Role of Jasmonates, Calcium, and Glutathione in Plants to Combat Abiotic Stresses Through Precise Signaling Cascade

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Plant growth regulators have an important role in various developmental processes during the life cycle of plants. They are involved in abiotic stress responses and tolerance. They have very well-developed capabilities to sense the changes in their external milieu and initiate an appropriate signaling cascade that leads to the activation of plant defense mechanisms. The plant defense system activation causes build-up of plant defense hormones like jasmonic acid (JA) and antioxidant systems like glutathione (GSH). Moreover, calcium (Ca\(^{2+}\)) transients are also seen during abiotic stress conditions depicting the role of Ca\(^{2+}\) in alleviating abiotic stress as well. Therefore, these growth regulators tend to control plant growth under varying abiotic stresses by regulating its oxidative defense and detoxification system. This review highlights the role of Jasmonates, Calcium, and glutathione in abiotic stress tolerance and activation of possible novel interlinked signaling cascade between them. Further, phyto-hormone crosstalk with jasmonates, calcium and glutathione under abiotic stress conditions followed by brief insights on omics approaches is also elucidated.

Keywords: abiotic stress, cell signaling, jasmonic acid, glutathione, calcium

INTRODUCTION

Different environmental conditions turn out to be the cause of stress in plants that tend to affect their growth, development, metabolism, and even cause death (Boguszewska and Zagdańska, 2012). These abiotic stresses such as salinity, heavy metals, temperature, drought, etc. are serious threats that affect crop productivity (Asgher et al., 2015; Raza et al., 2020). Plants have mechanisms due

Abbreviations: JA, jasmonic acid; Ca\(^{2+}\), calcium; GSH, glutathione; MeJA, methyl jasmonate; JAZ, jasmonate zip domain; Ile, isoleucine; ROS, reactive oxygen species; Na\(^{+}\), sodium; Pb, lead; CAT, catalase; APX, ascorbate peroxidase; LOX3, lipoxygenase3; AsA, ascobic acid; Cd, cadmium; HM, heavy metal; Cu, copper; RuBisCO, ribulose-1,5-bisphosphate carboxylase oxygenase; SOD, superoxide dismutase; POD, peroxidase; H\(_2\)O\(_2\), hydrogen peroxide; jar1, methyl jasmonate resistant1; coi1, coronatine insensitive1; oji1, ozone-sensitive and jasmonate insensitive; OPR3, 12-oxophytodienoate reductase 3; GST, glutathione s-transferase; CAM, calmodulins; GR, glutathione reductase.
to which they adapt themselves to different climatic conditions by modulating their growth and physiology. Phytohormones are associated with various physiological and metabolic processes in plants (Kumar et al., 2014; Asgher et al., 2018; Geetika et al., 2020). The phytohormones play notable roles in inducing the numerous complex processes of growth, development, and response to stress by retarding the signaling cascades in plants. Moreover, it has been suggested that these phytohormones have potential to eliminate the ill effects of abiotic stress (Thao et al., 2015; Asgher et al., 2018; Zaid and Mohammad, 2018). Plant growth hormones such as auxin, gibberellin, cytokinin, abscisic acid, salicylic acid (SA), ethylene, JA, and recently studied brassinosteroid, act as components of abiotic-stress signaling (Fahad et al., 2015; Sharma and Laxmi, 2016; Wani et al., 2016). Among these phytohormones JA has gained much importance during the recent years.

JA has a ubiquitous expression in the plant systems. JA and its derivatives do have remarkable roles as plant growth and stress regulators, involved in diverse plant developmental processes such as callus growth, seed germination flowering, primary root growth, and senescence (Fahad et al., 2015). It acts as an important signaling molecule either in biotic or abiotic stress response (Wasternack, 2015; Per et al., 2018; Ali and Baek, 2020; Jang et al., 2020). Some jasmonates are derived from fungus while its methyl ester form, i.e., methyl jasmonate (MeJA) is extracted from petals of jasmine (Jasminum grandiflorum) (Avanci et al., 2010). It is usually present in flowers and reproductive tissues, while sparsely present in minute levels in root and mature leaves. JA have the capability to enhance or suppress the plant response (Agrawal et al., 2003; Fahad et al., 2015). JA tends to boost the antioxidant machinery of the plants (Bali et al., 2020).

Ca\(^{2+}\) acts as one of the important secondary messengers in all life forms involving many cell signaling cascades (Berridge et al., 2000; Stael et al., 2012). Among the most important nutrient elements, Ca\(^{2+}\) has a role under optimal and stressful conditions in plants (White and Broadley, 2003). Different kinds of stimulus are perceived by Ca\(^{2+}\) for downstream cellular ramifications via activation of Ca\(^{2+}\) channels followed by an increase in Ca\(^{2+}\) concentration due to influx of Ca\(^{2+}\) thereby inducing Ca\(^{2+}\) signaling (Evans et al., 2001; Chinnusamy et al., 2004). During abiotic stresses, Ca\(^{2+}\) signaling plays an important role by stimulation of Ca\(^{2+}\) channels and causes an increase in cytoplasmic Ca\(^{2+}\) levels for further downstream retaliations (McAinsh and Pittman, 2009; Dodd et al., 2010; Sarwat et al., 2013; Liu et al., 2018).

Glutathione one of the non-protein tripeptide thiol compounds, known as “master antioxidant” or “super defender,” is ubiquitous in nature and present in all plant cells at relatively high concentrations (Dixon et al., 1998). GSH is known to play a pivotal role in root development, plant disease resistance, protection against chilling damage, cell proliferation, and salt tolerance (Mittova et al., 2003; Gómez et al., 2004; Vivanco et al., 2010). GSH holds a very important position in stress responses by determining the cell redox state of the cell (Noctor et al., 2012).

Recent findings suggest that JA has a prime role at the physiological and biochemical levels that is associated with the plant defense against abiotic stress. However, JA cannot work alone to alleviate abiotic stress but works in concord manner via various signaling cascades. Vast literature is available on role of JA and its crosstalk with other phytohormones under abiotic stress, but there is no literature that documents the role of Jasmonate, Calcium, and Glutathione in plants to combat Abiotic stresses through precise signaling cascade. So, this review exemplifies the role of Jasmonates, Calcium, and glutathione in abiotic stress tolerance and activation of possible novel interlinked signaling cascade between them. Further, phytohormone crosstalk with jasmonates, Calcium, and Glutathione under abiotic stress conditions following with brief insights on omics approaches is also discussed.

**BIOSYNTHESIS OF JASMONIC ACID**

Jasmonic acid (JA) belongs to the family oxylipins, produced from polyunsaturated fatty acid (PUFA) through its oxidative metabolism (Wasternack and Hause, 2002; Ahmad et al., 2016). Its synthesis occurs via octadecanoic acid pathway involving esterification of α-linolenic acid (C18) in galactolipid membranes of chloroplast (Wasternack and Strnad, 2018; Wang et al., 2020). Phospholipase A causes the release of α- linolenic acid followed by oxygenation by 13- lipoxygenase (13-LOX) to a 13- hydroperoxyoctadecatetraenoic acid, which is then converted by a 13-allelo oxidase synthase (13-AOS) to a highly unstable epoxide. Cyclization of this epoxide to cis-(+)-12-oxy-phytodienoic acid (OPDA) by the action of an allelo oxide cyclase (AOC). The next half of JA biosynthesis takes place in peroxisomes. Followed by subsequent reduction and three steps of β-oxidation after which shortening of the carboxylic acid side chain to (+)-7-iso-JA, which is released into the cytosol and epimerizes to (−)-JA. Then Conjugation with amino acids, such as isoleucine, is catalyzed by jasmonoyl–isoleucine (JA-ile) conjugate synthase (JAR1) which is the most active JA bio-compound (Wasternack and Hause, 2013; Ruan et al., 2019). JA and its metabolites, collectively called jasmonates, have an important role in mediating plant signaling in response to abiotic stress. JA signaling based gene expression is negatively regulated by jasmonate zip domain proteins (JAZ proteins). However, JA preferentially conjugates to isoleucine (Ile) to form Ile-JA or gets converted into MeJA (Wasternack, 2007; Wasternack and Hause, 2013). Ile-JA is in turn perceived Skip-Cullin–F-box complex (SCF\(^{COI}\)) which mediates degradation of the JAZ repressor via 26S proteasome degradation, thereby relieving the repression by JAZ, transcriptional regulator (Figure 1) (Melotto et al., 2008; Gifler et al., 2010; Zhou and Memelink, 2016). The JAZ repressors recruit the protein topless (TPL) and the novel interactor of JAZ (NINJA) together to form transcriptional repression complex that inhibits the expression of jasmonate-responsive genes through formation closed to open complex, thereby favoring further attachment of histone deacetylase 6 (HDA6) and HDA19 (Causier et al., 2012; Chini et al., 2016).

**BIOSYNTHESIS OF GLUTATHIONE**

Various kinds of stresses tend to fluctuate the status of glutathione (Gómez et al., 2004). The biosynthesis of this non-protein thiol
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FIGURE 1 | Jasmonic acid biosynthesis and its gene regulation. (A) Jasmonic acid biosynthesis in various cellular compartments involving plastid, peroxisome and cytosol. In plastid α-linolenic acid is converted into 12-oxo-phytodienoic acid that is exported via JASSY channel protein and imported via COMATOSE ABC transporter to peroxisome. Subsequent reduction, β-oxidation, and epimerization reactions lead to JA formation and is released into cytosol. Then JA Conjugates with isoleucine in cytosol to form jasmonoyl–isoleucine (Ile-JA). (B) Degradation of JAZ repressor proteins via SCF\textsuperscript{COI}1 regulating JA gene expression at transcription level Ile-JA is in turn perceived Skip-Cullin–F-box complex (SCF\textsuperscript{COI}1) which mediates degradation of the JAZ repressor via 26S proteasome degradation, thereby relieving the repression by JAZ, transcriptional regulator.

FIGURE 2 | Biosynthesis of Glutathione. The two ATP dependent steps involved in biosynthesis of Glutathione. Glutamate and cysteine leads to the formation of γ-glutamylcysteine and in the next step glutathione formation occurs by addition of glycine to γ-glutamylcysteine. This reduced glutathione (GSH) acts as substrate for numerous cellular reactions in cytosol and mitochondria to yield oxidized glutathione (GSSG). This reduced glutathione (GSH) acts as substrate for numerous cellular reactions to yield oxidized glutathione (GSSG). The balance between GSH and GSSG acts as an important role in maintaining homeostasis of the cell (Meister, 1995; Noctor et al., 2012).

compound involves two ATP dependent steps as shown in Figure 2. First, the reaction is catalyzed by glutamate-cysteine ligase (GCL) involving glutamate and cysteine leading to the formation of γ-glutamylcysteine, and in the next step glutathione formation occurs by addition of glycine to γ-glutamylcysteine in the presence of glutathione synthetase (GS). This reduced glutathione (GSH) acts as substrate for numerous cellular reactions to yield oxidized glutathione (GSSG).
Availability or localization of GCL and GS plays an important role in glutathione biosynthesis. Early reports suggest that in plant cells, GCL is localized in chloroplast and GS in cytosol as well as in chloroplast cells (Hell and Bergmann, 1988, 1990). Work on Arabidopsis suggest that GCL and GS are encoded by a single gene with alternate start sites leading either cytosolic or plastid targeted protein (Wachter et al., 2005). Glutathione biosynthesis compartmentalization is unique to plant systems (Galant et al., 2011; Noctor et al., 2012). Generally, over-expression of GCL, not GS, in plants raises glutathione content by increasing flux through the pathway. Increase in GCL activity that is from GSH to GSSG form takes place in response to 5 mM H$_2$O$_2$ treatment to Arabidopsis seedlings as depicted by immunoblot and activity assays (Hicks et al., 2007). Moreover, addition of cysteine, glutamate, or glycine does not enhance glutathione synthesis suggesting the role of GCL as a metabolic control point in the pathway (Meyer and Fricker, 2002). Metabolic studies suggest that feedback inhibition may not be a major control regulatory feature of glutathione (Meyer et al., 2001). Even though glutathione inhibits both GCL and GS (Jez et al., 2004). According to Previous reports glutathione biosynthesis pathway is controlled in a tightly regulated manner and hence supports the increased expression level of GCL and GS genes under various stress conditions (Xiang and Oliver, 1998; Lu, 2013).

