Signaling and Communication in Plants

Tariq Aftab
Mohammad Yusuf *Editors*

Jasmonates and Salicylates Signaling in Plants

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Signaling and Communication 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.

Aligarh, India
Al Ain, United Arab Emirates

Tariq Aftab
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Contents

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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

Akbar Hossain, Zahoor Ahmad, Debjyoti Moulik, Sagar Maitra, Preetha Bhadra, Adeel Ahmad, Sourav Garai, Mousumi Mondal, Anirban Roy, Ayman EL Sabagh, and Tariq Aftab

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

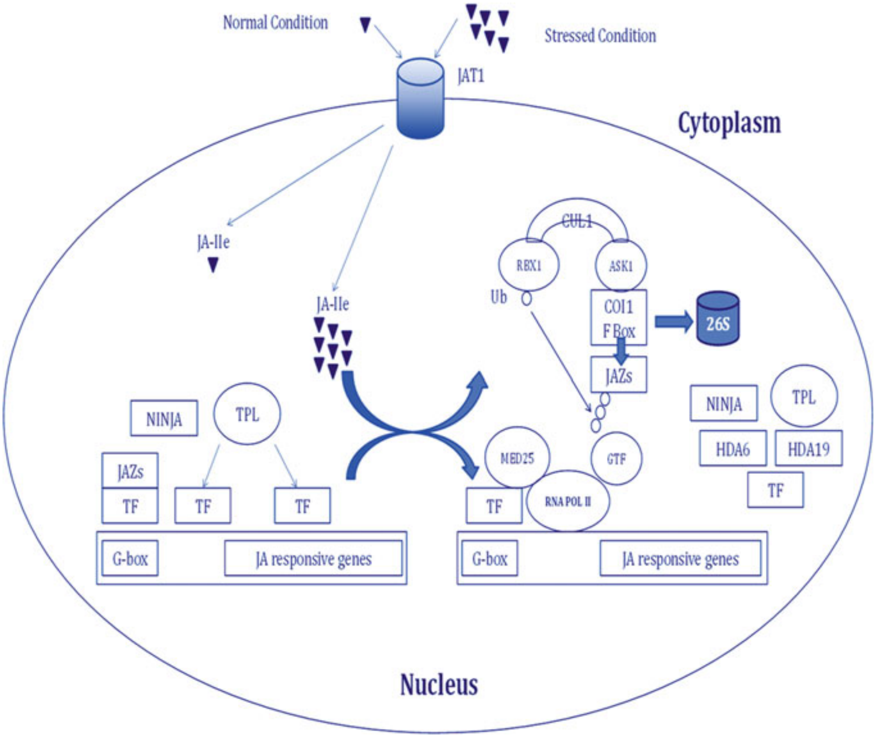

Fig. 1 Signaling pathway of Jasmonic acid during abiotic stress

synthesis form another pathway involving chorismate and isochorismate (Wildermuth 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 participation 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

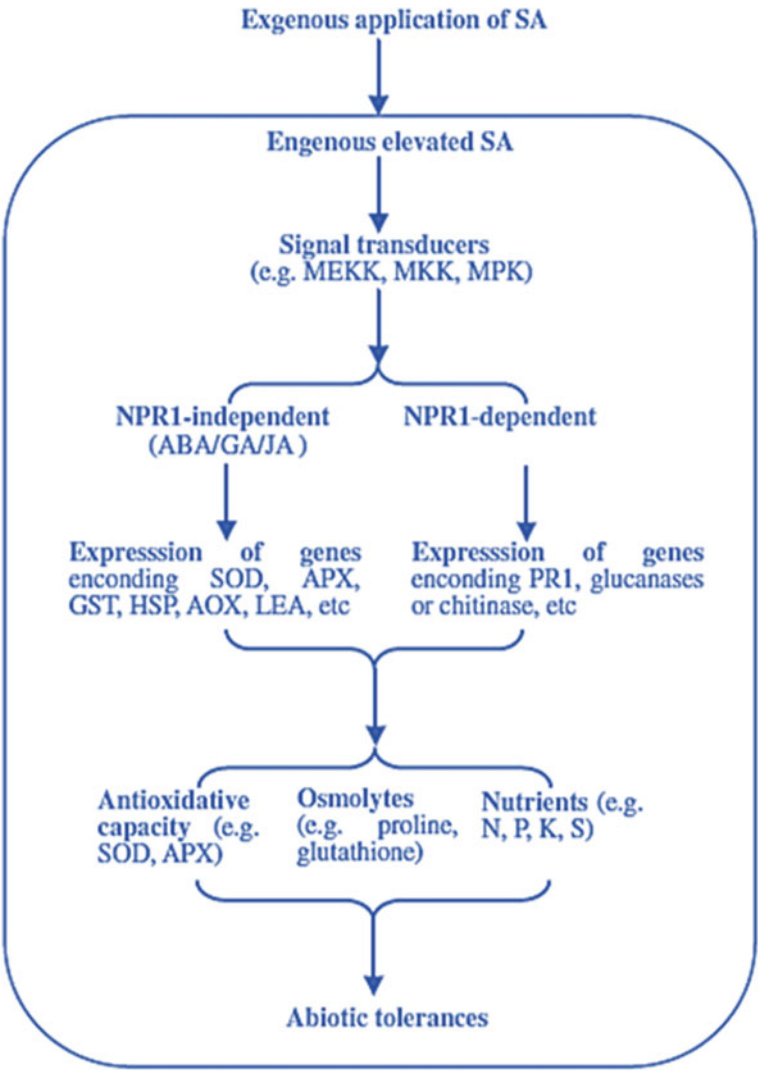

Fig. 2 Salicylic acid and its effect in plants

the spatial guideline of JA flagging. Reliably, two JA biosynthetic rice freaks, cpm2 and hebiba, were less delicate to salt because of lower Na+ collection in shoots, however, no distinction was identified in roots. So also, the maize JA biosynthesis freak opr7opr8 showed a diminished salt reaction in shoots yet showed an overstated reaction in roots with a progression of antagonistic physiological records. These perceptions propose that JAs intercedes plant development reaction to salt worry in a tissue/organ-subordinate way. What's more, the coi1 freak is touchier to salt worry at the underlying phase of seed germination yet shows no distinction at the late development stage after seed germination, suggesting JAs-interceded plant salt reactions can be additionally managed in a transiently explicit way.

Under salt pressure, JA treatment was joined by an expansion in endogenous ABA content and checked the NaCl-incited GA decrease in rice and chard plants, showing that other plant hormones are associated with the JAs-interceded salt reaction. ABA content was lower in the JAs biosynthesis freak aos and JAs levels were diminished in the ABA biosynthesis freak aba. Moreover, MYC2, the ace controller working in JAs flagging, transcriptionally initiates articulation of the ABA-inducible qualities RD22 and AtADH1 for plant adaption to osmotic pressure and, thus, PnJAZ1 was discovered to be actuated by ABA and in this manner advanced salt resilience in plants through mitigating exorbitant ABA motioning under salt pressure (Fig. 3). In synopsis, JA–ABA exchange assumes a significant function in the plant salt reaction (Ali and Baek 2020; Wang et al. 2020).

Fig. 3 Effect of Jasmonic acid in plants

5 Conclusion

Currently (2020) world population is 7.8 billion and approaching to reach 10.9 billion (the median line) at the end of the twenty-first century. To meet the food demand of the increasing population, cereal equivalent food production should be increased to 10,094 million tons by the year 2030 and 14,886 million tons in 2050. In the meantime, IPCC projected that at a consequence of climate change 50% yield losses of several crops may be occurred mostly due to abiotic stresses including high temperature, low temperature, salinity, drought and others abiotic stresses. While tolerance plants could alleviate the incompatible effect of abiotic stresses through several adaptive mechanisms. Among them, several phytohormones play a significant role in abiotic stress. The chapter overviewed earlier studies for better understanding of the role of phytohormones, particularly biosynthesis, transport and signalling mechanisms of jasmonates and salicylates. The information on jasmonates and salicylates will be helpful for the sustainability of crop production under present and future changing climate.

