawad *et al.*, 2014). Further stress also decreases the uptake of Mg which is a building block in chlorophyll synthesis (Ashraf and Harris, 2013). The exogenous supply of JA has been found to improve the Mg uptake which improves the chlorophyll synthesis and allows the plants to maintain better chlorophyll synthesis under drought stress (Asma and Lingakumar, 2015). Furthermore, an increase in chlorophyll synthesis due to JA treatment application could also be due to an increase in cytokinin concentrations (Kovac and Ravnikar, 1994). In a study, Ttayab *et al.* (2020) reported plants treated with MeJA + JA showed high levels of chlorophyll a, chlorophyll b, and carotenoids in untreated drought-stressed plants. In conclusion JA protect the photosynthesis apparatus be decreasing ROS which ensures better photosynthetic efficiency and subsequent assimilates production.

Jasmonic acid maintains osmolyte accumulation and hormonal balance under drought stress

Osmo-regulation plays an important role in plants to mitigate drought stress (Yazdanpanah *et al.*, 2011). Proline is an important osmolyte accumulated by plants that can minimize the toxic effect of drought stress (Redy *et al.*, 2003). Generally, the proline synthesis is increased under drought stress (Redy *et al.*, 2003) which helps the plants to maintain osmotic adjustment (Xu *et al.*, 2008). In a study, Tasgin *et al.* (2006) reported a significant increase in proline with the application of JA and SA in bean, wheat, and tomato under drought stress. Further, different authors also found an increase in soluble sugar accumulation under drought stress with JA application (Nazrali *et al.*, 2011). The concentrations of amino acids in wheat plants treated with JA were also enhanced under drought stress (Noshin Ilyas *et al.*, 2017). This increase in the amino acids has been well reported in different crops sorghum, chickpea, millet, and wheat (Yadav *et al.* 2004). It is reported that foliar application of MeJA can increase the drought tolerance capacity by increasing the sugars, phenolic, and flavonoids (Mohamed and Latif, 2017).

In a study Bandurska *et al.* (2003) noted that JA has different impacts on different compounds like ABA, proline, and spermidine. There was an increase in abscisic acid (ABA) and proline contents in plants with exogenous application of JA. Proline is an important osmolyte that regulates ROS production and protects the plants' drought induced oxidative damage (Nadarajah, 2020; Mahmood *et al.*, 2020). Jasmonic acid enhances the accumulation of proline that helps to detoxify the ROS in plants growing under drought conditions (Sirhindi *et al.*, 2016; Fugate *et al.*, 2018). JA regulates the transcriptional expression of genes involved in proline metabolism which in turn increases the proline synthesis under drought stress (Anjum *et al.*, 2011; Cao *et al.*, 2012; Awan *et al.*, 2021; Abdelgawad *et al.*, 2014). In a study, it was reported that proline content was higher in the shoot tips of plants treated with MeJA under drought conditions. Similarly, MeJA-treated soybean plants have excessive proline contents which helped to maintain RWC under drought conditions compared to controls (Anjum *et al.*, 2011). MeJA also increases proline, free amino acids content, and total protein which in turn improves the plant performance under drought stress (Abdelgawad *et al.*, 2014). The exogenous application of substantially improves hormonal balance and increases the synthesis of potential osmolyte which protect the plants from toxic effects of drought by increasing antioxidant activities and water uptake.

Jasmonic acid improves the accumulation of secondary metabolites under drought stress

Secondary metabolites are important compounds synthesized by plants that make them stronger against different stresses (Teoh, 2015). Phenolic compounds play a significant role in the detoxification of free radicals and protect plants from the negative effects of water stress (Petridis *et al.* 2012). Jasmonic acid increases the synthesis of phenolic compounds under drought stress (Table 2). For example, a study conducted on soybeans showed that MeJA enhanced the synthesis of phenolic compounds in different genotypes. The maximum concentration of phenolic was seen in soybean cultivar Giza 35 under drought stress treated with MeJA. Further, in another study, a significant increase in ferulic acid and vanillic acid concentration was seen with JA application (Mohamed and Latif, 2017). Hura *et al.* (2009) reported a significant increase in praulic acid content and phenolic compounds with JA application under drought stress. Buckwheat plants growing under drought stress also showed an increase in ferulic acid concentration with MeJA as compared to control (Gumerova *et al.*, 2015). In another study, Mohamed and Latif (2017) found that exogenous application of MeJA improves the flavonoids which helped soybean plants to counter the toxic effects of drought. In addition, Gholamreza *et al.* (2019) found that MeJA application under drought increased the flavonoid contents, while Kim *et al.* (2006a) found that after 48 hours of MeJA treatment (0.1 and 0.5 ppm) increased the total phenolic contents by 27% and 57%.

