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Jasmonates and Salicylates Signaling in Plants

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Preface

Demand for agricultural crops and nutritional requirements continues to escalate in response to increasing population. Also, climate change exerts adverse effects on agricultural crop productivity. Plant researchers have therefore focused to identify the scientific approaches that minimize the negative impacts of climate change on agriculture crops. Thus, it is the need of the hour to expedite the process for improving stress tolerance mechanisms in agricultural crops against various environmental factors, in order to fulfil the world's food demand. Among the various applied approaches, the application of phytohormones, has gained significant attention in inducing stress tolerance mechanisms.

Jasmonates are phytohormones with ubiquitous distribution among plants and generally considered to modulate many physiological events in higher plants such as defence responses, flowering, and senescence. Also, jasmonates mediate plant responses to many biotic and abiotic stresses by triggering a transcriptional reprogramming that allows cells to cope with pathogens and stresses. Likewise, salicylates are important signal molecules for modulating plant responses to environmental stresses. Salicylic acid may influence a range of diverse processes in plants, including seed germination, stomatal closure, ion uptake and transport, membrane permeability and photosynthetic and growth rate.

The present book covers a wide range of topics, discussing the role and signalling of jasmonates and salicylates in normal as well as challenging environments. Moreover, this is an unique reference book on the topic discussing the role of jasmonates and salicylates with the latest biotechnological approaches. We believe that this book will initiate and introduce readers to state-of-the-art developments and trends in this field of study.

The book comprises of 15 chapters, which are review articles written by experts, highlighting wide range of topics, discussing the role and regulation jasmonates and salicylates in plants under normal and stressful conditions. We are hopeful, this volume would furnish the need of all researchers who are working or have interest in this particular field. Undoubtedly, this book will be helpful for general use of research students, teachers, and those who have interest in these growth regulators.

We are highly grateful to all our contributors for accepting our invitation for not only sharing their knowledge and research, but for venerably integrating their

expertise in dispersed information from diverse fields in composing the chapters and enduring editorial suggestions to finally produce this venture. We also thank Springer Nature team for their generous cooperation at every stage of the book production.

Lastly, thanks are also due to well-wishers, research students, and editors' family members for their moral support, blessings, and inspiration in the compilation of this book.

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Dr. Tariq Aftab received his Ph.D. in the Department of Botany at Aligarh Muslim University, India, and is currently an Assistant Professor there. He is the recipient of a prestigious Leibniz-DAAD fellowship from Germany, Raman Fellowship from the Government of India, and Young Scientist Awards from the State Government of Uttar Pradesh (India) and Government of India. After completing his doctorate, he has worked as Research Fellow at the National Bureau of Plant Genetic Resources, New Delhi and as Postdoctoral Fellow at Jamia Hamdard, New Delhi, India. Dr. Aftab also worked as Visiting Scientist at Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben, Germany, and in the Department of Plant Biology, Michigan State University, USA. He is a member of various scientific associations from India and abroad.

He has edited 10 books with international publishers, including Elsevier Inc., Springer Nature, and CRC Press (Taylor & Francis Group), co-authored several book chapters, and published over 60 research papers in peer-reviewed international journals. His research interests include physiological, proteomic, and molecular studies in medicinal and crop plants.

Dr. Mohammad Yusuf is Lecturer in the Department of Biology, United Arab Emirates University, Al Ain, UAE. Mohammad received his Ph.D. in Plant Physiology and M.Sc. in Botany (Plant Physiology) from Aligarh Muslim University, India. He has worked as the SERB-Young Scientist and also an awardee of the prestigious Dr. D.S. Kothari Postdoctoral Fellowship from the Government of India. He has also been invited to present his work at Huazhong Agricultural University (HAU), Wuhan, China. Mohammad's research contribution includes more than 50 research articles in the international journal of repute and also more than 2500 google scholar citations with 26 h-index. He is exploring phytohormones mediated abiotic stress tolerance mechanism in crop plants through proline metabolism.

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Jasmonates and Salicylates: Mechanisms, Transport and Signalling During Abiotic Stress in Plants

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Abstract Population across the globe are increasing at an alarming rate. UN Population Division currently (2020) expects that the world population is now 7.8 billion, which will be reached 10.9 billion (the median line) at the end of the twenty-first century. To meet the food demand of increasing population cereal equivalent food demand needs to be increased by about 10,094 million tons by the year 2030 and 14,886 million tons in 2050. At the same time, climate change will impact on agricultural productivity, as a result of the extreme events of abiotic stresses. For example, on an average, about 50% yield losses of several crops are occurred mostly due to high temperature (20%), low temperature (7%), salinity (10%), drought (9%) and other abiotic stresses (4%). Other earlier studies, estimated that a large enhancement of biomass and grain yield loss (83% on average) of wheat was observed when salinity was combined with drought stress. Global wheat production is estimated to fall by 6% for each °C temperature increase further and will be become more variable over space and time. To alleviate the antagonistic effect of abiotic stresses, generally, plants take numerous adaptive mechanisms. Among them, several phytohormones play an

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important role in abiotic stress tolerance in plants. The chapter discussed the role of phytohormones, particularly biosynthesis, transport and signalling mechanisms of jasmonates and salicylates during abiotic stress tolerance in plants.

1   Introduction

In view of the global climate change, drought, salinity and heat stresses are the major abiotic constraints for wheat productivity and adversely affects the yield and quality through altering the physiological activity (Outoukarte et al. 2019; Yassin et al. 2019). On an average, about 50% yield losses of several crops are occurred mostly due to high temperature (20%), low temperature (7%), salinity (10%), drought (9%) and other abiotic stresses (4%) (Kajla et al. 2015).