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Salicylic Acid and Jasmonic Acid in Generating Salt Stress-Tolerant Plants

Ankur Singh and Aryadeep Roychoudhury

Abstract Salt toxicity is a severe environmental constraint which limits the growth and development of the plants. To overcome this unfavourable environmental situation, plants possess endogenous protective metabolites which reduce the toxicity of salt stress. Such metabolites cumulatively reduce salt-induced toxicity by reducing the accumulation of Na^+ ions via up regulating the endogenous protective mechanisms of plants. Two such protective compounds are salicylic and jasmonic acids, also characterized as well-known stress related phytohormones. The precursor of salicylic acid is phenylalanine and chorismate, whereas that of jasmonic acid is α-linolenic acid. After being synthesised in the tissues, they are further processed to give methylated or glycosylated products which are utilized by plants for the induction of systemic acquired resistance against various abiotic stresses. These two acids do not only play an independent role during abiotic stress, but also work in a complex signal network with other plant hormones which help to abrogate the toxicity caused due to excess accumulation of Na^+ ions and lower the level of other cytotoxic metabolites and reactive oxygen species during salt stress. This chapter focuses on the harmful effects of salt stress in various crops followed by metabolism and transportation of salicylic and jasmonic acids. The protective role of salicylic and jasmonic acid has been discussed along with their crosstalk with other plant hormones that synergistically help to ameliorate the salt-induced toxicity in plants.

1 Introduction

Production of agricultural crops around the world is severely hampered by abiotic stresses like drought, salinity, extreme temperature, metal and xenobiotic toxicity along with several biotic stresses like insects and other diseases which restrict the growth and development of plants. Unfavourable environmental conditions reduce the yield of the plants and are a major cause of concern for human food safety. The

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demand for food crops is estimated to be increased by 70% by 2050 for an additional 2.3 billion rise in population which is a major challenge for the agricultural production (Shabala 2013). In addition, the condition is further worsening due to the presence of excess salt in the soil which affect yield and quality of food grains. About 20% of the agricultural land is contaminated with excess salt and this amount is increasing day by day. Majority of the plant species that cannot survive under such harsh conditions are classified as glycophytes, whereas several crops can withstand a certain level of salt stress and are grouped under halophytes.

Excess salt in the soil perturbs the growth of the plants and also disturbs the homeostatic balance of the cells. Salt stress also enhances secondary stress in plants like osmotic stress, generation of reactive oxygen species (ROS) and ion toxicity due to excess accumulation of ions like Na^+ and Cl^- in the cells. The water absorption capacity of the roots decreases, which, together with stomatal transpiration, lead to the hyperosmotic stress in the cells (Munns 2005). Salt stress initially leads to osmotic stress which further damages the lipid membrane, disturbs the nutritional balance of cells, enhances the formation of ROS and degrades the photosynthetic apparatus (Roychoudhury et al. 2008). James et al. (2011) reported that under salt stress, higher Na^+ accumulation in wheat seedlings reduces the uptake of K^+ which is required for growth and development of plant. They also showed that lower accumulation of K^+ ions reduces the growth and may also lead to death of the seedlings. Salinity-induced formation of ROS causes overall oxidative damages to various cellular components like DNA, lipids and proteins which slow down major cellular functions.

Plants have developed various protective mechanisms like compartmentalization of ions that maintains the cellular osmotic balance, leads to the formation of osmoprotectants and other protective metabolites, causes activation of antioxidative enzymes and modulation of hormones which help them to survive under high salt stress. Roychoudhury et al. (2008) reported that exogenous application of 200 mM NaCl for 15 days causes higher accumulation of Na^+ ions in salt sensitive cultivars which in turn reduces the uptake of K^+ ions and thus hinders the growth and development of the seedlings as compared to that of salt tolerant variety. They also showed that higher accumulation of Na^+ induces the oxidative damage in the seedlings which was ameliorated by the enhanced accumulation of osmolytes like anthocyanins, proline, total amino acids, reducing sugars and enzymatic antioxidants like guaiacol peroxidase and catalase. The pivotal role of protective osmolytes and antioxidative machineries in various crops like tobacco, wheat, *Arabidopsis* and rice under salt stress has also been reported earlier (Hoque et al. 2007; Ahmad et al. 2010; Hossain et al. 2011; Nounjan et al. 2012; Tahir et al. 2012).

Chemical agents like salicylic acid (SA) and jasmonic acid (JA) have been reported to play a major role in defence response of the plants against salt stress. Numerous studies have demonstrated that exogenous application of SA and JA can abrogate the salt induced toxicity in various crops. Rivas-San Vicente and Plasencia (2011) reported that the effect of exogenous application of SA is mostly concentration- and plant species-dependent. Application of relatively lower amount of SA (less than 100 μM) promotes growth and development, whereas higher amount of SA (more than 1 mM) hampers the development of diverse plant species. The protective role of SA against salt stress in various plant species like wheat, tomato, mung bean, tobacco, etc. (Kang et al. 2012; Mimouni et al. 2016; Lee et al. 2014; Khan et al. 2014; Horvath et al. 2015) has been reported earlier. Hayat et al. (2010) reported that exogenous application of SA maintains the K^+/Na^+ balance in the cells which mitigated the salt-induced toxicity in the plants. At the same time, SA also takes an important part in mediating the plant growth and development via cross-talk with various plants hormones like gibberellin (GA), abscisic acid (ABA), ethylene and JA (Khan et al. 2014; Alonso-Ramirez et al. 2009; Yasuda et al. 2008). The other important plant hormone in this regard is JA. JA and their cyclopentanone derivatives produced in plants are altogether known as jasmonates which are well known lipid-derived phytohormones. JA was initially considered as stress-related hormone, but in recent times, its role in regulating the growth of the plants has also been identified. These multifunctional hormones are involved in various physiological processes of plants like fruit ripening, growth inhibition, reproduction, plant development, tendril coiling, trichrome formation and tuber formation in potato (Yoshida et al. 2009; Balbi and Devoto 2008). Various studies have reported that JA reduces salt stress in plants via reducing the accumulation of Na^+ ions which lowers the formation of ROS, by inducing the action of antioxidative enzymes, increased photosynthetic rate and by producing osmolytes like proline and amino acids which scavenge the ROS formed, maintain the integrity of lipid membrane and regulate the osmotic balance of cells (Bandurska et al. 2003; Walia et al. 2007; Khan et al. 2012). This chapter is focused to demonstrate the diverse actions of SA and JA in plants exposed to salt stress. We begin this chapter by explaining the metabolism and transportation of SA and JA in plants, followed by explaining the protective role of these metabolites along with their crosstalk with other hormones that regulate the tolerance capacity of plants towards salt stress.