Table 2. Effect of jasmonic acid on oxidative stress markers, and antioxidant activities under drought stress

Plant type	Stress condition	Dose and type of JA	Protective Role	References
Wheat	Drought was imposed by applying (PEG – 1.03 MPa)	0.1 mM	JA decreased the membrane damage and improved chlorophyll stability index, leaf proline, APX, CAT, POD, SOD, and total antioxidant activities.	Abeed <i>et al.</i> (2021).
Brassica	(15 % polyethylene glycol, PEG-6000)	0.5 mM	JA application decreased MDA and H ₂ O ₂ production, LOX (Lipoxygenase) activity, and increased activities of GR, Gly-1, MDHAR, DHAR, GR, GPR, Gly-1 and Gly-II activities.	Alam <i>et al.</i> (2014).
<i>Grewia asiatica</i> L.	60% field capacity	0.5 mM	Jasmonic acid increased the phenolics and APX, GPX, and SOD	Waheed <i>et al.</i> (2022).
Soybean	Drought was imposed by withholding irrigation	50 mM	Methyl jasmonate enhanced the activity of CAT, POD and SOD and leaf proline.	Anjum <i>et al.</i> (2011)
Peppermint	50% FC	50 mM	JA increased activities of SOD and DPPH.	Gholamreza <i>et al.</i> (2019).
Maize	45% FC	50 mM	The exogenous application JA increased CAT, POD and SOD activities.	Abdelgawad <i>et al.</i> (2014).
Brassica rapa L.	40%	10 mM	The activity of antioxidant enzymes POD, CAT, GR, APX and CAT was increased by JA application.	Ahmad Lone <i>et al.</i> (2022).
<i>Physalis peruviana</i> L.	50% FC	10, 100 mM	Methyl jasmonate treatments increased antioxidant activity and yield	Ghasemzadeh <i>et al.</i> (2023).
French bean	Drought stress was imposed day after the foliar spray of JA by withholding irrigation until end of study.	MeJA (20 µM) or SA (2 mM)	MeJA and SA enhanced enzymatic anti-oxidative activity by the up-regulation of SOD, APX, GPX, GR, GST CAT, POD, and MDHAR activities.	Mohi-Ud-Din <i>et al.</i> (2021).

CAT: catalase, APX: ascorbate peroxidase, SOD: superoxide dismutase, LOX: lipoxygenase, GR, glutathione reductase, MDHAR: monodehydroascorbate reductase, DHAR: dehydroascorbate reductase, DPPH: 2-diphenyl-1-picrylhydrazyl.