ROLE OF JASMONATES, CALCIUM, AND GLUTATHIONE IN ABIOTIC STRESS TOLERANCE

Abiotic stresses including heavy metals, salinity, temperature, drought, etc. represent a significant threat to plants by causing cellular damage and inhibiting normal physiological activities in plants thereby limiting productivity (Fujita et al., 2006; Asgher et al., 2015; Hasanuzzaman et al., 2017a) the detailed roles of JA, Ca$^{2+}$, and GSH under different abiotic stress conditions are discussed below.

Salt Stress

Alkaline stress is one of the most important stresses, especially in arid and semi-arid environments, that affects crop productivity at a global level (Parvin et al., 2019). Alkaline salt contamination to agricultural soil has been predicted in the past few decades mostly in Asian countries (Paz et al., 2012). Extreme alkaline stress can promote negative effects on plants at cellular level high sodium (Na$^+$) concentration, enhancing ionic stress (Chen et al., 2012). About 10% of the world’s cultivable land productivity is affected by salt and alkaline stress (Tanji, 2006). Salinity disturbs the allocation of minerals and membrane permeability. It decreases chlorophyll biosynthesis, metabolism of nitrogen, and carbon dioxide (Gupta et al., 2002; Kim et al., 2004). High salinity also causes the production of reactive oxygen species (ROS), hence leading to oxidative stress (Smirnoff, 1993). Application of plant growth regulators including phytohormones help to counter the different environmental stresses in plants. Earlier reports have shown that JA activates expression of α-linolenic acid metabolism genes which is a branch of JA biosynthesis (Wasternack, 2007). Moreover, it has been seen that JA accumulation occurs under salt stress in plant species like Solanum lycopersicum (Pedrazzani et al., 2003). The exogenous application of JA alleviated salt-induced injury in other variety of plants like barley (Walia et al., 2007), rice (Kang et al., 2005), and wheat (Qiu et al., 2014). Exogenous supplementation of (60 and 120 mM) MeJA increased growth and physiological attributes of Anchusa italica (Taheri et al., 2020). It has been recently reported that 45–60 μM MeJA significantly improved SOD, GPX, APX while 15–30 μM increased AsA, CAT, GSH activities in Glycyrrhiza uralensis seedlings under salt-stressed conditions, respectively (Lang et al., 2020). JA treatment led to up-regulation of the osmolyte synthesis, antioxidant system, and metabolite accumulation in tomato (Ahmad et al., 2018). Under increasing salt stress conditions abscisic acid (ABA) accumulated in tolerant varieties of rice while decreased in salt intolerant ones. Exogenous application of JA, however, led to an increase in ABA, especially in salt intolerant cultivars of rice, thereby ameliorating the salt stress (Kang et al., 2005). Exogenous application of MeJA effectively safeguards salinity stress symptoms in soybean seedlings by increasing the levels of ABA and relieving the repression of GA biosynthesis (Yoon et al., 2009). The lipoxygenase 3 (LOX 3) enzyme involved in JA biosynthesis of Arabidopsis is induced under salt treatment. However, LOX3 mutant seem to be hypersensitive toward salt treatment and could be complemented by exogenous JA treatment (Ding H. et al., 2016). Moreover, JA increased GSH related gene expression in plants in response to salt stress which in turn increases the antioxidant ability thereby protecting against oxidative stress caused by salt stress as seen in wheat seedlings (Qiu et al., 2014; Mir et al., 2018a). Ion homeostasis seem to be an important factor for plants under salt stress (Hasegawa, 2013). Plants have mechanisms by which they are able to sense salt stress via ionic and osmotic signals (Zhu, 2003). The Salt Overly Sensitive (SOS) pathway is a central mechanism in plant salt tolerance, which includes two calcium sensor proteins, SOS3 and SCA BP8; the protein kinase SOS2; and the Na$^{+}$/H$^+$ anti-porter SOS1. AtANNEXINs are a family of calcium-dependent membrane-binding proteins in plants. AtANNEXIN4 (AtANN4) plays a critical role in generating the calcium signal under salt stress that activates the SOS pathway in Arabidopsis. The SOS pathway suppresses AtANN4-mediated calcium transients through an interaction between SCA BP8 and AtANN4. AtANN4 likely functions during a very early stage of the plant salt stress response by generating a calcium signal. Afterward, an initial calcium signal is created in cells by AtANN4, SCA BP8, and SOS2 under salt stimulus. Phosphorylation of AtANN4 by SOS2 reduces the calcium-binding capability of AtANN4, which might alter calcium perception. The collaboration with SCA BP8 and phosphorylation by SOS2 represses the AtANN4-mediated calcium changes, there by provides a negative regulation loop. The negative feedback regulatory loop involving the SOS pathway decreases cytoplasmic sodium levels and elicits specific, long lasting salt stress reactions in plants (Ma L. et al., 2019). Phosphatases like calcineurin (protein phosphatase B) are important Ca$^{2+}$ sensors and result in a decrease in K$^+$ current and stomatal closure in plants. The specific to salt stress (SOS3) gene of
Arabidopsis was comprehended to encode calcineurin B homolog of yeast. However, SOS3 mutant acts as a Ca$^{2+}$ sensor to elicit downstream signaling under salt stress conditions which are hypersensitive to Na$^{+}$ and are partially suppressed by increasing the concentration of Ca$^{2+}$. Therefore, SOS3 mutant helps to unravel the basic role of Ca$^{2+}$ in regulating potassium nutrition and salt stress in plants (Sanders et al., 1999).

**Metal(l oid) Stress**

Metal contamination of agricultural systems has become a worldwide concern due to industrialization and anthropogenic activities like mining (Chary et al., 2008; Noriega et al., 2012). Essential micronutrients like Zn and Cu are required by plants to carry out activities of different metal dependent proteins and enzymes. There accumulation above certain threshold value results in oxidative stress and nutrition stress. It results in alteration in carbohydrate metabolism, inhibition of photosynthesis and transpiration. Changes in plant morphology and physiology are also evident under heavy metal (HM) stress (Qureshi et al., 2016). JA production in response to metal or metalloid has been reported in *Wolffia arrhiza* (Qureshi et al., 2016). JA production in response to metal or photosynthesis and transpiration. Changes in plant morphology threshold value results in oxidative stress and nutrition stress.

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**Lead Stress**

Lead (Pb) a non-essential element toxic to plants is absorbed by plants via roots, shoots, or foliage. Its entry into the plant cell causes inhibition of enzymatic activities, alteration of mineral nutrition, hormonal status, membrane structure, etc., leading to decreased growth and chlorosis (Seregin and Ivanov, 2001; Küpper, 2017). Change in enzyme activities causes inhibition of seed germination as reported in *Sporobolus alterniflorus* (Mrozek and Funicelli, 1982) and *Eichhornia crassa* (Malar et al., 2016). Moreover, it is also responsible for inhibition of growth in plants like privet (Zhou et al., 2018). High Pb content leads to generation of ROS that directly or indirectly induces oxidative stress (Verma and Dubey, 2003; Reddy et al., 2005). JA elicits lead detoxification in tomato through production of secondary metabolites and gene expression and by decreasing the expression of the RBO and P-type ATPase transporter genes (Bali et al., 2019a,b). It also leads to the induction of lipid peroxidation, perturbing the level of saturated to unsaturated fatty acids in plant (Verma and Dubey, 2003; Bidar et al., 2008). Pb toxicity in *W. arrhiza* increased when supplemented with 100 µM of JA by the formation of lipid peroxides which resulted in decreased fresh weight, chlorophyll a, carotenoid soluble protein content, and monosaccharide while 0.1 µM of JA protected *W. arrhiza* fern against Pb stress by preventing Pb accumulation, restoring plant growth, and primary metabolite level by promoting the activities of enzymatic antioxidants and non-enzymatic antioxidants, such as the content of AsA and GSH (Piotrowska et al., 2009). JA also causes changes in ascorbate glutathione pathway in plants like *Lycopersicum esculentum* under lead stress at various growth stages (Bali et al., 2018). GSH has chelating properties for heavy metals and therefore helps in ROS detoxification (Hossain et al., 2012). JA also exhibits diverse functional roles in alleviating Pb induced toxicity by increasing activity of antioxidant enzymes like activating GPX and GR that act as ROS scavenger and regeneration of the GSH/GSSG pool of the cell, respectively (Hasanuzzaman et al., 2018). Exogenous application of GSH improved tolerance in *Iris lactea var. chinensis* by mediating Pb accumulation and transport (Yuan et al., 2015).

**Cadmium Stress**

Cadmium (Cd), a non-redox heavy metal with long biological perseverance is highly toxic to plants (Asgher et al., 2015). It interferes with normal functioning of plants like photosynthesis, mineral, and water uptake (Baryla et al., 2001; Khan N.A. et al., 2016). Its toxicity in plants causes chlorosis, leaf rolling, and reduced growth of stem and root (Smeets et al., 2005; Mishra et al., 2006). It induces oxidative stress via generation of ROS causing serious damage to plants (Gallego et al., 2012). JA positively regulates plants in response to Cd stress (Zhao et al., 2016). Varying concentrations of JA and MeJA tend to alleviate the stress caused by Cd in soybean and *Oryza sativa*. 5 µM of MeJA improved antioxidant response and accumulation of antioxidants under Cd stress in O. sativa while 20 µM of JA reduced the damage caused by Pb stress in soybean (Noriega et al., 2012; Singh and Shah, 2014). These phytohormones cause increase in growth and photosynthesis besides changing the activity of different antioxidants and increasing GSH pools (Yan et al., 2013; Singh and Shah, 2014). Tomato seedlings susceptible to Cd show enhanced JA deficiency, this suggests that JA positively regulates the tomato plant to Cd stress (Zhao et al., 2016). Furthermore, JA acts as a signaling molecule for combating Cd stress and is also associated with expression of genes related to GSH biosynthesis (Maksymiec et al., 2007). Heavy metals compete with Ca$^{2+}$ on the plasma membrane by substituting Cd, thereby altering the plant metabolism (Mansour, 2004).
However, exogenous application of Ca\(^{2+}\) results in improving biochemical and physiological processes, besides enhancing activity of antioxidant enzymes, which provides tolerance against Cd stress as shown in faba bean (Siddiqui et al., 2012). Up regulation of antioxidant enzymes has been observed upon Ca\(^{2+}\) treatment to the Sesamum indicum under Cd stress (Abd-Allah et al., 2017). The same positive correlation was observed by exogenously applying GSH in combating Cd induced stress in *O. sativa*. It was reported that the difference in tolerance capability of sensitive and insensitive cultivars of *O. sativa* is associated with the tendency of the plant to elevate its GSH levels. Higher GSH levels halt the translocation of Cd and decreases its lethal effect. GSH treatment also enhances the chlorophyll level, photosynthetic performance and antioxidant capability of plants (Cai et al., 2011a; Fang et al., 2020).