2 Metabolism and Transportation of SA

2.1 Metabolism of SA

SA is synthesised in both plastid and cytoplasm. Chorismate and phenylalanine are the precursors of SA in plastid and cytoplasm respectively. In plastid, chorismate is converted to isochorismate by isochorimate synthase 1 (ICS1) which is further transformed to SA by isochorismate pyruvate lyase (IPL) (Strawn et al. 2007). In cytoplasm, phenylalanine is converted to trans-cinnamic acid by the action of phenylalanine ammonia lyase (PAL) which is later converted to benzoic acid and ultimately gives rise to SA by the action of benzoic acid-2-hydroxylase (BA2H) (Fig. 1). Sawada et al. (2006) reported that exogenous application of SA in rice seedlings when exposed to salt stress enhances the endogenous content of SA via phenylalanine pathway. Dempsey et al. (2011) showed the presence of SA in double

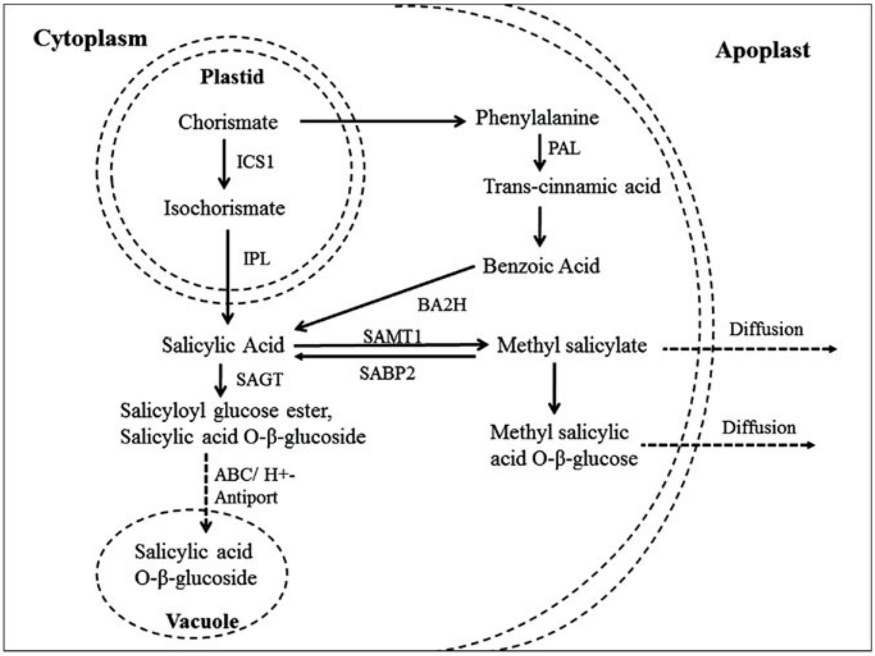

Fig. 1 Major steps involved in the biosynthesis of SA. Enzymes involved in the pathway are (i) Isochorismate synthase 1 (ICS1); (ii) Isochorismate pyruvate-lyase (IPL); (iii) Phenylalanine ammonia-lyase (PAL); (iv) Benzoic-acid-2-hydroxylase (BA2H); (v) SA carboxyl methyltransferase (SAMT1); (vi) SA-binding protein 2 (SABP2); (vii) SA glycosyltransferase (SAGT)

mutant *ics1/ics2 Arabidopsis* which suggests that chorismate pathway is not responsible for SA formation in plants. In addition, the plants which were deficient in ICS1 showed drastic reduction in the level of SA in cells.

At the transcriptional level, MYELOBLAST (MYB) 96 and MYB 30, WRKY 28, WRKY 46 and Wound Induced Mitogen Activated Protein Kinase positively regulate the expression of *ICS* gene which up regulates the synthesis of SA via chorismate pathway (Vidhyasekaran 2015). The RNA binding proteins (RBP) control the SA biosynthesis at post transcriptional level. Qi et al. (2010) reported that higher level of SA was noted in *Arabidopsis* having enhanced expression of AtRBP-defence related (AtRBP-DR) 1 transcription factor, whereas mutant line lacking the function of AtRBP-DR1 showed lower level of SA.

After synthesis, methyl or glucose moiety gets conjugated with SA. Salicylic acid carboxyl methytransferase (SAMT) mediates the conversion of SA to methyl salicylate (MeSA) (biologically inactive metabolite) at relatively low level of SA (Dempsey et al. 2011). Manosalva et al. (2010) showed that back conversion of SA from MeSA triggers the induction of systemic acquired resistance in plants. MeSA can be further changed to methyl salicylic acid O-β-glucose by adding a glucose moiety and is stored in the cytoplasm (Song et al. 2008). Addition of glucose at the hydroxyl group of the SA gives rise to O-β-glucoside (SAG) which is the most dominant form of conjugated SA and its addition to the carboxyl terminal end forms salicyloyl glucose ester (SGE) catalysed by SA glycosyltransferase (SAGT) (Dean and Delaney 2008). SAG is produced in the cytosol and is further stored within the vacuole. Dempsey et al. (2011) reported that SAG must be again converted to SA to induce the defence response in plants. They also showed that addition of non-hydrolysable analogue of SAG was unable to trigger the expression of SA marker gene PR-1.

2.2 Transportation of SA

Both short and long range movement of SA occurs within the plants. Intracellular movement of SA within the cells, tissues and organs occurs freely. Movement of SA across the plasma membrane occurs independently of ROS and Ca^{2+} at 20 μM SA, whereas the movement is highly dependent on the concentration of ROS and Ca^{2+} at 200 μM SA (Chen et al. 2001; Chen 1999). The transporter involved in the movement of SA within the cells is unknown. Shulaev et al. (1997) reported that diffusion of MeSA occurs within the cells. Dean and Mills (2004) demonstrated that movement of SA within the tonoplast occurred through ABC transporter-like proteins. However, the transportation pathway still remains unclear and further need to be investigated.

Long range movement of SA occurs through phloem for induction of systemic acquired resistance in other plant parts. Seskar et al. (1998) reported that among all the derivatives of SA, MeSA is transported both locally and long distance after infection, which makes them a long range signaling molecule and also prove their efficacy in the induction of systematic acquired resistance in plants. However, due to its inactive nature, MeSA is unable to induce any defence response in plants during its transportation. The movement of SA through the cuticle is also independent of the pH of cells (Niederl et al. 1998).

3 Metabolism and Transportation of JA

3.1 Metabolism of JA

Alpha-linoleic acid and hexadecatrienoic acid released from galactolipids of chloroplast membrane serve as the precursor of JA (Schaller and Stintzi 2009). Within the chloroplast, the released poly unsaturated fatty acids are further oxidised by lipoxygenase to form stereo- and region-specific hydroxides which are again dehydrated to yield unstable allene oxides or allylic epoxides. The unstable intermediates are further cyclized by allene oxide cyclases to give optically pure (9S, 13S)-oxophytodienoic

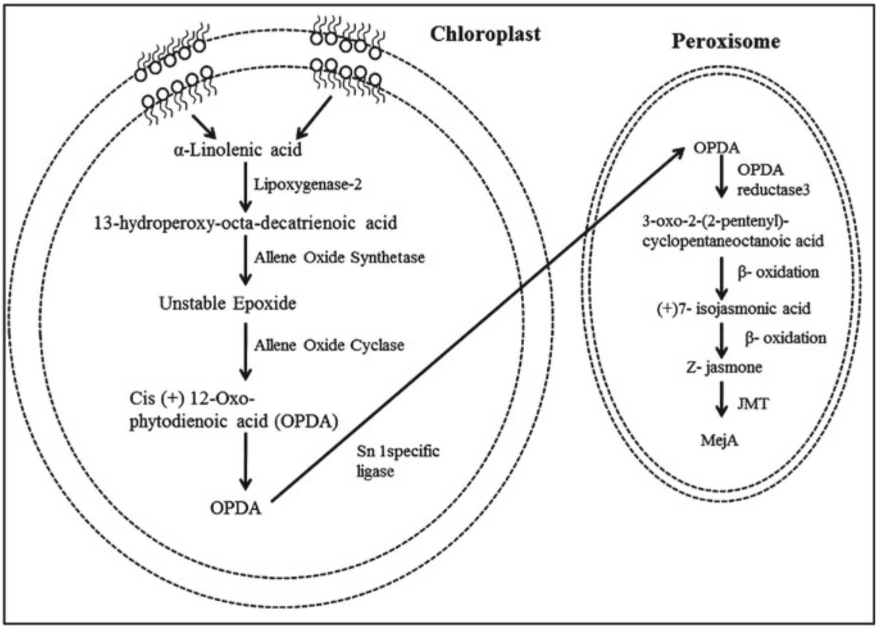

Fig. 2 Major steps involved in the biosynthesis of JA in chloroplast and peroxisome. Abiotic stress leads to membrane damage and formation of α-linolenic acid which initiates the pathway and acts as the precursor of JA