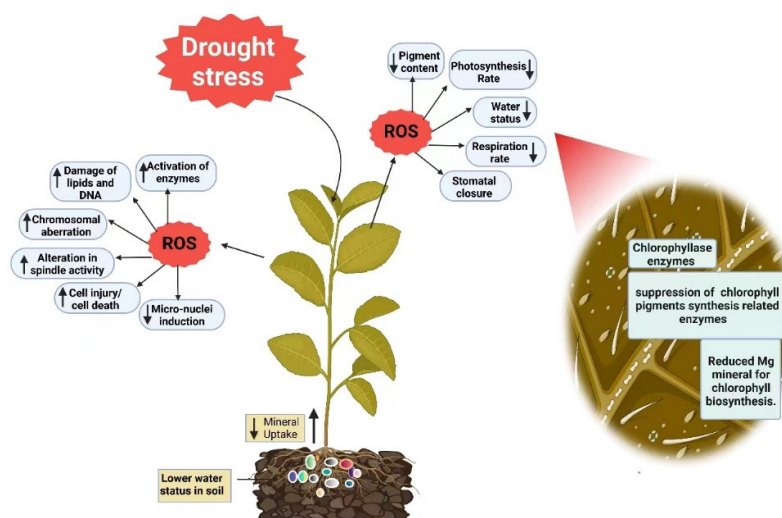


Figure 1. Drought stress reduce photosynthesis, plant water status, and transpiration and respiration rates and increase the ROS production that damage proteins, lipids, membranes, macro molecules and cause significant growth and yield losses

Flavonoids are the most important bioactive secondary metabolites and can act as secondary antioxidants in plants under drought stress (Agati *et al.*, 2012). Gholamreza *et al.* (2019) reported that ascorbic acid availability can considerably increase total flavonoid synthesis. In peppermint plants, it was seen that MeJA application increased the synthesis of phenolic acids, flavan-3-ols, flavonols, and flavonones (Gholamreza *et al.*, 2019). Further, these authors also found an increase in the concentration of rosmarinic acid, cumaric acid, caffeic acid, and hesperidin with MeJA application (Gholamreza *et al.*, 2019). To sum up JA improves the synthesis of secondary metabolites that make the plants stronger against drought stress.

Jasmonic acid strengthens antioxidant systems under drought stress

Drought stress often causes oxidative stress and results in an increase in antioxidant activities. Plant resistance to numerous stresses is linked with antioxidant capacity and improved levels of antioxidants can prevent the toxic effects of different stresses (Bor *et al.*, 2003). Foliar application of MeJA increased the transcription levels and activities of different antioxidants that can help to counter the toxic effects of drought (Shan and Liang, 2010; Ghasem *et al.*, 2012). In soybean plants drought stimulated enzymatic antioxidant activities which were further increased by exogenous application of MeJA (Anjum *et al.*, 2011). Similarly, these authors also found that MeJA application significantly increased the activities of CAT, POD and SOD which minimized the toxic effects of drought (Anjum *et al.*, 2011).

In another study, it was found that JA application (5 μM) significantly increased the APX, CAT and POD activities by 150%, 119% and 94% (Alam *et al.*, 2014). In another study, it was found that pre-soaking of plants with MeJA considerably increased the CAT, POD and SOD activities (Abdelgawad *et al.*, 2014) likewise, Majid and Akbar (2006) also found that MeJA (50 and 100 μM) promoted activities of antioxidants. Moreover, Tariq *et al.* (2011) found a substantial increase in activities of CAT, POD and SOD with MeJA treatments. They also found that MeJA enhanced the activities of all the antioxidants under stressed and non-stressed conditions. MeJA can induce the antioxidant plants that can mitigate the adverse impacts of water deficiency by scavenging ROS (Norastehnia and Nojavan-Asghari, 2006). Recently Rehman *et al.* (2023) also studied the effect of JA on antioxidant of corn plants. They found that JA supplementation increased the CAT

(36.35%), SOD (81.63%), guaiacol peroxidase (GPX; 37.09%), GR (58.64%) and glutathione S-transferase (GST: 40.26%) activities. On the other hand, Ahmad Lone *et al.* (2022) also found a remarkable increase in antioxidant activities (GR, CAT and POD) which countered the toxic effects of drought and protected the membranes by reducing MDA and electrolyte leakage (EL).

Dehydrins are the genetically disordered proteins and their synthesis is increased in response to stress conditions. The most important role of dehydrins in plants is to protect the cell structural cell structure integrity against drought stress (Close, 1996; Allagulova *et al.*, 2003; Hara, 2010; Nguyen *et al.*, 2020). The exogenous application of MeJA can increase the concentration the TADHN and mRNA under drought stress. For instance, in wheat plants exogenous application of MeJA significantly improved the expression level of TADHN and mRNA genes (Wang *et al.*, 2014; Kosova *et al.*, 2014). In another study, it was found that dehydrins accumulation in seedlings was significantly enhanced after pretreatment with MeJA (Kosova *et al.*, 2014). Further, Allagulova *et al.* (2020) and his colleague also found that MeJA mitigated the negative effects of drought stress which was linked with improved accumulation TADHN dehydrin (Allagulova *et al.*, 2020). The results of RT-PCR analysis of this study also showed that exogenous MeJA application enhanced dehydrin gene expression which protected the plants from toxic effects of drought (Allagulova *et al.*, 2020). Thus, JA improves antioxidant activities which countered the ROS and protect the plants cellular structures from oxidative damages.