Among the abiotic stresses, the frequency and severity of drought events in wheat-growing areas will be increased due to the possibility of climate change, and rapidly growing demands on available land and water resources (Trenberth et al. 2014). Approximately 65 million hectare land for wheat production was affected by drought stress in 2013 (FAO 2019). Drought is a non-uniform phenomenon that negatively influences plant growth, morphology, physiology and yield depending upon crop developmental stage, time, and severity of stress (Ahmad and Prasad 2011). Mild salinity and drought have important consequences for agriculture since it shows that when mildly saline areas are affected by drought the crop yield loss can be aggravated. Importantly, a large enhancement of biomass and grain yield loss (83% on average) was observed when salinity was combined with drought stress (Paul et al. 2019). Initial drought stress significantly reduced the total shoot, leaf relative water content, leaf dry weight, root dry weight, and chlorophyll and carotenoid content of drought acclimation plants in all the wheat genotypes (Amoah et al. 2019). Drought increases senescence by accelerating chlorophyll degradation, leading to a decrease in leaf area and photosynthesis. Rainfed and drought stress at the tillering stage resulted in a reduction of total dry matter of 28.2 and 16.2%, respectively, compared to irrigate (Mehraban et al. 2019). It has been confirmed by many researchers that

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water stress leads to growth reduction, which was reflected in plant height, leaf area, dry weight, and other growth functions (Kilic and Yağbasanlar 2010).

The primary effect of heat stress is the impediment of seed germination and poor stand establishment in many crops (Hossain et al. 2013). Ambient temperature around 45 °C severely affects embryonic cell in wheat which reduces crop stands through impairing seed germination and emergence (Essemine et al. 2010). Heat stress ranging from 28 to 30 °C may alter the plant growth duration by reducing seed germination and maturity periods (Yamamoto et al. 2008). Increasing temperature will influence the sustaining wheat production causing challenging the global food security due to the deleterious impacts of climate change (Tripathi et al. 2016). The effects of heat stress on plants are very complex resulting in accelerating of growth and development, changes in physiological functions, and reduced grain formation, which cause severely limit wheat yield (Mondal et al. 2013). Global wheat production is estimated to fall by 6% for each °C for further temperature increase and become more variable over space and time (Asseng et al. 2015). High temperature affects crops in different ways including poor germination and plant establishment, reduced photosynthesis, leaf senescence, decreased pollen viability, and consequently the production of fewer grains with smaller grain size (Asseng et al. 2011). The duration of heat stress was the most significant component in determining both seed number and seed weight, as well as the grain yield consequently, explaining 51.6% of its phenotypic variance. Irrespective of the developmental phase, the yield-related traits gradually deteriorated over time, and even a 5-day heat stress was sufficient to cause significant reductions (Balla et al. 2019).

Salinity is a major threat to agricultural productivity worldwide and presents a tremendous challenge for food security causing significant conversion of agricultural arable land into the unproductive wasteland, with about 20% of cultivated land and 33% of irrigated land being salt-affected and degraded in the world (Ahmad et al. 2019; FAO 2020). However, soil salinity is a major constraint for wheat production in many parts of the world affecting yield losses up to 60% and causing food insecurity (El-Hendawy et al. 2017). Salt stress caused 33, 51 and 82% reduction in germination vigour, seedling shoot dry matter and seed grain yield, respectively (Oyiga et al. 2016, 2018). Salinity in the arid and semi-arid region reduces the yield of wheat up to 50% (Dugasa et al. 2016). All phenological phases are accelerated under salinity stress in wheat. For example, the germination score is reduced about 7, 19 and 33% for 100, 150 and 200 mM NaCl, respectively, and 14 and 24% for 75 and 100 mM Na_2SO_4, respectively (Oyiga et al. 2016; Dadshani et al. 2019). Higher concentrations of salt create a lower osmotic potential of germination media which hampers the imbibition of water by seed, creates an imbalance in the normal activities of enzymes responsible for nucleic acid and protein metabolism, causes hormonal imbalance, and deteriorates the food reserves of seed (Hasanuzzaman et al. 2013).

To mitigate the adverse effect of abiotic stresses, plants follow several adaptive physiological mechanisms. Among these mechanisms, phytohormones play a significant role in abiotic stress tolerance in plants. The next sections of the chapter are discussed on the role of phytohormones, particularly biosynthesis, transport and

signalling mechanisms of jasmonates and salicylates during abiotic stress tolerance in plants.

2 Mechanisms of Phytohormones Jasmonates and Salicylates for Abiotic Stress Tolerance in Plants

Along with the globe, abiotic stresses like flooding, drought, cold, heat and salinity induce major crop losses. Production of more feed and food in response to the immense pressure exerted by a rapid increase in population demands avoiding such losses (Alexandratos and Bruinsma 2012; Gibbs et al. 2010). But the strength and timing of abiotic stress factors are expected to be more extreme and less predictable in the future (Bailey-Serres et al. 2012). Under the current climate change scenario, the area under multiple stresses is expected to be increased significantly (Ahuja et al. 2010). Responses to external and internal stimuli are regulated by plant hormones greatly. Traditionally, cytokinins, brassinosteroids (BRs), auxins (IAAs) and gibberellins (GAs) are known for plant development and ethylene, jasmonic acids (JAs) and salicylic acid (SA) are known for plant defence. However, plant hormones have multiple indirect or direct roles in plant functions. GAs and IAAs have a role in tolerance against both abiotic and biotic stresses, while ethylene, JA and SA have a role in abiotic stress tolerance and development of plant (Colebrook et al. 2014; Kazan 2013; Santino et al. 2013).

The JAs is a substance, initially identified the hormone that causes stress in higher plants and regulates endogenous growth. Similarly, JAs also shows regulatory effect by exogenous application on plants. Stress causes plant damages on a large scale. In this way, JAZ-MYC module plays an important role in the JAs signalling pathway. In the process of resisting environmental stress, JA shows antagonistic and synergistic effects with SA, ABA, ethylene and other plant hormones (Colebrook et al. 2014; Kazan 2013; Santino et al. 2013).