**Copper (Cu\(^{2+}\))**

Copper is a micronutrient that plays an important role in energy generation by means of ATP synthesis and carbon dioxide assimilation. It also alters ultra-structure and pigment composition of chloroplast. Therefore, being responsible for decline in the rate of photosynthesis via decrease in Ribulose-1, 5-bisphosphate carboxylase oxygenase (RuBisCO) inhibition of the electron transport chain and Photosystem II activities (Rakwal et al., 1996; Gang et al., 2013). High levels of Cu\(^{2+}\) exposure to *Theobroma cacao* seedlings caused damaging effects such as absence of starch grains and swelling of chloroplast double membrane (Souza et al., 2014). It has been reported that JA (1 µM, 1 nM, and 1 pM) enhances photosynthetic pigment accumulation and production of hydrogen peroxide (H\(_2\)O\(_2\)) mitigating enzymes, i.e., superoxide dismutase (SOD) and peroxidase (POD), suggesting that seed priming with JA can decrease the toxic effect of Cu\(^{2+}\) (Poonam et al., 2013). Moreover, addition of Ca\(^{2+}\) into nutrient solution improved the growth of Cu-treated seedling, by lowering the concentration of polyamines putrescine and increasing the levels of spermine and spermidine in the epicotyl of plants (Shen et al., 1998). Supplementation of Ca\(^{2+}\) to pea plants increases the Cu metal bio- absorption and maintains the homeostatic environment of the cell (Ben Massoud et al., 2019). A similar effect has been observed for GSH that helps in alleviating the effect of copper in rice seedlings by reducing copper uptake (Mostofa et al., 2015). Pretreatment with GSH caused the activation of oxidative stress scavenging mechanisms of plant thereby decreasing the level of ROS and Malondialdehyde concentration (Tahjib-Ul-Arif et al., 2020).

**Arsenic Stress**

Arsenic toxicity poses a serious health threat to all living organisms across the globe associated with anthropogenic activities like mining and smelting operations (Kumar et al., 2015; Singh et al., 2015). The As contamination in groundwater is a worldwide problem. It badly affects crop productivity and accumulates in different plant tissues, including grains, and affects the food chain (Verma S. et al., 2016; Ghosh et al., 2019). Naturally As exists in Inorganic arsenate As (V) and arsenite As (III) forms. Both forms are toxic but As (III) is more toxic than As (V) to plants as it has a tendency to bind proteins with sulphydryl groups and hinder with their functions (Verma S. et al., 2016). It also leads to ROS generation and inhibition of respiration by binding to cytochrome complexes with As, which gets sequestered into the vacuoles through ABC1/ABCC2 transporters (Schmöger et al., 2000; Dhankher, 2005). Furthermore, Lambda class of GST (GSTLs) has been seen to bind tightly to the flavonols and their derivatives (Chronopoulou et al., 2017). It has been suggested that GSTLs can recycle GSH adducts of oxidized flavonols back to the parent flavonols, maintaining the antioxidant pools (Hernández et al., 2009). Genome wide expression analyses have shown differential expression of OsGSTLs at various stages of plant development as well as under stress conditions (Kumar et al., 2013. However, the exogenous use of GSH in As-treated seedlings decreased As-induced oxidative stress, increased the AsA and GSH contents, and mediated As translocation from the roots to the shoots. Therefore, the results suggest that exogenous GSH application could be a favorable approach to enhance As stress resistance in rice (Farooq et al., 2018; Jung et al., 2019). The identification of calcium-dependent protein kinase CPK31 is a major component controlling As(III) tolerance in Arabidopsis. Genetic and biochemical studies show that CPK31 fulfils this function by interaction with NIP1;1, providing a novel role of CPK31 in controlling As(III) toxicity in plants via Ca\(^{2+}\) signaling (Mousavi et al., 2020).

**Nickel Stress**

Nickel (Ni) is among the common heavy metals that cause serious health complications even in trace quantity (Masindi and Muedi, 2018). Nickel induces the deficiency of Zn and Fe. It also hinders the uptake of other heavy metals such as Cd, Pb, Co, and Cr (Myśliwa-Kurdziel et al., 2004). Nickel toxicity disrupts the important macro and micronutrients uptake by hindering the translocation of these nutrients through root to aerial (Pandey and Sharma, 2002; Chen et al., 2009; Ameen et al., 2019). The
treatment of NiSO₄•7H₂O has led to decrease in chloroplast size and number. It was also seen to be responsible for the disorganization of ultrastructure of chloroplast like numbers of grana decreased, thylakoids deformation, the development of plasto globuli, and the membrane lipid composition alterations were stated in *Brassica oleracea* plants. These changes were due to the Ni induced drop in cell moisture content or subsequent peroxidation of membrane lipids due to oxidative stress (Ameen et al., 2019). The toxicity of Ni has been associated with oxidative stress in plants (Rao and Sresty, 2000; Boominathan and Doran, 2002). Nickel toxicity like other abiotic stresses led to production of ROS (Gill and Tuteja, 2010). Excessive Ni increases the concentration of superoxide anions, hydroxyl radicals, nitric oxide, and hydrogen peroxide (Stohs et al., 2000). The toxicity of heavy metals is directly linked with overall crop yield. The increasing concentration of Ni has deleterious effects on plants that finally triggered reduction in crop yield (Balaguer et al., 1993). Ni was also reported to be associated with inhibition of germination and production of chlorophyll (Zhou et al., 2009). Exogenous application of JA relieved the adverse effect of oxidative stress on biomass production, growth, and protein content in Ni treated plants by further enhancing the activity of antioxidant enzymes (Azeem, 2018; Mir et al., 2018b). However, exogenous or endogenous biosynthesis of JA make plants tolerant to any oxidative damage (Sirhindi et al., 2016). There is information that methyl ester of JA (MeJA) affects the pools of stress antioxidant enzymes activity to combat oxidative stress (Jung, 2004). Ni stimulated the activities of SOD, APX, and CAT. SOD is the primary enzyme of Asada-Halliwell pathway that causes dismutation of superoxide radicals under elevated levels of H₂O₂ followed by further hydrolysis into H₂O and O₂ by CAT and APOX or other POD enzymes present in various cellular organelles (Keramat et al., 2010; Sirhindi et al., 2015). Higher GSH reductase and catalase activities are present in a Ni-tolerant strain of the green alga, *Scenedesmus acutus f. alternans* (Randhawa et al., 2001). Also in transgenic Arabidopsis, GSH seems to be intensely associated with increased resistance the growth inhibitory and oxidative stress induced effects of Ni. This rise in GSH concentrations was reported to be determined by serine acetyltransferase (SAT) activity in conferring tolerance to Ni-induced oxidative stress in Thlaspi Ni hyperaccumulators (Freeman et al., 2004). However, the application of Ca²⁺ has been seen to be responsible for the higher efficiency of the antioxidants for increasing tomato tolerance to the Ni stress (Asrar et al., 2014).

**Drought Stress**

Drought is responsible for great famines of the past. It is one of the common threats to food security. Limited supply and increasing demand of water worsened drought effects (Somerville and Briscoe, 2001). Jasmonate zip-domain (JAZ) proteins are essential regulators of proteins of JA signaling in many plants including *A. thaliana* (Vanholme et al., 2007) and rice (Ye et al., 2009). It has been reported that enhanced expression of stress responsive OsJAZ1- gene of *O. sativa* showed higher sensitivity to drought stress, while the JAZ1 mutant plants were more hyposensitive to drought stress compared to wild plants, suggesting the role of JA in combating the drought stress in plants (Fu et al., 2017). Exogenous application of MeJA (75, 150, and 225 μM) improved many characteristics of *Satureja hortensis* such as growth, water content, proline level, antioxidant activity, and essential oil percentage as well as yield. However, among different concentrations used, 75 μM was more effective, like that seen in drought tolerance in different *Brassica* species by trehalose (5 mM) treatment (Hasanuzzaman et al., 2014; Miranshahi and Sayyari, 2016). Exogenously applied 0.1 μM of MeJA to the wheat seedlings decreased the drought-induced retarded growth, lesions of membrane by increasing the level of dehydrin protein expression in them (Allagulova et al., 2020). JA treatment to cowpea plant under drought stress improves relative water content, proline, chlorophyll content, and causes stomatal closure, so as to elevate the stress pertaining to drought (Sadeghpour, 2018; Tayyab et al., 2020). Exogenous application of 10 and 150 μM JA increases the antioxidant potential of sugar beet (Ghaifari et al., 2019) and bitter melon (Alisofi et al., 2020) respectively, under drought conditions thereby imparting tolerance to them. Differential expression of Me-JA induced miRNAs was seen by Me-JA treatment in wheat under drought stress. These miRNAs could play a significant role in the activation of a particular gene, so play an important function in combating drought stress (Ma C. et al., 2019). GSH also reduces the effect of drought stress via maintaining water status, proline content, and by acting as an antioxidant (Nahar et al., 2015a). Exogenous GSH application improves growth characteristics and yield of plants under drought stress (Chen et al., 2012; Nahar et al., 2015a). Recent studies indicate that apart from increasing antioxidant activity GSH has a role in maintaining the plant mineral homeostasis (Sohag et al., 2020). However, it has also been reported that application of Ca²⁺ and H₂O₂ to plants mitigated ill effects of the drought stress (Hasanuzzaman et al., 2014; Hu et al., 2018). Ca²⁺ also regulates the water status, proline, and H₂O₂ levels in maize plants under drought stress (Naeem et al., 2018).