Jasmonic acid nutrition improves plant growth, yield and quality under drought stress

Jasmonic acid (JA) plays a significant role in promoting plant primary root growth, cell expansion and cell differentiation (Cenzano *et al.*, 2003; Huang *et al.*, 2017). The exogenous application of MeJA and SA and their combined application can mitigate the adverse negative effect of drought on French beans by sustaining cellular water levels, membrane stability, photosynthetic activity and antioxidant activities (Huang *et al.*, 2017; Mohi-Ud-Din *et al.*, 2021). The positive effect of MeJA in improving the plant growth and development under drought is also reported in maize plants by Tayyab *et al.* (2020). Different authors also found that exogenous supply of MeJA improves the plants growth under drought stress by increasing biochemical, morphological, and physiological responses, including cell elongation, cell expansion, and cell differentiation (Anjum *et al.*, 2012; Alam *et al.* 2013; Anjum *et al.*, 2016; Huang *et al.*, 2017; Huang *et al.*, 2017).

In plants growing under drought stress, the exogenous application of MeJA reduce the harmful effects of drought and improved the plant height, fresh and dry weights, (Hasanuzzaman *et al.*, 2017). In another study, foliar application of MeJA and SA under water stress accelerated the root and shoot growth and biomass production chamomile plants (Nazrli *et al.*, 2014) (Figure 2). The increase in flowering and panicles was seen with exogenous application of MeJA and SA in plants growing under drought stress (Qin *et al.*, 2005; Yu *et al.*, 2019). The application of MeJA improves photosynthetic rate and photosynthetic efficiency which ensures better assimilates production thus resulting in better growth and production under drought stress (Dong *et al.*, 2007; Ma *et al.*, 2014). Further, jasmonic acid application also improves the radical elongation and increase the lateral roots which ensures better seedling growth in plants growing under drought stress (Zhang *et al.*, 2022). In another study it was found that exogenous application of JA minimized the growth retardation in pearl millet seedling and improved the root and shoot growth under drought stress (Awan *et al.*, 2021). Therefore, JA mediated increase in plant growth under drought stress is linked with membrane stability, leaf water contents, nutrient homeostasis, photosynthesis, osmolyte accumulation, hormonal balance, accumulation of secondary metabolites, and antioxidant activities.