Similarly, SA is also a signalling molecule and growth regulator in phenolic nature plants, which participates physiological process regulation like photosynthesis, growth and metabolic processes in plants. Several scientists show the result of the importance of SA with the response to abiotic stresses. To mitigate the oxidative stress, SA is very active molecule under adverse environmental conditions such as salinity (Khan et al. 2012), drought (Ndamukong et al. 2010), light (Tuteja and Gill 2013) and cold (Górnik et al. 2014; Ilyas et al. 2017; Sayyari et al. 2010). SA plays a physiological role and helps to develop abiotic stress tolerance in crop plants.

2.1 Interaction Between JA and SA Pathways Under Abiotic Stresses

Gornik et al. (2014) demonstrated that we can improve the resistance of seedlings to chilling when seeds are treated with SA or JA; while Ilyas et al. (2017) reported that in wheat improve the drought stress tolerance by the application of SA and JA but JAs shows more effective results than SA. However, by the use of SA and JA in combination than plant growth cannot influence significantly. Sayyari et al. (2010) reported that the use of methyl salicylate (MeSa) and methyl Jasmonic acid (MeJA) reduce the chilling injury. JAs and SA also protect against salt stress by followed the protein-coding gene expression mechanism (Khan et al. 2012). According to Farhangi-Abriz and Ghassemi-Golezani (2018) in soybean JAs and SA reduce the Na^+ concentration under different salt stress levels, although in the absence of salt stress, there was no effect on Na^+ concentration significantly. Consequently, SA has a lower effect on Na^+ reduction than JAs. A key regulator, glutaredoxin GRX480 shared by SA and JAs signalling pathways, which mediates protein redox regulation, it is because of their catalyse disulphide transition capacity (Meldau et al. 2012). Mitogen-activated protein kinase 4 (MAPK4) is a positive regulator in the JAs and negative regulator in SA signalling pathway in response to light stress by the research on *Nicotiana attenuate* (Tuteja and Gill 2013). Besides, SA and JAs can enhance abiotic stress responses by the exogenous application.

2.2 Against Heat Tolerance

Large changes from protein denaturation to transcription in plant physiology caused by elevated temperature (ET). Scientist suggests that Jas positively regulate and ET negatively regulate heat stress tolerance in *Arabidopsis*. Exogenous application of JA increases the heat tolerance. In agriculture, abiotic stresses play a key role in decreasing the productivity of crops. High and low, both temperatures are hazardous for crops. Increase in high temperature at the global level presents an alarming risk to the farmers. Tropical and subtropical areas of the world will be negatively affected by the tragedy of heat stress according to the worldwide environmental model analysis (Battisti and Naylor 2009). According to African report, due to rise of each 1 °C temperature beyond 30 °C, scientist analysis historical data almost 20,000 trails of maize crop proposed 1–2% yield losses under tropical and subtropical conditions (Lobell et al. 2011). In this condition, some pathways are activated by gene expression and ultimately some special proteins having low molecular weight like Heat shock proteins are synthesized by plants (Suri and Dhindsa 2008). JAs play an important role in heat tolerance has been seen in *Arabidopsis* (Clarke et al. 2009). Hasanuzzaman et al. (2013) reported that under unfavourable conditions, application of JAs under heat stress shows great defence response of plants. Foliar application of JAs increases the abscisic acid content in plant cells that help in

decreasing the adverse effects of heat stress (Creelman and Mullet 1997; Lehmann et al. 1995; Acharya and Assmann 2009). Transpiration rate of leaves is raising under high temperature and JA synthesis some osmoregulators in plant cells like soluble carbohydrates and proline and increases the water potential in plant cells (Bandurska et al. 2003). In the current environmental situation, both high (heat) and low (chilling and cold stress) temperature causing abiotic stresses in crop plants. Temperature stress affects plant physiological and biochemical processes (Larkindale and Knight 2002; Khan, Asgher, et al. 2013; Khan, Iqbal, et al. 2013; Kazemi-Shahandashti et al. 2014; Siboza et al. 2014).

SA-supplementation has been reported to differentially benefit several plant species exposed to chilling temperatures (Janda et al. 1999; Ding et al. 2002; Horváth et al. 2002; Kang et al. 2012; Kazemi-Shahandashti et al. 2014; Siboza et al. 2014) and high (He et al. 2002; Larkindale and Knight 2002; Clarke et al. 2004; Shi et al. 2006; Wang and Li 2006; Wang et al. 2010; Khan, Asgher, et al. 2013; Khan, Iqbal, et al. 2013). SA (0.5 mM) modulated antioxidant enzymes and improved chlorophyll fluorescence in *Z. mays* under low (2 °C) temperature stress (Janda et al. 1999).

2.3   Against Cold and Freezing Stress

For the development and growth of plants, one of the most challenging environmental stress is low-temperature stress. In the daily life period, at the optimal temperature, the optimum rate for growth and development is shown by plants (Fitter and Hay 2012). Molecular, physiological and biochemical changes occur in plants on diffraction of temperature from an optimal level. These changes are the defense mechanism of plants, as under thermal stress plants have to preserve optimum molecular and cellular homeostasis for maximizing the growth and development of plants (Fitter and Hay 2012). Generally, at 0–15 °C low-temperature stress effects plants. Through wide metabolic, physiological and gene expression reprogramming, plants respond to the lower temperature stress (Chinnusamy et al. 2007). Under low-temperature stress, long-distance signalling molecules like jasmonates got much attention in the last years (Lee et al. 2005). Tolerance to low-temperature stress could also be facilitated by ethylene, jasmonates and abscisic acid as stress regulators (Wasternack 2014; Kosova et al. 2012).

Under cold stress, increased contents of jasmonic acid were found in wheat (Kosova et al. 2012). Moreover, low-temperature stress positively controlled first enzyme involved in the biosynthesis of jasmonic acid (LOX) both in *Caragana jubata* and kiwi (*Actinidia delicosa*) (Zhang et al. 2006; Bhardwaj et al. 2011). Relief in chilling damage due to the jasmonates is a consequence of stimulation of antioxidants, ABA, lower activity of LOXs, polyamines, cryo-protective agents, and proteinase inhibitors production (Gonzalez-Aguilar et al. 2000; Cao et al. 2009; Zhao et al. 2013). Lee et al. (1997) demonstrated that jasmonic acid increased chilling stress tolerance in rice. Increased hydrolytic conductivity and inhibited stomatal opening induces preserved water status in chilled plants (Acharya and Assmann 2009).