**Flooding Stress**

Flooding influences agricultural productivity all over world (Jackson and Colmer, 2005). It restricts gaseous exchange between plants and their environment, thereby resulting in lowering of oxygen, carbon dioxide levels, and increasing levels of ethylene in plants (Bailey-Serres and Voessenek, 2008). Its interference in photosynthesis and respiration in plants hinders production of ATP via oxidative phosphorylation, besides leading to generation of ROS due to hypoxic and anoxic conditions (Gibbs and Greenway, 2003; Paradiso et al., 2016). Owing to flooding stress, plants experience compound stress like energy and carbon deficiency that leads to retardation of plant growth (Armstrong, 1980; Jackson, 1985). JA upregulates the ROS and H₂O₂ detoxification system in plant cells during floods (Nanjo et al., 2011). JA is reported to have a post-flooding recovery function in soyabeans by modulating the levels of nucleotidyl transferase activity (Khan and Komatsu, 2016). Studies have shown that GSH regulates the gene expression of JA at a basal level. Ca²⁺ also has a role in regulating the cell wall integrity besides the mitigating effect of oxidative stress during
flood conditions (Porto et al., 2013). Supplementation of GSH to rice plant increased its antioxidant potential and could be an important factor to rescue plants under flooding stress (Siddiqui et al., 2020). Exogenous application of Ca\(^{2+}\) causes the root elongation and inhibits the cell death at the root tips of soyabean under flood stress (Oh et al., 2014). Moreover, external supplementation of Ca\(^{2+}\) decreased the negative effects on their physiological parameters like stomatal conductance, photosynthesis, soluble protein content, fruit size, etc., and also seem to have roles in maintaining the integrity of root cells of pepper (Ou et al., 2017). In addition, early cytosolic Ca\(^{2+}\) transients also seem to be important in circumventing the effect of flood stress among plants (Subbaiah and Sachs, 2003).

### Ozone Stress

Stratospheric ozone layer depletion results in enhancement of the tropospheric ozone levels that adversely affect the terrestrial biosphere (Overmyer et al., 2000; Ainsworth et al., 2012). Ozone mediated changes at the cellular level in plants involves oxidative burst, accelerated cell senescence, and hypersensitive response kind of reactions (Vollenweider et al., 2003). Oxidative burst leads to lump and strand like protrusions on the cell wall with enhanced cellular oxidation (Günthardt-Goerg et al., 1997). ROS generation overcomes the cellular detoxification system. Its accumulation results in hypersensitive response with apparent symptoms like disruption of cellular structure, collapse of cell walls, incomplete degradation of cellular organelles, chromatin condensation, condensation of cell leftovers into apoptotic-like bodies, and nuclear degeneration leading to cell death (Vollenweider et al., 2003; Iriti and Faoro, 2007). JA plays a role in mitigating the ozone stress in plants (Tamaoki, 2008). JA insensitive mutants of Arabidopsis such as methyl-jasmonate resistant1 (jar1), coronatine insensitive1 (coi1), ozone-sensitive and jasmonate-insensitive (ojj1), JA-biosynthesis defective fad3/7/8triple mutant, and the 12-oxophytodienoate reductase 3 (OPR3) mutants are extremely susceptible to ozone (Staswick et al., 1992; Feys et al., 1994; Overmyer et al., 2000; Kanna et al., 2004). O\(_3\) tolerant cultivar of wheat is reported against cold stress (Li et al., 2012). Low temperatures increase the accumulation of certain key molecules and JA biosynthesis (Li Q. et al., 2016). The inducer of the CBF expression ICE-CBF pathway plays a core role in cold stress related response in plants. Under a normal set of conditions, ICE1 and ICE2 bind to the CANN13 sequence of the promoter region of CBF genes. These factors also bind JAZ1 and JAZ4, causing inhibition of ICE-CBF pathway. However, under cold stress conditions, the formation of more JA-Ile occurs which mediates the 26s proteasome degradation of JAZ factors that were previously bound to ICE1 and ICE2, hence activation of the ICE-CBF pathway occurs (Hu et al., 2017). It has been reported that external application of MeJA to a rubber tree eliminates the repression of JAZ proteins on ICE2 transcription factor that has an important role in the activation of CBF (C-repeat binding factor) cold signaling pathways involving genes CBF1, CBF2, COR47. So, the increase in the gene expression of CBF1, CBF2, COR47 genes tend to acclimate cold stress conditions in plants like rubber trees (Chen et al., 2019). Further, JA-related expression of genes involved in synthesis of GSH and GR occurs (Xiang and Oliver, 1998). It upregulates the antioxidant activities and protects the ultra-structure of the cell against cold stress (Li et al., 2012). Low temperatures increase the GSH level many folds which in turn alters the reduct status of GSH (Wildi and Lütz, 1996; Karpinski et al., 1997). GSH accumulation was seen to be more evident in cold tolerant varieties of rice decreased glutathione-s-transferase (GST) expression takes place which in turn affects the GSH/GSSG pool. Also, Ca\(^{2+}\) dependent differential gene expression is observed in Arabidopsis under ozone stress thereby elucidating important role of Ca\(^{2+}\) as well in combating ozone mediated stress in plants (Clayton et al., 1999; Short et al., 2012).

### Temperature Stress

Extreme differential temperature exposure causes stress in plants. Temperature stress (cold/low) alters the normal functioning of plants (Dhingra, 2015; Hatfield and Prueger, 2015), JA has role in surmounting the effect of extreme temperatures in plants (Zhao et al., 2013). Role of JA, Ca\(^{2+}\), and GSH under extreme temperature conditions are discussed below.

### Cold Stress

Cold (low) temperature stress, a major threat that prevents plants from resuming full potential, results in a decrease in the crop productivity worldwide (Yadav, 2010; Dhingra, 2015). It affects plant metabolism and growth via inhibition of electron transport chain and disturbance in the activity of enzymes that participate in plant metabolism (Dhingra, 2015). Low temperature exposure of a plant leads to oxidative stress. During which, the plant’s antioxidant machinery is activated to restore normal functioning of the plant. Antioxidants play key roles in cold acclimatization, low temperature stress tolerance, and maintenance of cellular redox homeostasis (Chen and Li, 2002; Khan et al., 2015). Exogenous application of MeJa to Arabidopsis (Hu et al., 2013) and loquat fruit (Cai et al., 2011b) imparted cold tolerance to them. However, it has been reported in cold tolerant Camellia japonica that upregulation of MYC – genes that are key regulators of JA signaling occurs in addition to an increase in the levels of precursor molecule α-linolenic acid of JA biosynthesis (Li Q. et al., 2016). The inducer of the CBF expression ICE-CBF pathway plays a core role in cold stress related response in plants. Under a normal set of conditions, ICE1 and ICE2 bind to the CANN13 sequence of the promoter region of CBF genes. These factors also bind JAZ1 and JAZ4, causing inhibition of ICE-CBF pathway. However, under cold stress conditions, the formation of more JA-Ile occurs which mediates the 26s proteasome degradation of JAZ factors that were previously bound to ICE1 and ICE2, hence activation of the ICE-CBF pathway occurs (Hu et al., 2017). It has been reported that external application of MeJA to a rubber tree eliminates the repression of JAZ proteins on ICE2 transcription factor that has an important role in the activation of CBF (C-repeat binding factor) cold signaling pathways involving genes CBF1, CBF2, COR47. So, the increase in the gene expression of CBF1, CBF2, COR47 genes tend to acclimate cold stress conditions in plants like rubber trees (Chen et al., 2019). Further, JA-related expression of genes involved in synthesis of GSH and GR occurs (Xiang and Oliver, 1998). It upregulates the antioxidant activities and protects the ultra-structure of the cell against cold stress (Li et al., 2012). Low temperatures increase the GSH level many folds which in turn alters the reduct status of GSH (Wildi and Lütz, 1996; Karpinski et al., 1997). GSH accumulation was seen to be more evident in cold tolerant varieties of rice decreased glutathione-s-transferase (GST) expression takes place which in turn affects the GSH/GSSG pool. Also, Ca\(^{2+}\) dependent differential gene expression is observed in Arabidopsis under ozone stress thereby elucidating important role of Ca\(^{2+}\) as well in combating ozone mediated stress in plants (Clayton et al., 1999; Short et al., 2012).

### Temperature Stress

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as compared to non-tolerant (Yu et al., 2020). Cold stress can inhibit some metabolic activity of plants (Shi Y. et al., 2018). Moreover, GSH interacts with JA, which is involved in regulating plant developmental processes and signaling networks under different types of stresses (Per et al., 2018). It has also been reported that Ca\(^{2+}\) influx is required for elicitor-induced synthesis of JA (Hu et al., 2009). Thus, JA induced signaling cascade may lead to activation of nifdefpine sensitive channels associated with the increase in cytosolic Ca\(^{2+}\) through release from intra-cellular stores (Sun et al., 2009). The decrease in temperature also causes significant increase in the cellular Ca\(^{2+}\) through increase in the influx of Ca\(^{2+}\) ions. Increased influx of radio labeled Ca\(^{2+}\) was seen in roots of plants in response to cold stress by the hypo-polarization of plasmalemma (Rincon and Hanson, 1986). Exogenous Ca\(^{2+}\) enhanced the tolerance potential of wheat under cold stress by regulating the levels of antioxidant machinery, photosynthetic rate, and membrane injury (Zhang et al., 2020).

Heat Stress
Constant rise in temperature due to greenhouse gases emission causes heat stress in plants. Plants are worst hit because of their sessile nature which makes them unable to shift to better place to handle the damaging effect of heat (Cassia et al., 2018). Heat stress greatly affects growth, physiological aspects, development, and yield of plant, thereby leading to generation of ROS in excess eliciting oxidative stress (Hasanuzzaman et al., 2013; Sarwar et al., 2018). It has been reported that applying JA helps to mitigate the effects of heat stress in plants via activating the oxidative defense and detoxification system (Sharma and Laxmi, 2016). Heat induced inhibition of photosynthesis is counteracted by Ca\(^{2+}\) salts that ameliorate the damage to Photosystem II as observed in tomato (Sakhonwasee and Phingkasen, 2017) and tobacco (Tan et al., 2011). Ca\(^{2+}\) ions tend to decrease the level of ROS production (Sakhonwasee and Phingkasen, 2017). Exogenous application of Ca\(^{2+}\) led to thermos-tolerance in common bean by up-regulating antioxidant enzyme activity and sugar accumulation in them (Naeem et al., 2020). GSH has also been found to protect plants under heat stress via improving photosynthetic attributes, osmolytes, and antioxidant levels in plants such as in Arabidopsis (Cheng et al., 2015). External application of GSH imparted heat tolerance in plants as seen in Cummins sativa (Ding X. et al., 2016). However, the involvement of GSH in mitigating heat mediated oxidative stress in plant is very well documented (Nahar et al., 2015a).

The response of exogenously applied JA, Ca\(^{2+}\), and GSH, respectively, to different plant varieties under various kinds of abiotic stresses is given below in the Table 1.