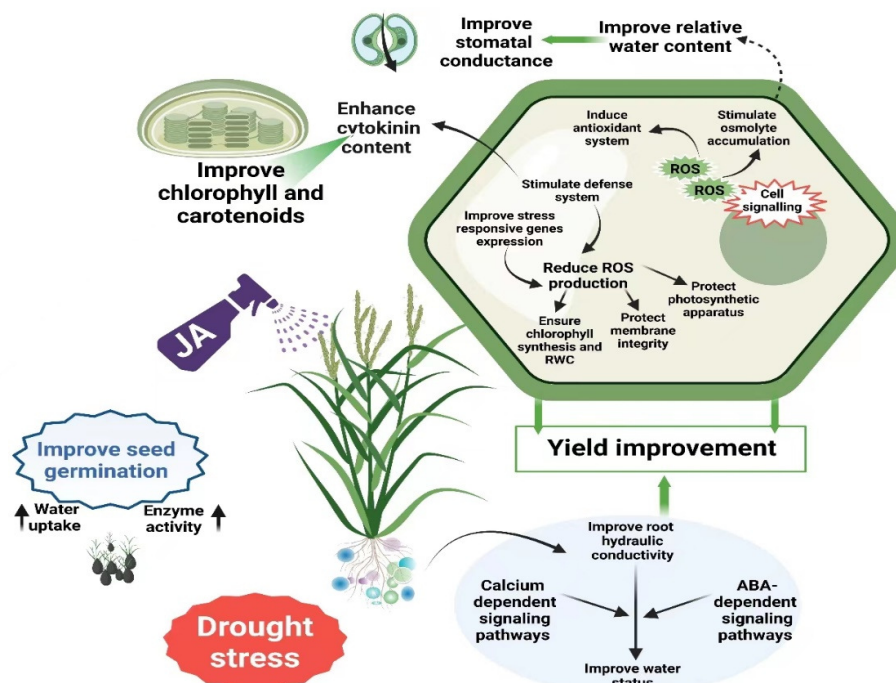


Figure 2. Exogenous application of JA improves seed germination, water uptake, leaf water status, chlorophyll synthesis, protect photosynthetic apparatus and reduce the ROS production by increasing antioxidant activities and osmolyte accumulation therefore, leads to increase in drought tolerance

Methods of jasmonic acid application to crops

Jasmonic acid can be applied to crops by different ways like seed priming and foliar application. For instance, maize seed soaked in 20 μM solution of MeJA showed an increase in plant growth, photosynthetic rate, yield and quality under drought stress (Tayyab *et al.*, 2020). In another study foliar spray of MeJA (20 μM) to soybean plants increased the plant growth, shoot length, shoot fresh and dry weight, photosynthetic pigment and relative oil content under drought stress conditions (Mohamed and Latif, 2017). Similarly, wheat plant exposed to drought stress with foliar applied MeJA (0.5 mM) showed marked improvement in dry biomass, grains per spike, grains weight and biological yield (Anjum *et al.*, 2016). In a study it is reported that foliar application of MeJA increased chlorophyll a/b ratio and soluble sugar content in *Huangguogan* plant under drought stress (Xiong *et al.*, 2020). Moreover, Nazim *et al.* (2021) found that foliar applied jasmonic acid (100 μM) to cotton crop showed an increase in vegetative growth. Lastly, Abeer *et al.* (2021) found that foliar application of JA (100 μM) at early stage of wheat crop improved the plant growth and antioxidant activities under drought stress (Abeer *et al.*, 2021).

Conclusions

Drought stress is a serious abiotic stress that is negatively affecting the plant growth and productivity across the globe. Drought stress can significantly reduce the growth and development of plants by disturbing the plant physiological and biochemical functioning and cause oxidative damages and water shortage. In recent time JA got a significant attention owing to its remarkable participation as developmental and defense signaling molecule under different stress conditions. The changes induced by JA under drought are with alterations in

plant physiological, biochemical, and molecular responses. Jasmoic acid under drought stress improves membrane integrity, plant water relations, chlorophyll synthesis, photosynthesis, antioxidant activities and osmolyte accumulation which can mitigate adverse impacts. Though role of JA under drought is not fully explored and there are many research gaps that must be fulfilled in future studies. The role of JA in seed germination under drought stress is not fully studied, therefore, it would be interesting to explore the role of JA in germination mechanism under drought stress. Nutrients play an important role to tolerate the toxic effects of drought, however, uptake of most of nutrients is seriously reduced under drought conditions. The role of JA on nutrient uptake under drought is rarely studied, thus, it is important to underpin how JA affects different nutrient channels, nutrient signaling and transporters under drought stress. The crosstalk of JA with different hormones and osmolytes is also poorly studied, and it is mandatory to explore the complex linking between JA and different hormones and osmolytes under drought stress. The recent genomic, transcriptomic, proteomic, and metabolomic approaches can facilitate to determine the complex relationship between different hormones and osmolytes under drought stress. Further, the potential omics approaches to identify JA-related genes, proteins and metabolites must be explored. Besides this, identification of JA-related metabolic pathways can provide new suggestions to understand signaling network under drought stress. In literature most studies are performed under control conditions, and there is a dire need to conduct the long-term field studies to further study the role of JA under drought stress.

Authors' Contributions

Conceptualization, T.A.K. and H.G.; writing—original draft preparation, H.H., H.W., M.I.U.H., I.A., F.L. and H.M. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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