acid (OPDA) which is transported out of the chloroplast by an unknown transporter (Holland and Jez 2018). OPDA is then transported into the peroxisome by ATP-binding cassette (ABC) transporter COMATOSE (CTS) (Theodoulou et al. 2005). Within the peroxisome, the OPDA reductase 3 converts OPDA into 3-oxo-2-(2-pentenyl)-cyclopentaneoctanoic acid which is further oxidised at β-position to give JA. Methylation of JA occurs through the enzymatic activity of JA carboxyl methyltransferase that use S-adenosyl-L-methionine (SAM) as methyl donor (Seo et al. 2001) (Fig. 2).

3.2 *Transportation of JA*

Due to technical constraints, it is not possible to accurately determine the level of JA in different subcellular compartments which limits our knowledge of intracellular movement of JA. Transportation of OPDA via CTS transporter represents the key point of JA entry into the peroxisome. Theodoulou et al. (2005) reported that *cts* mutant of Arabidopsis showed basal level of JA which was synthesised in response to wounding stress, thus suggesting passive diffusion or involvement of an unknown transporter in movement of OPDA in peroxisomes. Maynard et al. (2018) showed that accumulation of OPDA in cytosol due to impaired movement of OPDA in *cts* mutant plants leads to the activation of distinct OPDA-mediated signaling pathway.

Like SA, long range movement of JA plays an important role in the induction of systemic aquired resistance in plants. Radiolabelled tracking of JAs, methyl jasmonate (MeJA) and jasmonoyl-isoleucine (JA-Ile) showed long range distal movement of these metabolites from the site of damage (Bozorov et al. 2017; Thorpe et al. 2007; Sato et al. 2011). Similar to the movement of JA from older to younger leaves in *Nicotiana sylvestris*, Zhang and Baldwin (1997) reported long-distance movement of JA via phloem in *Nicotiana tabacum*. However, the pathway of JA-Ile is still not clear and the results are quite inconsistent. Bozorov et al. (2017) showed that during grafting, JA serves as the mobile oxylipin signal molecule, but Matsuura et al. (2012) reported that wounding stress induces de novo synthesis of JA/JA-Ile rather than transportation from local damaged site.

4 Protective Role of SA During Salt Stress

SA must bind to some specific receptors to activate its defence signaling. Kumar and Klessig (2003) reported that two enzymes, i.e., SA methyl transferase (SAMT) 1 and SA binding protein (SABP) 2 are essential for induction of local and systemic acquired resistance in plants upon infection with tobacco mosaic virus. SAMT1 is responsible for conversion of SA to its inactive form, i.e., MeSA, whereas SABP2 again converts MeSA to active SA via its SA-inhibiting methyl salicylate esterase activity (Forouhar et al. 2005). Sun et al. (2010) demonstrated that salinity stress induces the expression of SABP2 which enhances the tolerance ability of wild type tomato plants, as compared to its halophyte counterpart. Non-expressor of PR protein (NPR) 1 is regarded as the master regulator of SA-mediated defence response due to coactivator nature of *PR* gene expression (Wu et al. 2012). During control condition and at low concentration of SA, NPR1 is present in cytosol in oligomeric form which is biologically inactive. Upon being exposed to abiotic stress, the level of SA in cells increases which ultimately converts the oligomeric inactive form of NPR1 to monomeric active form (Dong 2004) triggered by NPR3 and NPR4 (Fu et al. 2012). Finally, NPR1 is transported to the nucleus which regulates the specific transcription factors that ultimately activates the SA-responsive *PR* genes. In addition, NPR1 also controls the expression of *ICS1* which is the crucial step after successful induction of defence response, since hyper accumulation of SA would lead to hypersensitivity (Zhang et al. 2010). Jayakannan et al. (2015) reported the involvement of both NPR1-dependent and NPR1-independent mechanism during salt stress in plants. Alonso-Ramirez et al. (2009) reported that higher expression level of *ICS1* cause reversal of salt-induced inhibition of germination of *Arabidopsis* seedlings which leads to the conclusion that the synthesis and accumulation of SA regulates the tolerance level of seedlings during salt stress. The protective effect of SA during salt stress is dose-dependent which was demonstrated by Lee et al. (2010) where they showed that exogenous application of 50 μM SA reversed the effect of salt stress in

SA-induction deficient (*sid*) *2* mutant of *Arabidopsis*, but application of 100 μM SA further enhanced the effect of salt stress. Exogenous application of lower amount of SA also rescued the salt-induced decrease in carbon fixation, transportation, antioxidative enzyme activity, stomatal conductance and photosynthetic rate (Stevens et al. 2006; Szepesi et al. 2008; Nazar et al. 2011). In contrast, higher amount of SA further induced the damages in seedlings leading to lowered chlorophyll, swelling of thylakoid grana, and coagulation of stroma that ultimately resulted in increased volume of chloroplast (Moharekar et al. 2003; Uzunova and Popova 2000). Thus, to better understand the role of SA in plant stress, further studies are needed in various plant species.

Being a signaling molecule, SA interacts with other plant hormones and plays a pivotal role in maintaining plant growth and development during stressed condition. SA is well known antagonist of ABA and based on this, Yasuda et al. (2008) reported that ABA hinders the development of systemic acquired resistance in plants by SA. They further reported that activation of systemic acquired resistance by SA checked the ABA-mediated signaling pathway in *Arabidopsis*. Miura et al. (2009) showed higher SA accumulation along with higher expression of SA-regulated genes and ABA sensitivity in *small ubiquitin-like modifier E3 ligase1* (*siz1*) mutant of *Arabidopsis*, being defective in small ubiquitin-related modifier (SUMO) E3 ligase. Thus, it can be concluded that salt tolerance in plants is mostly regulated by supersession of ABA signaling by SA. Another important growth regulator of plants during stressed environment is GA which balances the deficiency of SA in plants. Alonso-Ramirez et al. (2009) demonstrated that SA-deficient *sid2* mutant *Arabidopsis* showed better germination and development in presence of 50 μM GA and on treatment with 150 mM NaCl.

5 Protective Role of JA During Salt Stress

The protective action of JA upon exogenous application or being endogenously produced within the plant tissue is well known. JA can be sprayed to the plants or the seeds can be imbibed in JA solution prior to sowing (Khan et al. 2003). Endogenous content of JA in tomato plant maintained the cellular ROS balance which enhanced the tolerance level of the plants on being exposed to salt stress (Abouelsaad and Renault 2018). Exogenous application of JA reduced the uptake and accumulation of Na^+ ions, or induced the photosynthetic rate, ABA level, proline synthesis and activity of enzymatic antioxidants (Bandurska et al. 2003; Walia et al. 2007; Khan et al. 2012). Exogenous application of JA reduced the level of malondialdehyde and hydrogen peroxide and up regulated the expression level of antioxidative enzymes like superoxide dismutase, catalase and ascorbate peroxide which improve salt tolerance in wheat seedlings (Qiu et al. 2014). Walia et al. (2007) demonstrated that arginine decarboxylase and apoplastic invertase mediates salt tolerance in barley seedlings which are in turn regulated by JA. JA also reduced the excess accumulation of Na^+, reducing the level of toxic metabolites and ROS, enhancing the formation of osmoprotectants and activity of enzymatic antioxidants in various crops like *Limonium bicolor*, *Lycopersicon esculentum*, *Zea mays*, *Glycine max* and *Oryza sativa* (Yuan et al. 2018; Pedranzani et al. 2003; Shahzad et al. 2015; Sheteawi 2007; Kang et al. 2005).