The jasmonic acid applied exogenously enhanced tolerance in Arabidopsis against freezing stress. Arabidopsis plants deficient in jasmonates were more sensitive than wild type plants to freezing stress (Hu et al. 2013).

Nowadays, one of the most common approaches for developing tolerance to temperature stress in plants is the exogenous application of SA. Salicylic acid develops abiotic stress tolerance and is a signalling molecule being the endogenous phytohormone or growth regulator (Khan et al. 2012). There was a decrease in H_2O_2 accumulation and an increase in APX, CAT and SOD activities in response to exogenous application of SA in Musa under chilling stress (Kang et al. 2003). Rate of respiration and CO_2 assimilation reduction under cold stress is a consequence of disruption in activities of PEPC and RuBPC. While, SA application ameliorated the effects of cold stress by enhancing the activity of these enzymes (Yordanova and Popova 2007). In the fruits of *Prunus persica*, treatment of SA before the onset of cold stress enhanced the activities of heat shock protein and antioxidants due to which effects of chilling injury were reduced (Wang et al. 2006).

2.4 *Against Salt Stress*

Salinity by causing osmotic, oxidative and ionic stress restricts the productivity of plants as a stress factor (Kumar et al. 2013; Ismail et al. 2013; Golldack et al. 2014). Hindrance in the productivity of crops in more than 10% of the arable land is associated with alkalization and salinization worldwide (Parihar et al. 2015). In agricultural lands, 20% of lands are known to be under salt toxicity (Munns and Tester 2008). Recently JAs were studied as regulators for inducing salt tolerance in crops (Qiu et al. 2014; Dong et al. 2013; Zhao et al. 2014). JAs not only enhanced tolerance against salinity but also enhanced activities of APX, CAT, POD, and SOD in wheat (Qiu et al. 2014). In an ABA-dependent way, salt tolerance is also promoted by systemin that is a plant hormone promoting the production of JAs in tomato (Orsini et al. 2010). Wu et al. (2015) demonstrated that JAs promotes the expression of some genes involved in salt stress tolerance in rice. Ding et al. (2016) studied the germination of the JAs receptor coi1 mutant and oxylipins in the LOX3 mutant under salinity and found that JAs regulates these mutants as an early response to salinity.

In *Pisum sativum*, jasmonic acid normalizes the rate of protein synthesis and carbon fixation by reducing the salt toxicity (Velitchkova and Fedina 1998), in rice JAs enhances biomass production by alleviated salt inhibition (Kang et al. 2005). In the seedling of soybean, lowering in the salt toxicity symptoms was a consequence of foliar-applied JAs (Yoon et al. 2009). In safflower, through increasing grain yield, plant biomass, the maximum quantum yield of photosystem II (Fv/Fm), relative water content and increasing chlorophyll content, foliar sprayed jasmonic acid improved physiological performance under salt stress (Ghassemi-Golezani and Hosseinzadeh-Mahootchi 2015). Under salt stress, improvement in the potassium content of plants, reduction in lipid peroxidation and increase in antioxidant enzymes activity is also

a consequence of exogenously applied JAs (Faghih et al. 2017; Farhangi-Abriz and Ghassemi-Golezani 2018).

The salinity tolerance mechanisms were strengthened in *V. radiata* (Khan et al. 2014), *Medicago sativa* (Palma et al. 2013), *Brassica juncea* (Nazar et al. 2011, 2015), and *Vicia faba* (Azooz 2009) due to SA under salinity stress. Alleviation of oxidative stress and activation of the photosynthetic process by enhanced activity of antioxidant enzymes and enhanced chlorophyll content in *Torreya grandis* under salinity stress was also a consequence of salicylic acid (Li et al. 2014). The deficiency of SA is considered as a major reason for the diminished activity of antioxidants enzymes and increased damages due to salinity stress in *Arabidopsis* (Cao et al. 2009). For enhancing GST that is a H_2O_2 metabolizing enzyme priming of SA is an important technique (Csiszár et al. 2014). In *Triticum aestivum*, the activity of ascorbate (AsA)-GSH pathway enzymes and transcript level of antioxidant genes (*GS, MDHAR, GST2, GST1, GR, DHAR, GPX2* and *GPX1*) were enhanced with exogenous application of SA (0.5 mM) (Li et al. 2013). In *A. thaliana*, salinity tolerance was improved with the prevention of potassium loss and restoration of membrane potential in response to SA application under salt stress (Jayakannan et al. 2013).

The synthesis and accumulation of ABA as influenced by exogenous application of SA may also perform in reducing salt stress effects. SA plays role in modulating the responses of plants to salinity induced stresses like oxidative and osmotic stress. SA has also been a messenger or signal transducer under stressful conditions (Klessig and Malamy 1994). In recent studies, it was reported that SA applied exogenously alleviates the toxic effects of salinity stress on plants. The accumulation of certain osmolytes like proline and the enhanced activation of some enzymes like ascorbate peroxidase and aldose reductase by soaking seeds of tomato in salicylic acid enhanced its tolerance against salinity stress (Tari et al. 2002, 2004; Szepesi et al. 2005).

2.5 *Against Drought Stress*

In deteriorating production process in agriculture, drought plays the main role as a stress factor on yearly basis (Pandey et al. 2017). Drought stress affects productivity and growth of plants by a series of molecular, biochemical, physiological and morphological changes that alters the normal growth balance (Pandey et al. 2017). Drought elevates the harmful effects and intra- or inter-cellular solute concentrations in plants by reducing turgor and water potential of cells (Todaka et al. 2015). Various mechanisms are associated with the drought tolerance process; For example, stomatal closure, as it lowers the water loss associated with transpiration. Some hormones like JAs and ethylene are associated with the closure of stomata (Tanaka et al. 2005; Desikan et al. 2006; Acharya and Assmann 2009). JAs are well known for prompting the stomatal closure (Suhita et al. 2004; Munemasa et al. 2007). JAs also plays role in modifying the root hydraulic conductivity under water-limited

conditions to promote the uptake of water from the soil (Sánchez-Romero et al. 2014). ABA-independent and dependent, as well as calcium independent and dependent pathways, are greatly influenced due to the JAs (Sánchez-Romero et al. 2014). Drought tolerance is implicated due to JAs signalling pathways in rice (Seo et al. 2011).