### POSSIBLE INTERACTION BETWEEN JASMONATES, CALCIUM, AND GLUTATHIONE

Plants have different capabilities of combating abiotic stress depending upon their antioxidant expression system (Davenport et al., 2003). Plant hormones regulate the adaptive responses that are indispensable for a plant to adapt itself to abiotic stress. JA increases antioxidant responses against abiotic stress in plants. JA effectively reduces oxidative stress by measuring the decrease in thioarbituric reactive substance levels, increased GSH content, and scavenging of ROS via expression of enzymatic antioxidants (Maksymiec and Krupa, 2002; Chen Y. et al., 2011). Abiotic stress induces Ca\(^{2+}\) influx causing cold acclimation related necessary cellular alterations. Calcium signaling is one of the most vital signaling mechanisms that affect the JA-mediated signaling system inside plant cell via calcium channels (Fisahn et al., 2004; Beyhl et al., 2009; Lu et al., 2016). Generation and accumulation of ROS due to abiotic stresses triggers the opening of Ca\(^{2+}\) channels (Demidchik et al., 2018). Regulation and biosynthesis of JA is governed by levels of Ca\(^{2+}\) fluxuations (Wasternack and Song, 2017). However, in leaf cells of Arabidopsis JA tend to induce the increase in Ca\(^{2+}\) levels by mediating Apoplastic calcium influx (Lu et al., 2016). It causes significant increase in Ca\(^{2+}\) into the cell due to immediate influx of Ca\(^{2+}\) ions as seen in roots of winter wheat (Erlandson and Jensén, 2006), alfalfa (Monroy and Dhindsa, 1993), and maize (Rincon and Hanson, 1986). Drastic changes in Ca\(^{2+}\) levels of lnodicle cells of panicles of rice and guard cells of Arabidopsis by exogenous application of MeJA has been reported, but transient rise in Ca\(^{2+}\) levels can also occur by other JAs in the plant cell cytosol and nucleoplasm (Qin et al., 2005; Walter et al., 2007). Ca\(^{2+}\) channel blocker like ruthenium red disrupted the Ca\(^{2+}\) transients in potato plants that also hinders the JA formation (Fisahn et al., 2004). Basal level of JA expression was increased in Arabidopsis by gain of function of two pore calcium channel 1 (TPC1) (Bonaventure et al., 2007). JA has been found to cause Ca\(^{2+}\) influx via AtCNGC2 calcium channel in epidermal cells of Arabidopsis (Lu et al., 2016). Increase in cytosolic Ca\(^{2+}\) levels result in the activation of Ca\(^{2+}\) dependent protein kinases (CDPK), calmodulins (CAM), etc., resulting in further integration of stress response pathways. This increase in the cytosolic Ca\(^{2+}\) occurs due to Ca\(^{2+}\) influx from external or release stores. It has been observed that JA also tends to induce Ca\(^{2+}\) mobilization that in turn interacts with CAM or CAM like proteins (CML) to modulate the expression of JA responsive genes like JRI1 (Sun et al., 2006). Accumulation of CAM 1 type and CAM 3 type proteins was reported in tobacco plants followed by JA treatment (Yamakawa et al., 2001). CML42 of Arabidopsis is deciphered to have a crucial role in calcium mediated JA biosynthesis (Vadassery et al., 2012a). CAM gene, CAM binding protein, and CML expression also increased in response to MeJA (Bergey and Ryan, 1999; Yang and Poovaiah, 2002; Vadassery et al., 2012b). Moreover, CDPK has also seen to be upregulated by JA as they seem to trigger the formation of OPDA (Ludwig et al., 2005). Inhibitors of JA synthesis prevented the inhibitory effect induced by abiotic stress like heavy metals, on the accumulation of chlorophyll and photosynthesis (Maksymiec and Krupa, 2002). Uprgulation of MeJA mediated stress defense by changing the protein profile thereby controlling the photosynthesis and antioxidant metabolism (Chen Y. et al., 2011; Maserti et al., 2011). Changes in the intracellular redox environment of a plant due to generation of ROS in response to various abiotic stresses disturbs the plants cellular physiology (Ogawa et al., 2005). ROS
TABLE 1 | Abiotic stress response in relation with JA, Ca$^{2+}$, and GSH among different plant species.

| Stress type | Plant species | JA/GSH/Ca$^{2+}$ | Response | Growth pattern | Cotyledon number | References |
|-------------|---------------|-----------------|----------|---------------|-----------------|------------|
| MeJA        | *Pisum sativum* (L.) | 10$^{-5}$ M | Osmoregulation, increased proline content | Annual | Dicot | Fedina and Tsonov, 1997 |
|             | *Glycine max* (L.) | 20 and 30 µM | Increase in growth and proline content | Annual | Dicot | Yoon et al., 2009 |
|             | *Arabidopsis thaliana* (L.) | 5 and 10 µM | Compliments lox3 mutant rescues salt stress | Annual | Dicot | Ding H. et al., 2016 |
|             | *Triticum aestivum* (L.) | 0.1 µM | Increases cytokinin production and plant growth | Annual | Monocot | Avalbaev et al., 2016 |
|             | *Solanum lycopersicum* (L.) | 10, 20, 30, 40, 50, and 60 µM | Increase in levels of osmo-protectants and enzymatic antioxidants | Annual | Dicot | Manan et al., 2016 |
|             | *Brassica napus* (L.) | 100 µM | Increases relative water content, soluble sugar, photosynthesis | Annual | Dicot | Ahmad et al., 2018 |
| JA          | *Pisum sativum* (L.) | 10$^{-5}$ M | Decreased activity of sodium and chloride ions, increased endogenous level of proline | Annual | Dicot | Velitchkova and Fedina, 1998 |
|             | *Oryza sativa* (L.) | 30 µM | Increases ion uptake, growth, ABA levels | Annual | Monocot | Kang et al., 2005 |
|             | *Hordeum vulgare* (L.) | 12 µM | Induction of genes having role in imparting salt tolerance | Annual | Monocot | Walia et al., 2007 |
|             | *Brassica napus* (L.) | 10$^{-6}$, 10$^{-9}$, and 10$^{-12}$ M | Sugar accumulation | Annual | Dicot | Kaur et al., 2013 |
|             | *Triticum aestivum* (L.) | 2 mM | Increase in concentration of GSH, enhanced activity of SOD, CAT, APX | Annual | Monocot | Qiu et al., 2014 |
| GSH         | *Oryza sativa* (L.) | 2 mM | Positive influence on yield contributing traits | Annual | Monocot | Wang et al., 2014 |
|             | *Arabidopsis thaliana* (L.) | 400 µM | Abscisic acid, auxin and jasmonic acid biosynthesis | Annual | Dicot | Cheng et al., 2015 |
|             | *Vigna radiata* (L.) | 1 mM | Activation of glyoxalase system and improved antioxidant system | Annual | Dicot | Nahar et al., 2015b |
|             | *Solanum lycopersicum* (L.) | 5 mM | Increased GSH biosynthesis, improved activity of SOD, CAT, POD | Annual | Dicot | Zhou et al., 2017 |
|             | *Glycine max* (L.) | 2 mM | Improved stress tolerance and yield attributes | Annual | Dicot | Akram et al., 2017 |
| Ca$^{2+}$   | *Solanum lycopersicum* (L.) | 5 and 10 mM | Increased growth, physiology and fruit production | Annual | Dicot | Parvin et al., 2015 |
|             | *Glycine max* (L.) | 6 mM | Positive effect on growth and metabolic activities. | Annual | Dicot | Yin et al., 2015 |
|             | *Oryza sativa* (L.) | 3 and 5 mM | Elevated antioxidant enzyme levels | Annual | Monocot | Tahjib-Ul-Arif et al., 2018 |
| Lead        | *Wolffia arrhiza* (L.) | 0.1 µM | Preventing Pb accumulation by restoring plant growth and primary metabolite level | Perennial | Monocot | Piotrowska et al., 2009 |
|             | *Solanum lycopersicum* (L.) | 0.1, 1, and 100 µM | Increase osmolytes concentration and ascorbate glutathione cycle | Annual | Dicot | Bali et al., 2018 |

(Continued)
### TABLE 1 | Continued

| Stress type | Plant species | JA/GSH/Ca\(^2\)+ | Response | Growth pattern | Cotyledon number | References |
|-------------|---------------|-------------------|----------|----------------|------------------|------------|
| **GSH**     |               |                   |          |                |                  |            |
|             | Gossypium sp. (L.) | 50 µM            | Stabilized ultra-structure and increased antioxidant activity | Perennial | Dicot | Khan M. et al., 2016 |
|             | Triticum aestivum (L.) | 1 mM             | Enhancement of enzymatic and non-enzymatic antioxidant activities and improved seedling growth | Annual | Monocot | Hasanuzzaman et al., 2018 |
| **Cadmium** |                |                   |          |                |                  |            |
|             | Glycine max (L.) | 20 µM            | Increased antioxidant response | Annual | Dicot | Noriega et al., 2012 |
|             | Vicia faba (L.) | 0.01 mM          | Restoration of growth and pigment system | Annual | Dicot | Ahmad et al., 2017 |
|             | Brassica napus (L.) | 25 µM           | Osmolytes and antioxidant activity increased | Annual | Dicot | Ali et al., 2018 |
| **MeJA**    |                |                   |          |                |                  |            |
|             | Oryza sativa (L.) | 5 µM             | GSH homeostasis, JA biosynthesis | Annual | Monocot | Singh and Shah, 2014 |
|             | Arabidopsis thaliana (L.) | 0.01 µM | Suppression of genes involved in Cd uptake | Annual | Dicot | Lei et al., 2020 |
|             | Hordeum vulgare (L.) | 20 mg/L    | Improved photosynthesis | Annual | Monocot | Chen et al., 2010 |
|             | Oryza sativa (L.) | 50 µM           | Enhanced photosynthetic performance | Annual | Monocot | Cai et al., 2011a |
|             | Gossypium sp. (L.) | 50 µM           | Reverses stressful effects, leaf ultra-morphology revived | Perennial | Monocot | Daud et al., 2016 |
|             | Populus sp. (L.) | 100 µM          | Increased Cd detoxifying gene transcript | Perennial | Monocot | Ding et al., 2017 |
| **Ca\(^2\)+** |              |                   |          |                |                  |            |
|             | Vicia faba (L.) | 2%               | Antioxidant enzyme up regulation | Annual | Dicot | Siddiqui et al., 2012 |
|             | Brassica juncea (L.) | 50 mM      | Improved photosynthesis | Annual | Dicot | Ahmad et al., 2015 |
|             | Arabidopsis thaliana (L.) | 3 mM     | Alleviated the inhibition of Cd on the root growth | Annual | Dicot | Li P. et al., 2016 |
|             | Sesamum indicum (L.) | 50 mM        | Improved growth and proline levels | Annual | Dicot | Abd-Allah et al., 2017 |
| **Copper**  |                |                   |          |                |                  |            |
|             | Oryza sativa (L.) | 0.5 mM          | Phytoalexin production | Annual | Monocot | Rakwal et al., 1996 |
|             | Cajanus cajan (L.) | 1 µM, 1 nM,    | Osmolytes and antioxidant enzyme increased | Perennial | Dicot | Poonam et al., 2013 |
|             | Triticum Aestivum (L.) | 5 mM     | Increased transcript of glutathione-s- transferase | Annual | Monocot | Li et al., 2013 |
| **MeJA**    |                |                   |          |                |                  |            |
|             | Phaseolus coccineus (L.) | 10^{-5} M | Promoted plant growth and development | Perennial | Dicot | Hanaka et al., 2015 |
| **GSH**     |                |                   |          |                |                  |            |
|             | Triticum aestivum (L.) | 2.5 mM/L  | Accumulation of nitrogen, sulfur, and phosphorous | Annual | Monocot | Peng et al., 2012 |
|             | Glycine Max (L.) | 0.16 and 0.32 Mm/L | Enhances amylase activity | Annual | Dicot | Chen, 2012 |
|             | Oryza Sativa (L.) | 100 mg/L       | Increased germination rate and vigor index | Annual | Monocot | Mostofa et al., 2015 |
| **Ca\(^2\)+** |              |                   |          |                |                  |            |