JA does not have any independent role in response to abiotic stress, but works in conjunction with various other phytohormones to enhance the tolerance capability of the plants that helps them to survive under harsh environmental condition. Treatment of rice seedlings with salt solution induced the level of ABA and GA in presence of JA (Seo et al. 2005). During salt stress, the level of JA and ABA increases, whereas the level of SA and indole acetic acid declines that maintain the growth and development of plants during salt stress (Wang et al. 2001). Zhai et al. (2013) reported that treatment of *Glycine max* with MeJA induced the expression of ethylene response factors (ERFs) which confers tolerance to salt stress. Farhangi-Abriz and Ghassemi-Golezani (2018) demonstrated that exogenous application of SA and JA reduced Na^+ accumulation in soybean when exposed to various salt concentrations. They also concluded that JA reduced the accumulation of Na^+ in tissues more efficiently as compared to that of SA. The crosstalk of JA with other phytohormones mostly regulates plant growth during unfavourable environmental conditions.

6 Conclusion and Future Perspectives

Salt stress is one of the major environmental stresses which hamper the proper development and yield of the plants. Salt stress reduces both quality and quantity of the grains which is a serious cause of concern for the growing population. On an average, about 20% of the agricultural land is contaminated with excess salt and this number is increasing day by day. Thus, to protect themselves, plants have endogenous defense machineries which include protective metabolites like osmolytes and enzymatic antioxidants. Exogenous application of SA and JA protects the plants against salt-stressed situations via further elevating the action of these protective metabolites. SA and JA also control various signaling pathways and interact with stress-related hormones like ABA, GA and ethylene to abrogate the salt-induced toxicity in the plants. Although the action of SA and JA against salt stress in various plants is well documented, the detailed mechanism behind is not well known till date so that further studies are required. Due to their low abundance and lack of proper technical methods, the precise transport mechanism of both SA and JA is not clear and hence a clear pathway cannot be explained effectively. Another contrasting result was observed during exogenous application of several concentration of SA to various crops where higher dose further enhanced the damages caused by salt stress. This issue also needs to be further addressed.

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Role of Jasmonic and Salicylic Acid Signaling in Plants Under UV-B Stress

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Abstract Jasmonic acid (JA) and Salicylic acid (SA) are the essential plant hormones responsible for the plant's proper growth and development. These signaling molecules have a significant role in plants along with the regulation of defense mechanisms locally and systemically under various biotic and abiotic stresses. Among abiotic stresses, ultraviolet-B (UV-B) radiation coming to the Earth's surface due to depletion of the stratospheric ozone layer is of serious concern to all living organisms. UV-B is an important factor, negatively influencing the growth and yield of plants on this Earth, ultimately posing a threat to food security. Therefore, understanding the signaling behavior of JA and SA under UV-B stress will be definitely beneficial for the maintenance of agricultural productivity worldwide. Plant responses related to morphological, biochemical, physiological, growth, and yield have been extensively studied under UV-B stress, although studies conducted with UV-B exposure and its impact on plant's endogenous JA and SA contents are limited. On the other hand, some studies have also explored the regulatory impact of exogenously supplied JA and SA to the plants. More accumulation of endogenous JA and SA contents has been observed under elevated UV-B exposure in plants. JA and SA play synergistic as well as antagonistic roles during the regulation of defense responses under various stresses. An inverse relationship between JA and SA are well established under UV-B stress in pea, soybean, and mungbean cultivars. Increased JA content provided better plant resistance while increased SA level imposed higher oxidative stress to plants when exposed to elevated UV-B. Oxidative stress caused by the higher accumulation of SA is well correlated with its inhibitory impact on catalase and ascorbate peroxidase activity leading to more generation of Reactive oxygen species (ROS) under

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UV-B exposure. JA has an inhibitory effect on the accumulation of SA by the regulation of NAC transcription factors like ANAC019/055/072 where MYC2 binds to the promoter regions of these NAC transcription factors, which further inhibits ISOCHORISMATE SYNTHASE1 (ICS1) expression, which is responsible for initiating the expression of BSMT1 (BENZOIC ACID/SA CARBOXYL MEHYLTRANSFERASE 1) during SA biosynthesis. Therefore, the present chapter will focus on the effect of UV-B stress in plants with special emphasis on JA and SA signaling, their antagonistic and synergistic behavior in plant defense, and ROS interaction.

1 Introduction

Sun is the ultimate energy source, necessary for all the living beings along with the photosynthetic life on this Earth's surface. Ultraviolet (UV) radiation is a part of the solar spectrum, mainly divided into three parts UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (below 280 nm). UV-B reaching the Earth's surface is of major concern, due to the depletion of the stratospheric ozone layer. Anthropogenic emissions of chlorofluorocarbons (CFCs) were considered important factors for ozone depleting substances (ODSs) after Molina and Rowland (1974), and in 1985, Farman et al. deciphered the 'Antarctic ozone hole'. Later in 1987, the Montreal protocol was signed to cut the emissions of ODSs. After its successful implementation, it is now predicted that its recovery to pre-1980s status can be achieved by the end of 2050 (Chipperfield et al. 2015). But, as per Anderson et al. (2012), current climate changing scenarios and increasing intensity and frequency of thunderstorms are directly injecting water molecules and sulphate aerosols up to the stratosphere, which is destroying ozone molecules via chemical reactions. Further, in 2014, Laube et al. reported that three new CFCs and one hydrochlorofluorocarbon (HCFC) are depleting stratospheric ozone, as they were not covered under the Montreal Protocol. Later, NASA (2015) predicted that the ozone hole might return to its pre-1980s level by 2075. Since it is a very complex phenomenon; therefore, UV-B coming to Earth's surface will be dangerous for all living organisms until the recovery of ozone concentration in the stratosphere.

Short wavelength UV radiation has potentially damaging effects on DNA of all living beings on this Earth's surface. Tanning of skin and sunburn is a common phenomenon after exposure to UV-B radiation, leading to skin cancer in humans. Since plants lack locomotion, therefore they cannot escape from direct sunlight, hence they possess different adaptive mechanisms and structures to avoid higher UV-B radiation coming to them. High UV-B radiations have a potentially damaging impact on morphology, physiology, molecular biology, and biochemistry of green vegetation on this Earth, including crop plants, which is of serious concern to food security worldwide. UV-B impacts vary among different plant species and cultivars of the same species, depending upon their sensitivity and the intensity and exposure of UV-B (Kakani et al. 2003; Choudhary and Agrawal 2017). Bronzing (accumulation of coloured pigments like carotenoids, anthocyanins, and various phenolic compounds in the epidermal region of leaves), glazing (waxy compounds accumulation on the exposed surfaces of plants) and development of more trichomes (glandular hairs) on exposed surfaces of the plants are the first line of defence to avoid UV-B penetration deep inside the plant cells (Kakani et al. 2004; Choudhary and Agrawal 2016). Cupping and curling of leaves take place due to the destruction of Auxin synthesis on the exposed area, which is another avoidance mechanism adopted by plants to minimize UV-B exposure. Besides these, spongy parenchyma developments, increased leaf thickness, and reduced stomatal density are common responses against UV-B exposure (Kakani et al. 2003; Choudhary and Agrawal 2017).