In comparison to biotic stresses, the role of JAs under abiotic stresses like drought is less known. Earlier studies demonstrated that level of jasmonic acid increases in roots and leaves of the plants under drought (Kiribuchi et al. 2005). To alleviate the dangerous effects of water deficit stress on the plants, one of the useful approaches is the exogenous application of jasmonic acid that is a plant growth regulator. Abdelgawad et al. (2014) said that under drought stress, to alleviate oxidative stress and increase antioxidant enzymes in maize, exogenous application of jasmonic acid is useful. Moreover, Kumari et al. (2006) also indicated that jasmonic acid decreased oxidative damage to peanut seedlings by enhancing antioxidant activity that resulted in the reduced lipid peroxidation. Alam et al. (2014) concluded that drought-induced reactive oxygen species are inhibited by foliar application of JAs, as it accelerated the activity of antioxidant enzymes like catalase, ascorbate peroxidase and glutathione peroxidase in Brassica species. But the mechanism of modification of antioxidant system by JAs is not clear yet. Possibility for changes in post-transcriptional, translation or gene transcription is there. However, the changes in metabolism at the subcellular level that are controlled by JAs could also be the reason due to its organ-specific nature (Comparot et al. 2002).

Under drought conditions supplementation of SA at 500 µM to *H. vulgare* also increased the rate of CO_2 assimilation that might be due to the increase in the stomatal conductance (Habibi 2012). The Exogenous application of SA not only lowers oxidative stress but also modulates important nonenzymatic (including GSH) components of AsA–GSH pathway and glyoxalase system (Gly I and Gly II) and enzymatic (including monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; GR; GSH peroxidase, GPX) components in plants exposed to drought (Alam et al. 2013). In drought-tolerant *Z. mays* cultivar, the antioxidant system was strengthened by 1.0 µM SA applied as the foliar application (Saruhan et al. 2012). In *Mitragyna speciosa*, gene expression was induced by SA application at the rate of 5.0 µM (Jumali et al. 2011). SA treated plants induced Cytochrome P450 (CYP), CAD and SAD biosynthesis along with antioxidants, HSPs and chaperone encoding genes in the 292 expressed sequence tags (ESTs) analyzed randomly. *Triticum aestivum* exposed to drought showed potential participation of SA in about 76 proteins that are recognized (Kang et al. 2012).

In enhancing drought tolerance in wheat seedlings pre-treatment of salicylic acid at 0.5 mM found beneficial as it alleviated substantial water loss (Kang et al. 2003). It was investigated by proteomics that 37 protein spots were regulated with pretreatment of SA under drought stress. Under drought conditions, SA also upregulated ATP synthesis by regulating proteins involved and about 21 other protein spots including RuBisCo and related enzymes (Kang et al. 2003).

2.6 Against Heavy Metals' Stress

Heavy metal ions in trace element quantities are required for development, growth and metabolism in plants but excess quantities of these elements are toxic for plants. These elements play an inhibitory or stimulatory role in plants when these are present in the plant available form in soils. Heavy metal stress inhibits the photosynthetic process and enhances leaf senescence resulting in reduced plant growth (Maksymiec et al. 2007). Xiang and Oliver (1998) found that the toxicity of copper and cadmium in soil increased the contents of jasmonates in *Arabidopsis thaliana*. Actually, lipoxygenase activity increases in this condition that accelerates the synthesis of jasmonates (Tamás et al. 2009). Toxic effects of aluminium were lowered by the exogenous application of jasmonate, as methyl jasmonate increases enzymatic antioxidants like superoxide dismutase as well as nonenzymatic antioxidants like phenolic compounds (Heijari et al. 2008). In *Cassia tora* and *Brugmansia candida*, plant tolerance to the toxicity of aluminium was improved by the foliar application of methyl jasmonate, as it increased peroxidase activity, decreased oxidative stress and stimulated lignin accumulation in the cell wall (Spollansky et al. 2000; Xue et al. 2008). Cadmium (Cd)-induced oxidative damage by the generation of ROS and lipid peroxidation are mitigated by the foliar spray of JAs in soybean (Keramat et al. 2009). The low dose of Jas protects plants from copper toxicity as it adjusts photosynthetic pigment (Poonam et al. 2013). Farooq et al. (2016) described that JAs not only reduced the generation of ROS and lipid peroxidation but also improved chlorophyll fluorescence and biomass of canola under arsenic stress when applied exogenously. In *Cajanus cajan* (L.) Mill sp., priming of JAs lowered the hazardous effects of copper toxicity (Poonam et al. 2013). Chen et al. (2014) stated that the exogenous application of methyl jasmonate reduced the uptake of cadmium by lowering transpiration.