(Continued)
### TABLE 1 | Continued

| Stress type | Plant species | JA/GSH/Ca\(^{2+}\) Response | Growth pattern | Cotyledon number | References |
|-------------|---------------|--------------------------------|----------------|------------------|------------|
| Drought JA  | Glycine Max (L.) | 4.5 and 9 mM/L | Maintenance of membrane integrity | Annual | Dicot | Chen et al., 2006 |
|             | Vigna radiata (L.) | 5 mM | Solution improved the growth of Cu-treated seedling and lowering the concentration of Polyamines putrescine and increased concentrations of spermine and spermidine in epicotyl of plants | Annual | Dicot | Shen et al., 1998 |
|             | Brassica sp. (L.) | 0.5 mM | Increase in physiological, antioxidant and glyoxalase system activities | Annual | Dicot | Alam et al., 2014 |
|             | Allium cepa (L.) | 25, 50, and 100 \(\mu\)M | Pigment and compatible solute enhancement | Annual | Monocot | Ahmad and Murali, 2015 |
|             | Beta vulgaris (L.) | 5 and 10 \(\mu\)M | Increased germination rate | Annual | Dicot | Ghafari and Tadayon, 2019 |
| MeJA        | Brassica oleracea (L.) | 10 \(\mu\)M | Increased Net photosynthetic rate and antioxidant machinery activation | Annual | Dicot | Wu et al., 2012 |
|             | Triticum aestivum (L.) | 0.25 \(\mu\)M | Water status and antioxidant capacity increased | Annual | Monocot | Ma et al., 2014 |
|             | Satureja hortensis (L.) | 75, 150, and 225 \(\mu\)M | Improved many characteristics of plant like growth, water content, proline level, antioxidant activity | Annual | Dicot | Miranshahi and Sayyari, 2016 |
| GSH         | Arabidopsis thaliana (L.) | 400 \(\mu\)M | Changes at translational level of numerous hormones | Annual | Dicot | Cheng et al., 2015 |
|             | Vigna radiata (L.) | 1 \(\mu\)M | Improved their antioxidant components under drought stress | Annual | Dicot | Nahar et al., 2015a |
| Ca\(^{2+}\) | Zoysia japonica (L.) | 5 and 10 mM | Improved photosynthesis, growth and antioxidant response | Perennial | Monocot | Xu et al., 2013 |
|             | Zea mays (L.) | 5 mg/L | Improved photosynthesis, growth and soluble sugar content | Annual | Monocot | Naeem et al., 2018 |
|             | Nicotiana tabacum (L.) | 10 mM/L | Stabilization of gaseous exchange and photosynthetic organelles | Annual | Dicot | Hu et al., 2018 |
| Flooding JA | Citrus spp. (L.) | 1 mM | Increase in abscisic acid levels | Perennial | Dicot | de Ollas et al., 2013 |
| Ca\(^{2+}\) | Zea mays (L.) | 0.75% (W/V) | Regulates the cell wall integrity and mitigates effect of oxidative stress during flood stress conditions | Annual | Monocot | Porto et al., 2013 |
|             | Glycine max (L.) | 50 mM | Increase the root elongation and inhibited the cell death of root tip of under flood stress | Annual | Dicot | Oh et al., 2014 |

(Continued)
| Stress type       | Plant species                      | JA/GSH/Ca$^{2+}$ | Response                                                                 | Growth pattern | Cotyledon number | References               |
|-------------------|-----------------------------------|------------------|--------------------------------------------------------------------------|----------------|------------------|--------------------------|
| Ozone stress      | Capsicum annuum (L.)              | 10 mM            | Regulates osmotic and antioxidant metabolism                             | Annual         | Dicot            | Yang et al., 2016        |
|                   | Arabidopsis thaliana (L.)         | 1.4 µM           | Inhibited cell death and lesion containment                              | Annual         | Dicot            | Overmyer et al., 2000    |
|                   | Arabidopsis thaliana (L.) (JA insensitive mutants) | 10 µM           | Extremely susceptible to ozone                                            | Annual         | Dicot            | Kanna et al., 2004       |
|                   | Transgenic Nicotiana tabacum (L.) | Overexpression of glutathione synthetase in plastid | Ozone tolerance developed                                                | Annual         | Dicot            | Welburn et al., 1998     |
|                   | Populus sp. (L.)                  | Overexpression of Glutathione reductase | Ozone tolerance developed                                                | Perennial      | Monocot          | Foyer et al., 1995       |
| Heat              | Vitis sp (L.) seedling            | 50 µM/L          | Thermotolerance                                                          | Perennial      | Dicot            | Chen et al., 2006        |
|                   | Solanum lycopersicum (L.)         | 1 Mm             | Operating efficiency of photosystem II increased                         | Annual         | Dicot            | Sakhonwasee and Phingkasan, 2017 |
|                   | Nicotiana tabacum (L.)            | 20 Mm            | Improved stomatal conductance and thermostability                        | Annual         | Dicot            | Tan et al., 2011         |
| Cold              | Prunus persica (L.)               | 0.1 Mm/L         | Maintenance of fruit quality                                              | Perennial      | Dicot            | Meng et al., 2009        |
| MeJA              | Cucumis sativus (L.)              | 100 µM           | Enhances chilling tolerance by regulating antioxidant enzymes            | Annual         | Dicot            | Li et al., 2012          |
|                   | Arabidopsis thaliana (L.)         | 30 µM            | Induced freezing tolerance                                               | Annual         | Dicot            | Hu et al., 2013          |
|                   | Eriobotrya japonica (L.)          | 10 µM            | Alleviates the chilling injury in the fruits of plants                   | Perennial      | Dicot            | Cai et al., 2011b        |
| Ca$^{2+}$         | Solanum lycopersicum (L.)         | 27 mM            | Improvement carbon fixation, electron transport, etc.                    | Annual         | Dicot            | Zhang G. et al., 2014    |
|                   | Cynodon dactylon (L.)             | 1, 5, 10, and 20 mM | Antioxidant activation and metabolic homeostasis                        | Perennial      | Monocot          | Shi et al., 2014         |
| GSH               | Eriobotrya japonica (L.)          | 50, 100, and 300 mg/L | Increase in membrane fluidity and decrease in lipid peroxidation       | Perennial      | Dicot            | Wu et al., 2010          |
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is sequestered via production of antioxidants like GSH (Noctor and Foyer, 1998). Moreover, in response to JA and heavy metals increase in GSH in plants occurs via the expression of genes transcribing the enzymes for GSH production (Schafer et al., 1997; Xiang and Oliver, 1998). JA also leads to increased activity of GCL and GS. Increase of GCL activity causes more glutathione disulfide or oxidized glutathione (GSSG) formation. GSSG in turn causes release of Ca$^{2+}$ thereby also affecting Ca$^{2+}$ signatures (Gómez et al., 2004; Hicks et al., 2007; Sun et al., 2009). Moreover, in response to GSH and GSSG treatment, Ca$^{2+}$ release occurs in plants as seen in tobacco leaf. Ca$^{2+}$ related response is linked to overall GSH supplied to the leaf. Therefore, GSSG has an effect on calcium signatures (Gómez et al., 2004). However, JA biosynthesis and signaling is in turn regulated by Ca$^{2+}$ (Wasternack and Hause, 2013). Glutathione status is modulated by various abiotic stresses that affect the abundance of transcripts related with JA signaling, synthesis, and downstream cascade (Gómez et al., 2004; Han et al., 2013). OPR3, one of the JA biosynthetic enzyme expressions, increased with Ca$^{2+}$ treatment (Chotikacharoensuk et al., 2006). It is also found that Ca$^{2+}$ signaling results in increased levels of OPR3 and JA (Gust et al., 2005).

It is inferred that there must be crosstalk between the JA induced influx of apoplast and ionistol triphosphate sensitive Ca$^{2+}$ stores as JA induced influx of extracellular Ca$^{2+}$ concentration can be via nifedipine sensitive Ca$^{2+}$ channel in the plasma membrane and expression of downstream genes to JA (Sun et al., 2006; Ladyzhenskaia and Korabueva, 2008). It has also been demonstrated that for JA synthesis influx Ca$^{2+}$ is necessary for elicitor induction (Hu et al., 2009). However, JA-induced signaling cascade may lead to activation of nifedipine sensitive channels to increase in cytosolic Ca$^{2+}$ which in turn causes release of Ca$^{2+}$ from intra-cellular stores (Sun et al., 2009). JAs also might be involved in transducing signaling pathways and upregulation of the GSH metabolic genes and encourages the synthesis of GSH which eliminates peroxides via ascorbate-glutathione cycle (Smeets et al., 2005; Rouhier et al., 2008). MeJA has found to be responsible for increased expression of JA and glutathione biosynthesis enzymes (Jung et al., 2007).

The whole cross talk or interaction between JA, Ca$^{2+}$, and GSH is summarized in **Figure 3**.

**PHYTO-HORMONE CROSS TALK UNDER ABIOTIC STRESS**

Plant hormones have critical roles in mediating the abiotic stress tolerance under unfavorable environmental conditions (Alhaithloul et al., 2020). Abiotic stresses lead to the induction of signal transduction pathways that helps a plant to adapt itself to changing environmental milieu (Dolferus, 2014; Ingole et al., 2021; Kolbert et al., 2021). It leads to the ROS generation and various phyto-hormone accumulation along with remodeling of gene expression in accordance with activation of preferable defense response. These phytohormones mediated signaling and interaction renders them ultimate entity for conferring abiotic stress tolerance in plants (Nguyen et al., 2016;}

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**FIGURE 3** Signaling pathways involved in abiotic stress tolerance. (A) Abiotic stresses causes ROS accumulation that leads to activation of Ca$^{2+}$ signaling and MAPK pathways to combat abiotic stresses in plants by maintaining cellular homeostasis. (B) Exogenous application of JA, Ca$^{2+}$ and GSH, respectively, to plants prior to or under abiotic stress mediates activation of Ca$^{2+}$ signaling and MAPK pathways via possible crosstalk mechanisms so as to further strengthen the cellular homeostatic mechanisms of plants, thereby imparting abiotic stress tolerance.
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Verma V. et al., 2016; Singh et al., 2019). Phytohormones cross talk in abiotic stress and its link with development of plant stress tolerance in accordance with JA, GSH and Ca\(^{2+}\) is discussed below.