Reduction in shoot length, root length, leaf area, number of leaves, seed germination, flowering, biomass, and yield are common harmful impacts of high UV-B radiation on plant's morphological characteristics (Kakani et al. 2003; Choudhary and Agrawal 2017). Enhanced UV-B radiation leads to higher production of reactive oxygen species (ROS) accountable for lipid peroxidation and oxidation of proteins and nucleic acids, along with the DNA damage, due to the formation of pyrimidine—pyrimidone dimmers (6,4-PPs) as well as cyclobutane pyrimidine dimers (CPDs) (Kakani et al. 2003; Choudhary and Agrawal 2017). In order to scavenge these, ROS plants have enzymatic (e.g., catalase, superoxide dismutase, ascorbate peroxidase, etc.) and non-enzymatic (eg. Anthocyanin, flavonoids, phenols, etc.) antioxidative defense mechanisms (Kakani et al. 2003; Choudhary and Agrawal 2017). Moreover, plants also pose different photo repair mechanisms for damaged DNA under UV-B radiation as excision, photoreactivation and recombinational repair (Gill et al. 2015). Damage to photosynthetic machinery due to UV-B radiation includes photosynthetic pigments, thylakoid membranes, light-harvesting complex, cyt. b/f complex, PSI and PSII, Rubisco and stomatal parameters (Kakani et al. 2003; Choudhary and Agrawal 2017). Plants well correct these disturbances in photosynthetic machinery up to some extent via synthesis of various new enzymes and proteins like restoration of D1 and D2 protein activities and the synthesis of UV-B screening compounds like phenols and flavonoids (Kakani et al. 2003; Choudhary and Agrawal 2017). These accumulated phenolics and flavonoid compounds are then transported towards the root zone, causing a deleterious impact on the rhizosphere's microbial community via excessive secretion and their antimicrobial nature (Lou et al. 2011; Choudhary et al. 2013; Choudhary and Agrawal 2017). Further, the balance of plant growth hormones in plants are also disturbed under UV-B exposure, directly affecting several plant growth performances and indirectly involving the symbiotic partnership of plants with the rhizosphere's microbial community (Choudhary et al. 2013; Choudhary and Agrawal 2017).

Among various plant growth regulators, Jasmonic acid (JA) and Salicylic acid (SA) have a vital and complex role in plants under UV-B stress. These signaling molecules are present in very low concentration and can regulate cellular processes in plants locally and systemically. JA and SA are both crucial components of signaling pathways during the activation of plants' protection mechanisms. Responses to various abiotic and biotic stresses are well coordinated through JA and SA and their derivatives like methyl jasmonate (MeJA) and methyl salicylate (MeSA). Increased accumulation of JA and SA has been reported in mung bean (up to 94 and 124%)

and pea (up to 91 and 53%) cultivars under UV-B stress (Choudhary and Agrawal 2014a, b). Differential accumulation of JA and SA in mung bean and pea has been observed depending upon the cultivar's sensitivity and resistance to UV-B. Interestingly, the antagonistic roles of JA and SA have been well established in these studies, as the cultivars having a higher accumulation of JA are more resistant, while cultivars having a higher accumulation of SA are susceptible to UV-B stress. The sensitivity of plants due to higher SA accumulation may be the effect of its inhibitory activities on ascorbate peroxidase and catalase activity (Rao et al. 1997; Durner and Klessig 1995; Vicente and Plasencia 2011). Later, Choudhary and Agrawal (2014a, b) have also observed that the mung bean and pea cultivars showing higher SA accumulation have more H_2O_2 levels and decreased activity of catalase and ascorbate peroxidase. Inverse relationships of SA and JA are also well reflected in rice plants after wounding (Lee et al. 2004).

To understand the complex mechanism of JA and SA in plants during UV-B stress, present chapter will mainly focus to JA and SA signaling, their antagonistic and synergistic behavior in plant defense, and the interaction to ROS.

2 Role of Jasmonic Acid Under UV-B stress in Plants

Jasmonic acid belongs to the group of lipidic plant hormones formed through fatty acids oxygenation (Bartoli et al. 2013) via octadecanoid (α-linolenic acid; 18:3) and hexadecanoid (hexadecatrienoic acid; 16:3) pathways (Fig. 1). In *Arabidopsis*, three reaction sites are known, i.e., chloroplast, peroxisome, and cytoplasm (Yang et al. 2019). This plant growth regulator is endogenous and generally distributed throughout the higher plants. JA is present in all the vegetative plant parts like leaves and stems, but the highest amount is reported in fruit parts mainly from immature pericarp (Meyer et al. 1984). It was first discovered as Methyl-Jasmonate (MeJA) by Edouard Demole in 1957 from the essential oil extract of *Jasminum grandiforum* L. (Demole et al. 1962) while, Aldridge et al. (1971) first isolated JA as free acid from the fungal culture filtrate of *Lasiodiplodia theobromae*. At present, three different forms i.e., Jasmonic acid (JA), Methyl Jasmonate (MeJA), and Jasmonate isoleucine conjugate (JA-Ile) are known (Ruan et al. 2019). Earlier, JA was considered as a plant growth inhibitor in rice (Yamane et al. 1981) and wheat (Dathe et al. 1981) seedlings, along with the senescence promoting substances in *Artemisia absinthium* (Ueda and Kato 1980) and *Cleyera ochnacea* (Ueda and Kato 1982). But, now it is firmly recognized that JA is the key plant growth regulator associated with plant's tolerance mechanisms against various biotic and abiotic stresses. Jasmonates (JAs) are connected with the plant's defense responses were first elucidated in tomato leaves during expression of proteinase inhibitors (Farmer and Ryan 1992; Browse 2009). It interacts with pathways of various other plant growth regulators (like auxin, abscisic acid, ethylene, gibberellins, salicylic acid, and brassinosteroids) in order to maintain plant growth and defense strategies, along with the tolerance to biotic and

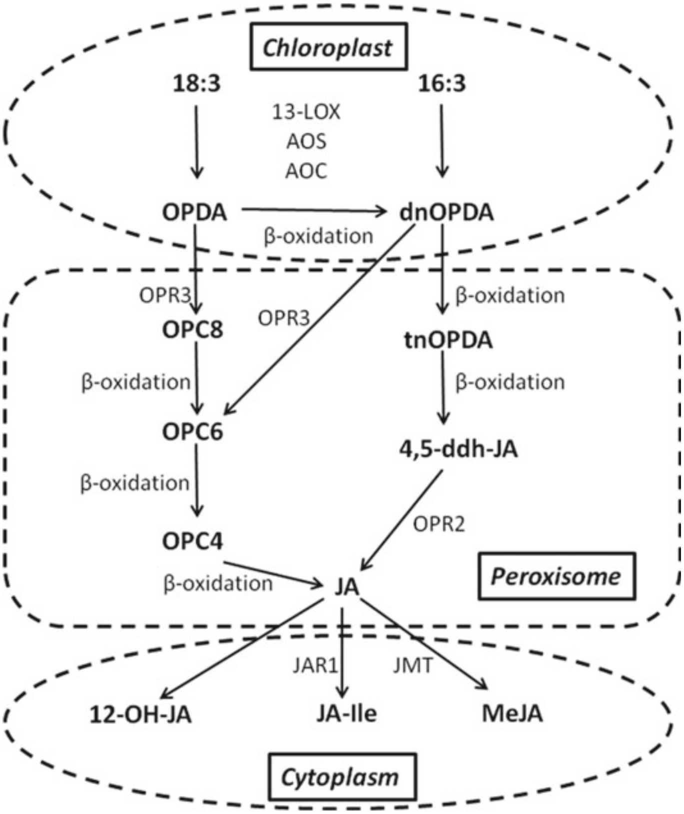

Fig. 1 Schematic representation of the JAs biosynthetic pathway in plants. 18:3, α-linolenic acid; 16:3, hexadecatrienoic acid; LOX, lipoxygenase; AOS, allene oxide synthase; AOC, allene oxide cyclase; JAR1, jasmonate resistant 1; JMT, JA carboxyl methyltransferase; OPR3, OPDA reductase, OPDA, 12-oxo-phytodienoic acid; dnOPDA, dinor-12-oxo-phytodienoic acid; tnOPDA, tetranor-OPDA; OPC8, 8-(3-oxo-2-(pent-2-enyl)cyclopentyl) octanoic acid; OPC6, 6-(3-oxo-2-(pent-2-enyl) cyclopentyl) hexanoic acid; OPC4, 4-(3-oxo-2-(pent-2-enyl) cyclopentyl) butanoic acid; 4,5-ddh-JA, 4,5 didehydrjasmonate; JA, jasmonic acid; JA-Ile, jasmonoyl-L-isoleucine; 12-OH-JA, 12-hydroxyjasmonic acid