In *Oryza sativa* exposed to lead, exogenous application of SA improved photosynthetic traits and growth of plants (Chen et al. 2007), similarly in Cu (0.05, 0.10, 0.15, and 0.20 mM)-exposed *Phaseolus vulgaris* (Zengin 2014) and Cd (10, 15, and 25 μM) exposed *Zea mays* (Krantev et al. 2008), SA applied exogenously improved growth. In recent studies, it was depicted that under metal toxicity, the activity of enzymes like carbonic anhydrase and Rubisco, photosynthetic pigments, photosystem II (PSII) and photosynthesis process were regulated by the application of SA (Al-Whaibi et al. 2012; Noriega et al. 2012; Zhang et al. 2015). Control of H_2O_2 accumulation that is mediated by SA induced tolerance to Cd stress in *Linum usitatissimum* (Belkadhi et al. 2014). The SA applied exogenously increases the concentration of endogenous SA that minimizes the contents of H_2O_2 to prevent membrane damage in rice (Chao et al. 2010). Chlorosis induced by Fe deficiency is also minimized by SA application in plants (Kong et al. 2014). SA also plays a physiological role in plants by inducing stomatal closure, flowering, development and regulating plant morphology (Miura and Tada 2014; Mohsenzadeh et al. 2011). SA also attributes nodulation in legumes, cell growth and seedling germination (Vlot et al. 2009). Pre-treatment of SA protects different plants from metals like Cd, Hg and Pb (Ghani et al. 2015; Gondor et al. 2016; Zhou et al. 2009). Application of

SA lowers the oxidative damage caused by chromium toxicity in maize plants by inducing enzymatic and no-enzymatic antioxidants (Ahmad et al. 2011; Islam et al. 2016). Under Mn, Cu and Zn stress, Song et al. (2014) demonstrated the enhancement in activities of SOD and CAT enzymes mediated by SA in barley. Upregulation of the antioxidant (GR, APX, CAT, and SOD) enzymes and increased activities of defense responsive genes in response to SA application under Cd stress ameliorated the metal stress in *Arabidopsis thaliana* (Wael et al. 2015). Seed priming with SA lowered oxidative stress and improved relative water contents and root growth (Moussa and El-Gamal 2010).

3 Signalling Pathway of Jasmonates and Salicylates During Abiotic Stress in Plants

3.1 *Jasmonates Signalling Pathway in Response to Abiotic Stresses in Plants*

In plants' cell, Jasmonyl isoleucine (JA-Ile) is the most bioactive JAs; however, under normal condition, the concentration of JA-Ile is very low (Fonseca et al. 2009). In stress condition, it has been established that the JA-Ile accumulates in plant leaves as a protective physiological mechanism (Li et al. 2017). JAs transfer protein 1 (JAT1) acts as a transporter for subcellular localization of Jasmonates (Wang et al. 2019). JAT1 has been found in both cell membrane and nuclear membrane and transports the jasmonates from the cytoplasm to nucleus and apoplast and therefore JAT1 is known as Jasmonates regulatory protein (Wang et al. 2019). The presence of JAs in apoplast activates the JAs signalling pathway and the signals transmitted to other cells through the vascular bundles and/or via air transmission even in distal regions (Thorpe et al. 2007). The localization of different JAs synthases in the sieve element of vascular bundles facilitates the re-syncretization of JAs during their transportation (Heil and Ton 2008; Hause et al. 2000). The concept of re-synthesization has been proven by the formation of JA precursor 12-oxo-PDA in the sieve elements of phloem (Hause et al. 2003). Methyl Jasmonate (*MeJA*) is highly volatile in nature, having greater penetrating ability into cell membrane as compared to JA and therefore, MeJA can smoothly diffuse to distant leaves and adjacent plants (Farmer and Ryan 1990).

The promoters of jasmonates-responsive genes are not activated by various transcription factors (TFs) due to the low concentration of JA-Ile under normal condition. A range of jasmonates-zinc finger inflorescence meristem domain (JAZ) proteins suppress the different TFs, known as transcriptional repressors (Table 1). The effective transcriptional repression complex is formed by protein topless and the protein novel interactor of JAZ; this repression complex inhibits the jasmonates responsive genes expression by closing the open complex through the further involvement of histone deacetylase 6 (HAD 6) (Hause et al. 2003). In *Arabidopsis*, thirteen JAZ proteins have been discovered which contain two conserved domains: the central

Table 1 Transcription factors interacting with jasmonates-ZIM domain protein and their functions

JAZ domains	JAZ-Interacting DNA-binding transcription factors	Physiological functions	References
JAZs	MYC2/3/4/5	Root elongation, wounding responses, defense, metabolism, hook development	Ali and Baek (2020), Loh et al. (2019), Liu et al. (2019), Um et al. (2018), Major et al. (2017), Sun et al. (2017), Wang et al. (2017), Kachroo and Kachroo (2012), Qi et al. (2011), Niu et al. (2011), Chung and Howe (2009) Chung et al. (2008)
JAZ1/8/10/11	MYB21/24	Stamen development and fertility	
JAZ1/2/5/6/8/9/10/11	TT8/GL3/EGL3/MYB75/GL1	Trichome development and anthocyanin synthesis	
JAZ1/3/4/9	FIL/YAB1	Chlorophyll degradation and anthocyanin accumulation	
JAZ9/11	OsRSS3/OsbHLH148	Confer drought and salt tolerance	
JAZ1/4/9	ICEI/2	Increase freezing tolerance	
JAZ4/8	WRKY57	Promote leaf senescence	
JAZ1/3/9	EIN3/EIL1	Root elongation, defense, root hair and hook development	
JAZ1/3/4/9	TOE1/2	Repression of flowering during early vegetative development	
JAZs except JAZ7/12	BHLH03/13/14/17	Root elongation, fertility, defense, anthocyanin synthesis	

ZIM domain and the C-terminal JA-associated domain (Pauwels and Goossens 2011). The protein–protein interaction is facilitating by different domains in JAZ proteins (Gimenez-Ibanez et al. 2015). The JAZ-NINJA-TPL repressor complex is formed via the interaction of JAZ with TFs and NINJA (includes an ethylene-responsive element-binding factor associated amphiphilic repression (EAR) motif) and recruiting TPL (Pauwels and Goossens 2011). In *Arabidopsis*, JAZ5, JAZ6, JAZ7, JAZ8 and JAZ13 carry an additional EAR motif that facilitates to direct interaction with TPL without the presence of NINZA (Shyu et al. 2012). The amino acid sequence having a bipartite

structure containing a loop and amphipathic alpha hexil that binds the coronatine or JA-Ile and coronatine insensitive 1 (COI1) respectively; these amino acids sequence is known as JAZ degron (Sheard et al. 2010).