**JA Phyto-Hormone Cross Talk Under Abiotic Stress**

Under multiple environmental stresses, plant hormones allocate limited resources to respond to the most serious stress and develop various signaling pathways to regulate the balance between plant growth and defense response (Tian et al., 2003; Matyszek et al., 2005; Sharma et al., 2013). Understanding the similarities and differences of plant hormone signaling may be important in agricultural production. The crosstalk between plant hormones is of vital importance in plant stress response (He et al., 2017). JA does not work independently but acts in a complex signaling network combined with other plant hormone signaling pathways (Ahmad et al., 2016; He et al., 2017; Hu et al., 2017; Westernack and Strnad, 2018). Kazan (2015) elucidated the immense role of JA and ethylene in abiotic stress. JA and ET are known to regulate plant tolerance against abiotic stress like drought cold salinity through coordination or antagonistically (van der Fits and Memelink, 2000; Zhai et al., 2013). Ethylene response factors (ERFs) that confer roles in abiotic stress combating mechanism are induced by JA signaling apart from ethylene, thereby facilitating cross talk between them (Ramegowda and Senthil-Kumar, 2015). ERF-domain transcription factor ORA59 of *A. thaliana*, ET INSENSITIVE3 (EIN3) and its homolog EIN3-like 1 (EIL1), as well as JAZs-MYC2 are involved in the crosstalk between JA and Ethylene signaling pathways (Zhu, 2003, 2014; Zhang X. et al., 2014; Zhu and Lee, 2015). JA interacts with ABA under abiotic stress to cause a physiological response to overcome abiotic stress factors (Gomez-Cadenas et al., 2015). MYC2 and JAZ have roles in cross talk between them (Chen Q. et al., 2011). JA cross talk with ABA imparts cold stress tolerance (Hu et al., 2013). MYC2, the core regulator of the JA signaling mechanism, contributes in the ABA signaling cascade in response to drought stress (Abe et al., 2003; Liu et al., 2014). Moreover, JA and SA also have the same regulator glutaredoxin GRX480 which maintains protein redox regulation due to its ability to catalyze disulfide transitions (Meldau et al., 2012). Mitogen-activated protein kinase 4 (MAPK4) is a negative regulator of SA signaling and positive regulator of JA signaling cascade in light stress (Sharma, 2013). The C-terminus of JAZs mediates interaction between JAZs and MYC2 and between JAZs and DELLAs. So, DELLAs can completely interact with JAZs (Hou et al., 2010). In absence of gibberelic acid (GA), DELLA can interact with JAZ and mediates release of MYC2 thereby inhibiting JA biosynthesis and mediating activation MYC2 downstream gene activation (MYB21 and MYB24) (Song et al., 2011). But in the presence of GA, DELLA gets degraded, thus allowing JAZ-MYC2 interaction (Hu et al., 2013). On the contrary, JA delays GA-mediated degradation of DELLA (Yang et al., 2012). JA and auxin signaling coordinately regulate the plant growth and development. COI1, MYC2, and JAZ are the core components in the crosstalk of JA and auxin signaling pathways. In response to exogenous auxin, the activation of auxin–TIR–AUX/IAA–ARF signaling occurs, mediating JA synthesis. The endogenous JA prompts the expression of auxin synthase gene (ASA1) and auxin content. JA leads to formation of a complex of COI1 and JAZ leading to the degradation of JAZ, thereby activating the transcriptional activities of MYB21/MYB24 and causing flower development (Chen Q. et al., 2011). JA also interacts with Cytokin in through MYC2 transcription factor. MYC2 is reported to be a negative regulator of cytokinin response by facilitating expression of inhibitor of cytokinin signaling AHP6. JA is involved in decreased expression of PIN-FORMED 7 gene that is involved in the development of xylem and it has been reported that extra xylem formation takes place in roots of Arabidopsis under drought stress (Jang and Do Choi, 2018). So, this opposite interaction between JA and Cytokinin has a role in JA dependent stress response. It is also suggested that differential cytokinin expression under stressful conditions leads to JA – cytokinin interaction at a metabolic level (Le et al., 2012; Jang and Do Choi, 2018). So JA interacts with a different kinds of hormones to regulate the growth and development of plants such as GA, auxin, cytokinin, Ethylene, and SA (Figure 4). These interactions may help to optimize growth and development of plants under abiotic stress conditions.

**Glutathione Phytohormone Cross Talk Under Abiotic Stress**

Adverse climatic conditions lead to abiotic stress in plants. Peroxiosomal or cytosolic atmosphere leads to electron absorption and subsequently causes oxidative damage via ROS generation (Hasanuzzaman et al., 2017b). ROS-mediated abiotic stress induces apoptosis or whole plant death in many plant cultivars (Petrov et al., 2015; He et al., 2018). It imparts signals that regulate stress adaptation (Hmamdi and Van Breusegem, 2018). Plants have an antioxidant defense system comprising of non-enzymatic and enzymatic antioxidants in cell organelles, which aids in ROS removal up to a certain level (Gill and Tuteja, 2010). Among this well-defined antioxidant system, Glutathione regulates numerous metabolic functions. Glutathione peroxidase is responsible for ROS detoxification (Hasanuzzaman et al., 2017a). Glutathione increases the plant tolerance to different abiotic stresses, including salinity, drought, high temperature (HT), low temperature, and toxic metal stress (Hasanuzzaman et al., 2013). Exogenously given GSH imparts abiotic stress tolerance in plants (Nahar et al., 2015a,b). Hormonal regulation of GSH and its role in abiotic stress tolerance have been reported in many research findings. Transcriptome analysis revealed that GSH treatment leads to biosynthesis of Auxin, JA, and ABA along with activation signaling cascades pertaining to them (Cheng et al., 2015). GST overexpression in *A. thaliana* plants have signaling and regulatory roles in plant development by maintaining GSH pools (Chen et al., 2012). The increased activities of GST and GPX contributes to improved salt stress in the auxin autotrophic tobacco callus lines (Csizsár et al., 2004). Phytohormones like JA, ABA, Auxin, ethylene,
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FIGURE 4 | Crosstalk between phytohormones with JA under abiotic stress conditions via different transcription factors. JA interacts with other phytohormones such as SA, ETH, ABA, GA, AUX, and CK in order to regulate plant abiotic stress. JA signaling inhibits SA by modulating mitogen activating protein kinase (MAPK4). Similarly, crosstalk of JA and ETH signaling pathway occurs through interaction of three TFs viz ERF, JAZ, and MYC2 thereby regulating plant stress response. MYC2 also participates in crosstalk of JA and ABA signaling pathway. DELLA interacts with JAZ in absence of GA to release MYC thereby inhibiting JA biosynthesis and causing activation of MYC downstream genes. However, in the presence of GA, DELLA gets degraded so allowing JAZ-MYC interaction. COL, MYC2, and JAZ are the core components in the crosstalk of JA and AUX signaling pathways. JA mediated inhibition of CK signaling by MYC2 and AHP6 transcription factors. (AUX, auxin; SA, salicylic acid; ETH, ethylene; ABA, abscisic acid; GA, gibberellic acid; CK, cytokinin). 

cytokinin, and brassinosteroid induced GST expression in plants (Marrs, 1996; Moons, 2005; Deng et al., 2007). Exogenous Glutathione application brought higher levels of ABA (Chen, 2012). 2, 4-D and NAA (two synthetic auxins) and IAA induced expression of GST8 in Arabidopsis (Bianchi et al., 2002). Moreover, exogenous or endogenous auxin positively regulates the expression intensities of numerous abiotic stress-related genes along with GSH/GSSG pools and GR activity (Shi et al., 2014). JA also regulates GSH concentration and genes for GSH metabolism in Arabidopsis (Akter et al., 2010) and Agropyron cristatum, (Sasaki-Sekimoto et al., 2005). It functions as signaling molecule during MeJA signaling in guard cells in Arabidopsis, in addition to intracellular GSH regulating MeJA-induced movements of stomata (Koornneef and Pieterse, 2008). Exogenous SA caused changes in the levels of GSH, GR transcriptomics and activity in maize genotypes and soybean cell suspension thereby mediating abiotic stress tolerance (Knörzer et al., 1999; Kellös et al., 2008). Changes in both SA and GSH expression due to overexpression of the SA gene in rice were correlated with oxidative abiotic stress tolerance (Kusumi et al., 2006). Ethylene has been reported to regulate GSH biosynthesis positively in ozone exposed Arabidopsis leaves (Freeman et al., 2005). The inhibitor of GSH biosynthesis l-buthionine sulfoximine (BSO) effectively reduced the suppression of the JA-responsive gene PDF1.2 by SA, which suggests that SA-mediated control of the cellular redox state is an important trigger for JA signaling (Koornneef and Pieterse, 2008).

Calcium – Phytohormone Cross Talk Under Abiotic Stress

Plant hormone signaling cascades not only crosstalk with one another, but have also been reported to interact with other signaling molecules such as the Ca$^{2+}$ and mitogen-activated protein kinase (MAPK) pathways during an abiotic stress conditions (Ludwig et al., 2005; Roychoudhury and Paul, 2012; Roychoudhury and Banerjee, 2017). The overlap between hormone-regulated gene expression profiles as adaptive responses of plants to environmental stresses suggests the presence of a complex network with widespread interactions between the different hormone signaling pathways (Suhita et al., 2003, 2004). However, phytohormones like JA and ABA induced the Ca$^{2+}$ transients. The primary role of JA and ABA in the plasma membrane seem to be different to each other. JA aims to encounter the Ca$^{2+}$ channels whereas ABA stimulates effector molecules in the plasma membrane like phospholipase C and D. But at the intracellular Ca$^{2+}$ level, both signaling cascades converge. The intracellular Ca$^{2+}$ level is regulated to a much greater extent by JA rather than by ABA. It has been reported that JA interaction with ABA-regulated stomatal closure by increasing influx of Ca$^{2+}$ causes activation of CDPK-dependent signal pathways, contributing to the drought stress...
responsiveness (Shi S. et al., 2018). Treatment of Arabidopsis leaves with MeJA or ABA results in less stomatal aperture reduction within 10 min (Munemasa et al., 2007). Though the chemical inhibitors or in ABA-deficient mutants led to inhibition of ABA biosynthesis along with suppression of the MeJA-induced Ca\(^{2+}\) oscillations in guard cells (Hossain et al., 2011). Therefore, during stomatal closure MeJA interacts with ABA leading to further Ca\(^{2+}\) signaling cascade. Ca\(^{2+}\) increase, however, fosters the stomata closure by enhancing Slow Anion Channel-Associated 1 (SLAC1) and cytoskeletal rearrangement of plasma membrane (Waidyarathne and Samarasinghe, 2018). Ca\(^{2+}\) dependent ABA regulation is related to induction of enzymatic antioxidants (SOD, CAT3, APX, and GR) and non-enzymatic antioxidants [glutathione, ascorbic acid, carotenoids (Ahmad et al., 2010)]. Some drought-responsive CPKs also have some functions like, in rice, OsCPK9 regulates both drought stress tolerance and spikelet fertility through an ABA-dependent manner (Wei et al., 2014). Nevertheless, the precise role of Ca\(^{2+}\) in ABA signaling needs to be further explored (Waidyarathne and Samarasinghe, 2018). Gene expression of ethylene-induced ACC oxidase (VR-ACO1) in tissue of root of mung bean was reported due to Cytosolic Ca\(^{2+}\) transients. In fact, inhibitors and chelators of Ca\(^{2+}\) significantly inhibited the ethylene based gene expression of VR-ACO1, respectively (Jung et al., 2000). Ca\(^{2+}\) was seen to augment the conversion of ACC to ethylene in primary roots of Zea mays (Hasenstein and Evans, 1986). However, ethylene was found to be responsible for activation of plasma membrane Ca\(^{2+}\)-permeable channel to increase the Ca\(^{2+}\) level in suspension cells of tobacco (Nicotiana tabacum) (Zhao et al., 2007). So, this relationship between ethylene and Ca\(^{2+}\) seems to be an essential component in abiotic stress response (Acosta-Motos et al., 2017). It has been found that involvement of ethylene in Ca\(^{2+}\) induced adventitious rooting under salt stress (Yu et al., 2019). Ca\(^{2+}\) plays a pivotal role in the overall downward polar transport of auxin and in the absence of Ca\(^{2+}\) basipetal auxin, transport was halted. However, Ca\(^{2+}\) supplementation can overcome the inhibition of this basipetal transport of auxin (Lee et al., 1983; Allan and Rubery, 1991). So, the transport of auxin plays noteworthy role in the dispersal of Ca\(^{2+}\) to developing tissues (Ranuelos et al., 1987). The auxin transport pathway seems to be involved in the remodeling of root system architecture in Ca\(^{2+}\) mediated alleviation of metal toxicity like Cd toxicity (Li P. et al., 2016).