abiotic stress in plants (Yang et al. 2019; Wang et al. 2020). Apart from development and stress responses, JAs also play an important role during the plant–microbe interactions and the establishment of symbiotic relationships. Further, long-range signaling between the plants is mediated by MeJA as a volatile compound.

JA has a significant role in plant defense responses under UV-B stress, as light plays an essential role in JA's biosynthesis and signal transduction. Studies carried out on plants concerning UV-B stress with JA are limited, and the role of JA under UV-B stress needs to be explored more. Higher accumulation of endogenous level of JA is well correlated with the better tolerance mechanism under UV-B stress in mung bean and pea cultivars (Choudhary and Agrawal 2014a, b). Accumulation of JA in these crop plants was cultivar specific, as the cultivar having more accumulation of JA under UV-B stress showed more tolerance along with the better anti-oxidative defense system (both enzymatic and non-enzymatic antioxidants). JA is mainly involved in activation of antioxidative defense mechanism (via peroxidase, superoxide anion radical, NADPH-oxidase, etc.), accumulation of soluble sugars and amino acids (i.e. methionine and isoleucine) along with the stomatal regulation (Karpets et al. 2014; Wasternack 2014; Acharya and Assmann 2009). Besides its role in plant defense, it also acts as a key regulator in the establishment of a symbiotic association of plants with rhizobia, as JA is necessary for the stimulation of nod genes (Rosas et al. 1998). Better nodulation along with the nitrogenase, nitrate reductase (NR) and nitrite reductase (NiR) activity was also noticed in cultivars of mungbean and pea having higher accumulation of JA in comparison to the cultivars with low endogenous JA level under UV-B stress (Choudhary and Agrawal 2014a, b). Several studies with different biotic and abiotic stresses in plants have also shown increments in the endogenous level of JA like infection of pests, pathogens, and diseases (Kiribuchi et al. 2005), cold stress (Cao et al. 2009), drought stress (Anjum et al. 2011), salt stress (Takeuchi et al. 2011) and light stress (Riemann et al. 2008). Consequently, induction in defensive proteins, phenol, lignin, and proline was observed in plants with the increased resistance capacity under stress (Kim et al. 2009; Shan et al. 2009). Further, expression of genes (i.e. AOC, AOS1, CO11, AOX2, and JAZ) and transcription factors (i.e. bHLH148 and MYC2) are involved at the molecular level (Hu et al. 2017; Robson et al. 2010; Zhao et al. 2013; Seo et al. 2011).

Exogenously supplied JA of 1.0 and 2.5 mM in concentration counteracted the harmful impacts of UV-B radiation in wheat seedlings (Liu et al. 2012). Induced tolerance against UV-B via JA in wheat was well coordinated with the accumulation of substances related to osmotic adjustments in plants and anthocyanin deposition along with enhanced superoxide dismutase (SOD) activities. Exogenous application of 1 mM JA was able to recover SOD activity under UV-B stress as exhibited in bluegrass (Zhang and Ervin 2005). Consistent results were also reported in rice seedlings with the interaction of salt stress and exogenous JA (Moons et al. 1997), pea seedlings with JA treatment only (Kumari et al. 2006) and in barley seedlings with MeJA treatment only (Popova et al. 2003). JA provoked antioxidative defense mechanisms in wheat seedlings against UV-B up to some extent as Liu et al. (2012) have also observed a significant decrease in catalase and peroxidase activities. Further, UV-B radiation is responsible for membrane damage and higher lipid peroxidation in plants (Choudhary and Agrawal 2017). Popova et al. (2003) have observed that the pretreatment of 2.5 mMMeJA can alleviate the lipid peroxidation resulting due to UV-B stress in plants. In contrast, enhancement in MDA content is reported under the application of JA alone to the plants (Fedina and Benderliev 2000).

Higher accumulation of proline under UV-B stress in plants is also a common phenomenon (Singh et al. 2009; Choudhary and Agrawal 2017). Beyond osmotic adjustments, proline also plays an essential role in the stabilization of proteins and enzymes, helpful for membrane integrity, $NADP^+$/NADPH ratios, along with free radical scavenging. Exogenously supplied JA has improved UV-B tolerance via induction of proline content in plants, and it has been speculated that this alteration in proline metabolism is mainly accountable for the expression of genes related to redox control (Hare and Cress 1997; Liu et al. 2012). Consistent results were also reported in barley seedlings under UV-B exposure after MeJA treatment (Fedina et al. 2009). Several studies reported induction of secondary metabolites after UV-B exposure in plants, which helps counteract the negative impact of UV-B directly or in some way via suppression of ROS formation and diminution of oxidative damage (Du et al. 2011; Choudhary et al. 2017). On the other hand, JA is also known to stimulate secondary metabolites (like anthocyanin, β-carotene, stilbene) along with increased phenolics, terpenoids and alkaloids (Wang et al. 2008; Morales et al. 2010). The application of exogenous JA resulted in increased anthocyanin content of plants related to JA specific COI1 protein that can induce late biosynthetic genes for anthocyanin, i.e., *LDOX*, *DFR*, and *UF3GT* (Shan et al. 2009). Liu et al. (2012) reported an enhanced anthocyanin content of wheat seedlings under the combined treatment of 2.5 mM JA and UV-B stress. Still, they did not observe any changes in flavonoids and phenolics content. Higher accumulation of flavonoids and phenolics is an adaptive mechanism to scavenge UV-B radiation and prevent the damage of mesophyll cells. A higher anthocyanin content of plant leaves is helpful for the mitigation of photooxidative injuries along with the scavenging of ROS (Neill and Gould 2003). Choudhary et al. (2013) reported increments of about 31 and 37% in total phenol and flavonoids content, respectively, under elevated UV-B exposure in mung bean plants. Choudhary and Agrawal (2014b) had observed more increments in kaempferol (up to 72%) and quercetin (up to 118%) content of pea cultivar having a higher accumulation of endogenous JA after elevated UV-B exposure. Similar results were also reported in mung bean cultivars with the increments of 70% in kaempferol and 164% in quercetin flavonols (Choudhary and Agrawal 2014a).