The formation of JA-Ile in the cytosol and its transportation is accelerated by the abiotic stresses in plants. Among various JAs, only JA-Ile can promote COI1-JAZ bindings (Thines et al. 2007). The ubiquitin–proteasome complex comprises suppressor of kinetochore protein 1 (SKP1)-cullin-F-box (SCF). The *Arabidopsis COI1* mutant lacks all responses to JA (Feys et al. 1994). The association of SKP1 and cullin with F-box protein results in SCF-type E3 ubiquitin ligase formation (Xie et al. 1998). This F-box protein COI recognizes the JA-Ile which is formed and transported to the nucleus at the time of abiotic stresses. Within the SCF complex, JA-Ile helps the interaction of JAZ with COI1 (Xie et al. 1998), with inositol penta kis phosphate acting as a cofactor in the formation of the CO1-JAZ co-receptor complex (Mosblech et al. 2011). The proteasome degradation of JAZ protein and the release of TFs to facilitate the expression of Jasmonates responsive genes regulate the JAs mediated defences and growth of plants under stress situation. The communication between the genes specific TF, RNA polymerase 2 and transcription machinery is carried by Mediator 25 (a subunit of the Arabidopsis mediator complex) (Bäckström et al. 2007). Previously, it has been well evidenced that the matching pairs of TFs with JAZ repressors to express the jasmonates-responsive genes is mainly responsible for JAs functioning in every aspect (Qi et al. 2011). JAs perception and signal transduction during abiotic stress is illustrated in Fig. 1.

3.2   Salicylates Signaling Pathway in Response to Abiotic Stresses in Plants

SA induction in response to various abiotic stress helps in plant defense system for maintaining homeostasis. As this compound is 7-C compound phenolics which is synthesized naturally in mevalonic acid and shikimic acid pathway protects plants in stress conditions. Most of the responses under various stresses involve some common phenomenon. Heavy metal causes hypersensitive response and major two pathways take the lead role. Cinnamic acid is one of the intermediate products of Salicylates which is converted from phenylalanine by phenylalanine ammoni-alyase, a key enzyme in stress response mechanism in plants (Chen et al. 2009). Phenylpropanoid pathway regulation is the most important phenomena under stress condition. Methylesalisylates induces gene expression under stress condition which induces higher expression of Cinnamate-4-hydroxylase and phenylalanine ammonia-lyase, two most important enzyme of the Phenylpropanoid pathway. Higher activity of PAL and Cinnamate-4-hydroxylase leads to increased production of phenolics compound in plants as reported in rice (Bi et al. 2007) and higher PAL activity causes *Musa* plants tolerance to saline and heat stress (Chen et al. 2008). Isochorismate pyruvate lyase and isochorismate synesthetes two major enzymes in salicylic acid
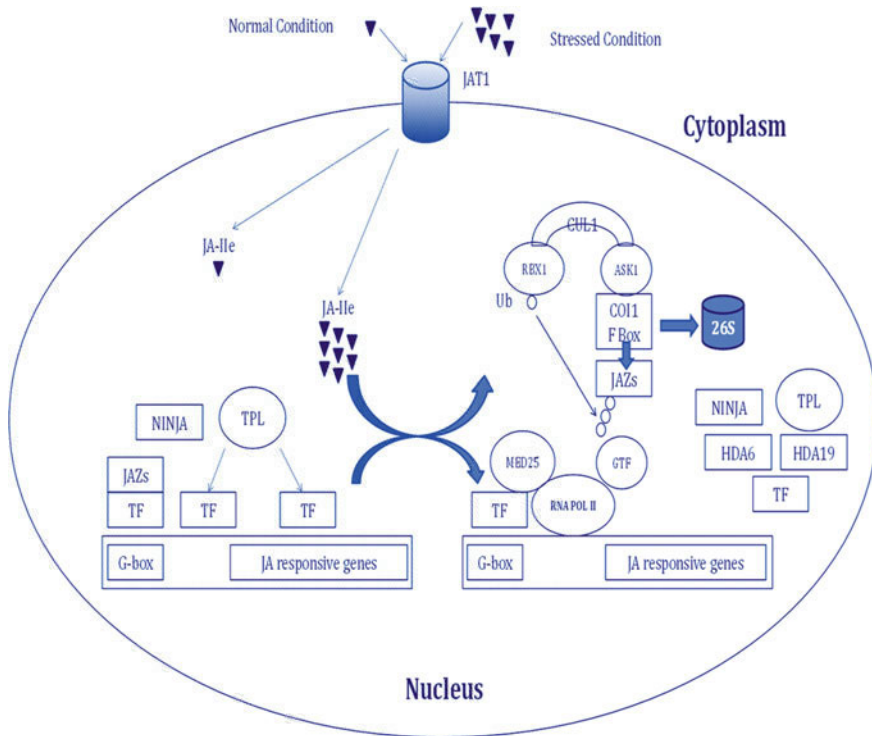
Fig. 1 Signaling pathway of Jasmonic acid during abiotic stress

synthesis form another pathway involving chorismate and isochorismate (Wilder-muth 2006). SA based Isochorismate synthase (*ICS1*) regulation under drought tolerance has been shown in Arabidopsis (Hunter et al. 2013). In case of heavy metal stress SA forms various proteins which conjugate with chelating compounds. Under stress condition salicylic acid enhances the accumulation of sulfur compound and glutathione indirectly increases various chelating compound (Kohli et al. 2017). Besides independent activity salicylic signalling also acts with some other signalling molecule including phytohormones, this interaction helps to survive plants under various abiotic stresses. Calcium-dependent salicylic signalling along with the partic-ipation of antioxidant defense causes heat and cold stress survived under changing climate (Wang and Li 2006). Exogenous SA treatment helps in Ca channel opening which triggers protection under stress condition. Salicylic acid causes higher catalase activity under H_2O_2 based catalase activity inhibition and *GSH* play an important role by metabolizing H_2O_2. Another H_2O_2 catalysing enzyme is also increased under salicylic treatment. In *Brassica* spp *GSH* synthesis also have been reported upon external salicylic treatment under various stress. SA mediated expression changes in GST gene family *SlGSTT2, SlGSTT3, SlGSTF4* in *Solanum* under saline stress protection has been reported (Csiszar et al. 2014). Higher expression of several genes