OMICS APPROACHES TO STUDY THE ROLES OF JA, Ca\(^{2+}\), AND GSH UNDER ABIOTIC STRESS

The intricate molecular controlling systems that have roles in abiotic stress adaptation and tolerance in plants can be interpreted using an ‘omics’ approach (Chawla et al., 2011). The omics technologies have paved the way toward the development of well-established protocols that provide in-depth insights about the gene functionality including their phenotypic effect in defined biological frameworks. Comparative genomic analysis between the plant models like Thellungiella halophila and A. thaliana have remarkable cold, drought, and salinity tolerance. So, plants tend to modify their omics profile to withstand the fluctuating environment for their existence (Gong et al., 2005). Almost 50% of the plant genes were activated by stresses including drought and salinity. The abiotic stress responding genes can be divided into two classes based either on their response in terms of timescale or on their involvement in tolerance, some seem to respond quickly within seconds or minutes, while others respond slowly (Ramanjulu and Bartels, 2002). It has been reported that about 15% more unknown genes were expressed in the plant subjected to salt stress than in the unstressed plant suggesting that the exposure of plant to abiotic stress results in the surge in expression of genes. In response to various abiotic stresses in plants, proteomic studies has been mostly accepted to explore the protein profiles that might lead to the progression of new strategic ways to improve stress tolerance (Cushman and Bohnert, 2000).

Researchers have used various omics approaches to decipher an integrated model of plant response to different abiotic stresses (Zhu et al., 2017; Bajwa et al., 2018; Parida et al., 2018; Zhang et al., 2018). Treatment of plants with MeJA showed remarkable change in their protein profile. Nearly 194 proteins were differentially expressed in various plant physiological processes. Functional analyses revealed that carbohydrate catabolism was upregulated along with some proteins involved in JA biosynthesis pathway and stress defense (Chen Y. et al., 2011). Multi-omics analysis determined vigorous cascade of transcriptional reprogramming via TF MYC2 and MYC3 that tend to target lots of JA-responsive genes, thereby enabling expression of cohorts of genes that have distinct roles within the JA response. This depicts the complexity of the hormone-response based genome regulatory program. Further, functional importance of MYC2 and MYC3 target genes in JA responses has been validated. Mutations in six genes caused evident disturbances in JA responses, both hypersensitivity and hyposensitivity (Zander et al., 2020).

Microarray experiments of wheat and barley cultivars under boron toxicity conditions suggest that genes related to jasmonate biosynthesis and GST can have roles in boron tolerance mechanisms in cereals (Öz et al., 2009). Moreover, plants have a complex antioxidant defense system to scavenge ROS under stress conditions (Hossain et al., 2009). Transgenic plants over express enzymes involved in oxidative stress protection like GPX, SOD, and GR (Tang et al., 2006). The differential expression of Medicago GST (MtGST) were upregulated whereas some of them were downregulated under abiotic stress. Two cluster groups - MtGSTU46 to MtGSTF8 and MtGSTL4 to MtGTH5 genes were mostly increased in both drought and salinity stresses. Among them, MtGSTU8, MtGSTU17, MtGSTF8, MtGSTT2, and MtGSTZ1 members were mostly upregulated in all cases of these two abiotic stresses (Hasan et al., 2021). AtGSTU19 and AtGSTF2 favors the glutathionylation and binds to JA hormone precursor oxylipin 12-OPDA. So, GST seems to be involved in the export of 12-OPDA from the chloroplast to the site of JA synthesis (peroxisome) (Dixon and Edwards, 2009). Interestingly, greater 12-OPDA level in plants promoted less stomatal aperture and drought tolerance (Savchenko et al., 2014). This points to a potential crosstalk among 12-OPDA (JA) and GSTs as GSTs are quickly induced by 12-OPDA and JA
participates in activation of the plasma membrane Na\(^+\) in abiotic stress response. SOS3/ScaBP8/CBL10 and SOS2/CIPK24/SnRK3 which have important functions. SnRK3-type kinases including SALT OVERLY SENSITIVE (SOS) 2 have a specific role in abiotic stress responses (Iqbal et al., 2020). About 30 CDPK genes have been reported in Arabidopsis that have role in abiotic stress responses (Hrabak et al., 2003). Arabidopsis has Ca\(^{2+}\)-binding calcineurin B-like (CBL) proteins dependent 25 SnRK3 type kinases including SALT OVERLY SENSITIVE (SOS2)/CIPK24/SnRK3 which have important functions in abiotic stress response. SOS3/ScabP8/CBL10 and SOS2 participate in activation of the plasma membrane Na\(^+\)/H\(^+\) antiporter (SOS1) prerequisite for salinity tolerance (Luan, 2009). Transcriptomics has revealed that CaM binds to regulate various transcription factors called as CAMTAs generating the stress response (Reddy et al., 2011). CAMTAs comprise bZIP, MYB, WRKY, and NAC families of transcription factors (Popescu et al., 2007; Yoon et al., 2008). Several CBLs have a myristoylation site that stimulates membrane association (Ishitani et al., 2000; Kolukisaoglu et al., 2004; Cheong et al., 2007). Moreover, different combinations of CBLs and CIPKs genes have been identified in plants. Genes encoding CBLs or CIPKs are attributed only to the plant kingdom by computer analysis deciphering their function being restricted to plants (Kolukisaoglu et al., 2004). Differential expression of CBL genes indicating their role in abiotic stress response has been reported also (Kudla et al., 2010). So, different omics tools have been employed to understand plants' responses to abiotic stress conditions. It involves the integration of multiple omics. Systematic use of omics approaches such as metabolomics, transcriptomics, proteomics, and fluxome are means to connect the global data generated via phenomics has led to expansion toward stress biology for revealing the mechanisms of stress responses. The expression of abiotic stress and adaptation to a specific abiotic stress.

### CONCLUSION AND FUTURE PERSPECTIVE

Jasmonic acid plays a key role in plant regulatory and developmental processes. It has a potent role in alleviating abiotic stress conditions in plants. This review of literature is of the opinion that JA biosynthesis and signaling is dependent on Ca\(^{2+}\) levels, however, JA itself can modulate the Ca\(^{2+}\) transients. Ca\(^{2+}\) transients are also seen in varied abiotic stresses as an early response. In addition to this, one of the plant antioxidants GSH also has a pivotal role in abiotic stress response and tolerance. GSH tends to interact with JA and also facilitates the expression of genes involved in JA biosynthesis. Moreover, it has been seen that release of Ca\(^{2+}\) from internal plant stores is also mediated by GSH. Exogenous application of JA also results in an increase in cytosolic Ca\(^{2+}\) concentration. This all implies possible interactions between JA, Ca\(^{2+}\), and GSH which helps in mitigating plant abiotic stress. This kind of study will help to adopt different approaches pertaining to abiotic stress tolerance. So, JA biosynthesis and signaling, calcium transients, and GSH seem to be co-related with each other. This review clearly suggests (1) Ca\(^{2+}\) signaling leads to JA formation then followed by GSH. (2) JA also facilitates the expression of GSH and vice versa. (3) JA and GSH both mediate the release of Ca\(^{2+}\) from internal plant stores. This type of interaction between the JA, Ca\(^{2+}\), and GSH decipher the novel mechanism of abiotic stress tolerance in plants. Detailed functional characterization of JA, Ca\(^{2+}\), and GSH will help us to decipher the core mechanism and identification of various novel entities that could have an important role in this cross talk. It will further help us to understand plant stress biology and unravel the intricate molecular mechanisms that help plants to combat the effect of abiotic stresses which are otherwise a major threat to agricultural productivity. Therefore, it may be concluded that JA, Ca\(^{2+}\), and GSH can enhance abiotic stress tolerance via initiating the possibly correlated signaling cascade.

### AUTHOR CONTRIBUTIONS

SA and NG: conceptualization and compilation of data. SA, NG, and SQ: writing part. SA, NG, MM, MA, NA-S, and AAA: designing of figures and generation of table.

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Mueller et al., 2008). However, GST binding might regulate the temporal signaling of oxylipins under stress. Elevated GST expression correlates with increased stress tolerance as observed in tomato (Sun et al., 2010) and wheat (Gallé et al., 2009). Moreover, OsGSTSL2 overexpression imparted a rise in tolerance level against drought, cold stress, and salinity (Kumar et al., 2013). However, the cytosolic Ca\(^{2+}\) transients have been reported under various stresses such as heat, cold, salinity, and water (Mahajan and Tuteja, 2005; Tuteja and Mahajan, 2007; Riveras et al., 2015). The promoter region analysis of the Ca\(^{2+}\) shows biased nature toward abiotic stress responsive genes. Three among four Ca\(^{2+}\) regulated promoter regions were reported to be indispensable for abiotic stress responses (Iqbal et al., 2020). About 30 CDPK genes have been reported in Arabidopsis that have role in abiotic stress responses (Hrabak et al., 2003). Arabidopsis has Ca\(^{2+}\)-binding calcineurin B-like (CBL) proteins dependent 25 SnRK3-type kinases including SALT OVERLY SENSITIVE 2 (SOS2)/CIPK24/SnRK3 which have important functions in abiotic stress response. SOS3/ScabP8/CBL10 and SOS2 participate in activation of the plasma membrane Na\(^+\)/H\(^+\) antiporter (SOS1) prerequisite for salinity tolerance (Luan, 2009). Transcriptomics has revealed that CaM binds to regulate various transcription factors called as CAMTAs generating the stress response (Reddy et al., 2011). CAMTAs comprise bZIP, MYB, WRKY, and NAC families of transcription factors (Popescu et al., 2007; Yoon et al., 2008). Several CBLs have a myristoylation site that stimulates membrane association (Ishitani et al., 2000; Kolukisaoglu et al., 2004; Cheong et al., 2007). Moreover, different combinations of CBLs and CIPKs genes have been identified in plants. Genes encoding CBLs or CIPKs are attributed only to the plant kingdom by computer analysis deciphering their function being restricted to plants (Kolukisaoglu et al., 2004). Differential expression of CBL genes indicating their role in abiotic stress response has been reported also (Kudla et al., 2010). So, different omics tools have been employed to understand plants’ responses to abiotic stress conditions. It involves the integration of multiple omics. Systematic use of omics approaches such as metabolomics, transcriptomics, proteomics, and fluxome are means to connect the global data generated via phenomics has led to expansion toward stress biology for revealing the mechanisms of stress responses. The expression of abiotic stress and adaptation to a specific abiotic stress.

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