like *GPX1, GPX2, GST1, GST2* under salt stress upon SA treatment has been reported in *Triticum aestivum* (Li et al. 2013). In its upstream activity, SA has been reported to induce HSPs, chaperon and various alcohol dehydrogenase and cytochrome P450 (Jumali et al. 2011). Non-express or of the pathogenesis-related gene (*NPR1*) induced in association with various stress response mechanism and MAP kinase activity are also mediated by SA signalling (Chai et al. 2014). Transcriptional reprogramming, calcium homeostasis, secondary metabolite synthesis is interconnected in SA upstream pathway under stress condition. Exogenous SA application (1 Mm) reduces oxidative stress and improves the activity of PSII and ultimate enhancement in photosynthetic capacity under heat stress and during recovery (Shi et al. 2006). Pyrroline 5-carboxylate reductase and γ-glutamyl activity have been enhanced by SA application under salinity stress. Enhanced proline production by salicylic acid treatment in *Lens esculenta* increases salinity tolerance (Misra and Saxena 2009). Stress tolerance involving brassinosteroids is mediated through SA signalling and interactions. Along with SA, JAs modulates the functioning of PR protein expression in an antagonistic mode. Hormonal regulation is the key mechanism for SA mediated stress tolerance. As SA induced inhibition of amino cyclopropane carboxylic acid which inhibits ethylene production and confers heat stress tolerance (Khan et al. 2003).

4 Molecular Mechanism of Jasmonates and Salicylates-Induced Abiotic Stress Tolerance in Higher Plants

4.1 Salicylic Acid (SA)

Foundational obtained obstruction (SAR) is an elevated condition of protection against a wide range of microbes initiated all through a plant following nearby contamination. The incited obstruction is recognized in the immunized foundational tissue of a microbe tainted plant. Limited assault by a necrotizing microbe actuates SAR to ensuing assault by an expansive scope of typically harmful microorganisms. SA gathering is needed for actuation of nearby safeguards on the underlying site of the assault, and in the far off microorganism free organs in lieu of the enlistment of SAR.

SA aggregation and motioning in the removed microorganism free organs are prepared to additional increment to more elevated levels upon encounter with a microbe. SA examinations have uncovered that few salicylate biosynthetic qualities are up-controlled in the midribs or entire leaves of grapevine tainted with the phytoplasma 'Ca. *P. solani*', e.g., VvICS, which encodes isochorismate synthase, and VvSamt, which encodes S-adenosyl-L-methionine: SA carboxyl methyltransferase, that catalyzes the development of the unpredictable ester methyl salicylate from SA. What's more, evaluation of SA and its forms in the primary leaf veins

through contaminations of grapevine with Ca, *P. solani* indicated a 26-overlap increment in SA2-O-glucopyranosyl, and essentially higher free and absolute SA, when contrasted with uninfected grapevine. SA glucopyranoside and salicylate were likewise extraordinarily expanded in the grapevine primary leaf veins tainted with the flavescence dorée phytoplasma. SA flagging has demonstrated to be needed for the appearance of SAR. Isochorismate synthase movement is useful for SA combination. The *Arabidopsis* ics1 freak, which is insufficient in isochorismate synthase 1 action, has discovered to be SAR inadequate.

Transgenic plants communicating the SA-debasing protein salicylate hydroxylase encoded by the *Pseudomonas putida* nahG quality were being discovered to be inadequate in communicating SAR. The FMO1 quality is needed for the fundamental gathering of SA in far off microorganism free leaves, and the FMO1 quality is required for the enlistment of SAR. Methyl esterase 1 is required for SAR in potato, and MES is needed for amassing of free SA in the distal foundational tissue, the tissue that does not get the essential (starting) contamination. NPR1 quality is an ace controller of the SA-interceded acceptance of protection qualities (Fig. 2). PR1 straightforwardly ties SA enacts SA flagging framework. NPR1 is associated with setting off SAR, and the npr1 freak of *Arabidopsis thaliana* is inadequate in SAR (Bailey et al. 2009; Chen et al. 2013; Denancě et al. 2013).

4.2   *Jasmonic Acids (JAs)*

As a pressure-related hormone, JAs is additionally accounted for association with salt-prompted development restraint. The levels of were raised and JAs flagging was initiated because of stress due to salinity. The F-box protein Coronatine Insensitive1 (COI1), otherwise called the JAs receptor, frames the SCFCOI1 E3 ligase complex with SKP1 and CULLIN1, which intercedes Jasmonate ZIM area (JAZ) debasement by the 26S proteasome. When JAZ were being eliminated, the hindered record factor (e.g., MYC) actuates the statement of JAs-responsive qualities. Enactment of JAs motioning in light of salinity pressure inevitably prompts the restraint of essential root development. Transformations of COI1 and MYC2/3/4 alongside the balanced out JAZ freak jaz3-1 all gave more noteworthy cell prolongation under salt pressure. Also, the JA-safe freak jasmonates insensitive3 (jai3) was found to recoup before and demonstrated an expanded development rate during salt pressure, expressing JAs intervenes development suppression in the salt reaction. Exogenous use of JAs lightened salt stress through keeping up ROS or particle homeostasis. In tomato, the high-JAs-aggregation res freak showed more prominent salt resistance with expanded K+ collection.

Reliably, decreased JA creation or collection prompted touchiness to saltiness in tomato and rice, though raised JA biosynthesis upgraded salt resilience in *Arabidopsis* and wheat. In synopsis, JA-interceded development, restraint may be a significant versatile technique in salt conditions. Salt-directed qualities elevated by JAs would, in general, be instigated in the inward tissue layer of roots in light of saltiness, suggesting