The decrease in chlorophyll and carotenoids content of plants under UV-B stress has been depicted in several studies (Choudhary and Agrawal 2017). Tsuchiya et al. (1999) had observed degradation in chlorophyll under MeJA treatment; however, Kovac and Ravnikar (1994) had reported contradictory results to this under JA treatment. Chl a, b and a/b did not change, whereas the decline in carotenoids was reported under combined treatment of UV-B and 2.5 mM JA (Liu et al. 2012). Similar findings were also observed in barley seedlings by Fedina et al. (2009). The negative impact of elevated UV-B on plants' photosynthetic process had been widely investigated (Kakani et al. 2003; Choudhary and Agrawal 2017), and PSII was revealed to be the most susceptible factors of photosynthetic apparatus under UV-B stress (Yang et al. 2007). Reduction in photosynthesis (up to 62%), stomatal conductance (up to 40%), and water use efficiency (up to 32%) along with the significant reductions in fv, fm, and fv/fm ratio had been observed in four soybean cultivars under elevated UV-B exposure (Choudhary and Agrawal 2015). Inhibition in PSII photochemistry in plants under UV-B stress leads to more excitation energy that could damage PSII, if not dissipated timely (Yang et al. 2007). Exogenous JA pretreatment had also improved the physiological functions under UV-B stress through better fv/fm ratio, PSII functions, non-photochemical quenching (NPQ), and Electron transport rate (ETR) process in wheat seedlings (Liu et al. 2012). Better photosynthetic rate along with the water use efficiency, stomatal conductance, and fv/fm ratio were also reported in mung bean cultivar having a higher accumulation of endogenous JA concentration under UV-B stress (Choudhary and Agrawal 2014a).

Overall JA has been proved to be beneficial under UV-B stress by improving the defense system of plants by enhancing enzymatic and non-enzymatic antioxidants, metabolites, photosynthetic functions, and various other physiological parameters, and ultimately these changes are reflected in the maintenance of crop yield. Mung bean and pea cultivars with higher accumulation of endogenous JA levels under elevated UV-B exposure were able to maintain better yield (Choudhary and Agrawal 2014a, b).

3 Footprints of UV-B Stress in Plants: Salicylic Acid (SA) Induced Signalling

Salicylic acid (SA) is a β-hydroxy phenolic acid and synthesized in pronounced amount in plants. SA functions as a chemical messenger which is capable of managing biological processes at even minuscule concentration. Unlike other metabolites, SA was considered to be a relatively unimportant secondary metabolite until Raskin (1992a, b) revealed its innate immunity, in the twentieth century. To synthesize SA, there are two pathways: isochorismate synthase (ICS) and phenylalanine ammonia lyase (PAL), both of which start with chorismate (Vlot et al. 2008). The dominance of pathways may vary with plant species and they may show equal dominance in some, like in soybeans (Lefevere et al. 2020). There could be differential regulation of SA within a plant species as it is found in rice. Shoots show much higher SA levels than roots (Duan et al. 2014). PAL and ICS pathways are independent pathways and 95% of SA synthesis occurs through ICS pathway; therefore it can be deduced that a small fraction of SA under UV-B treatment is through PAL pathway as observed in *Arabidopsis* and *Nicotiana benthamiana* (Seguel et al. 2018). During flowering, vadoo lily inflorescence exhibited marked heat production (thermogenesis). This happened because of volatilizing compounds that helped in the stimulation and attraction of insect pollinators. Rhoads and Mcintosh (1992) observed that thermogenesis happened via mitochondrial alternative respiratory pathway. Mostly the energy generated in this pathway is released as heat, which is generated by electron flow, while ATP is generated at just one step.

But both PAL and ICS pathways are highly significant for SA biosynthesis, and the intermediates from both the pathways contribute to SA synthesis. Numerous studies were conducted to analyse the higher levels of SA on plants under UV-B, and SA reduced the damaging effects (Mahdavian et al. 2008). Both ICS and PAL routes initiate with chorismate as the substrate, produced from phosphoenolpyruvate (PEP) and erythrose-4-phosphate (E4P) shikimate pathway which is a seven-step enzymatic reaction localized in plastid. Shikimate pathway is up-regulated upon UV-B irradiation and increases the carbon flow for PAL and ICS pathways (Zhang et al.

2012). Upon UV-B exposure, salicylic acid induction-deficient 2 (SID2) or Isochorismate synthase-1 (ICS1) and -2 (ICS2) act as isochorismate synthase which transform chorismate into IC in the chloroplast. Enhanced disease susceptibility 5 (EDS5) acts as a transporter to convey IC from the chloroplast into the cytoplasm, whose role under UV-B is not yet characterized. IC is initially transformed into isochorismoyl-9-glumate (IC-9-Glu) by an enzyme isochorismoyl-glutamate synthase (IGS) in plants. PBS3 is an enzyme involved in acyl-adenylate/thioester-formation and is from GH3 (glycoside hydrolase 3) protein family (Nobuta et al. 2007). PBS3 is involved in SA biosynthesis. SA is formed from IC-9-Glu and 2HNG (2-hydroxy-acryloyl-N-glutamate), which is also known as N-pyruvoyl-L-glutamate (NPG) which is also a by-product. The majority of SA is synthesized under UV-B via the ICS catalysed pathway (Catinot et al. 2008; Wildermuth et al. 2001; Garcion and Métraux 2006). *ICS2* interacts with many other genes (Fig. 2). The description of the genes that directly interact with *ICS2* is given in Table 1.

In 1961, phenylalanine ammonia-lyase (PAL) was for the first time isolated from barley, which is known to convert phenylalanine into t-coumaric acid (t-CA) and ammonia. Aldehyde oxidase 4 enzyme was identified in developing seeds of *Arabidopsis*, which is responsible for catalysing the conversion of BZA (benzaldehyde) to BA (benzoic acid). Further, an enzyme BA 2-hydroxylase (BA2H) is involved in forming SA from BA. ICS and PAL routes initial steps are closely associated with plastid, but most of the important enzymes needed in these pathways are encoded from nuclear genes. Both ICS and PAL pathways have a close nexus with other metabolic pathways like shikimate and aromatic amino acid biosynthetic pathways (Fig. 3). Chorismate obtained from the shikimate pathway is an antecedent

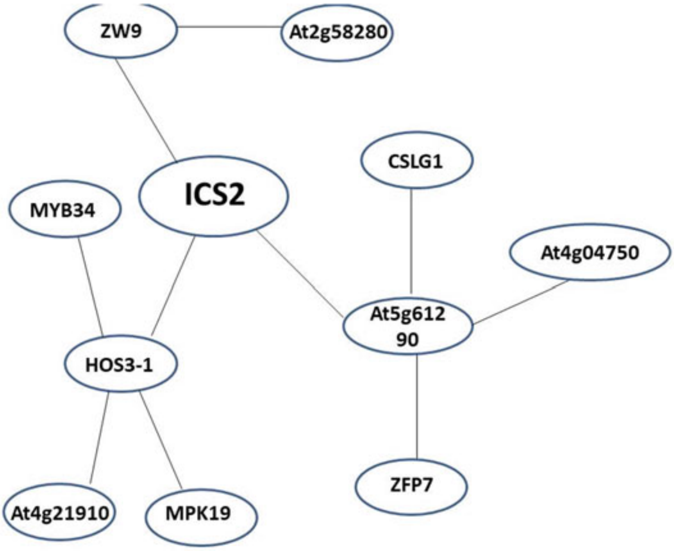

Fig. 2 ICS2 interaction with many other genes involved in signalling

Table 1 Description of genes involved in the interaction with *ICS2*

Gene	Function	Biological process
HOS3-1	GNS1/SUR4 membrane protein family	Fatty acid elongation and Saturated fatty acid synthesis
CSLG1	Cellulose synthase like G1 plant type	Primary cell wall biogenesis
MPK19	MAP kinase 19	Intracellular signal transduction
ZFP7	Zinc Finger protein 7	Negative regulation of abscisic acid-activated signalling pathway
MYB34	Myb domain protein 34	Response to Jasmonic acid
At4g21910	MATE efflux family protein	Transmembrane transport
At4g04750	Major facilitator superfamily Protein	Carbohydrate transmembrane Transport activity
At5g61290	Flavin binding monooxygenase family protein	Oxidation–reduction process
ZW9	TRAF-like family protein	Transcription factor
At1g58280	Phosphoglyceratemutase Family protein	–

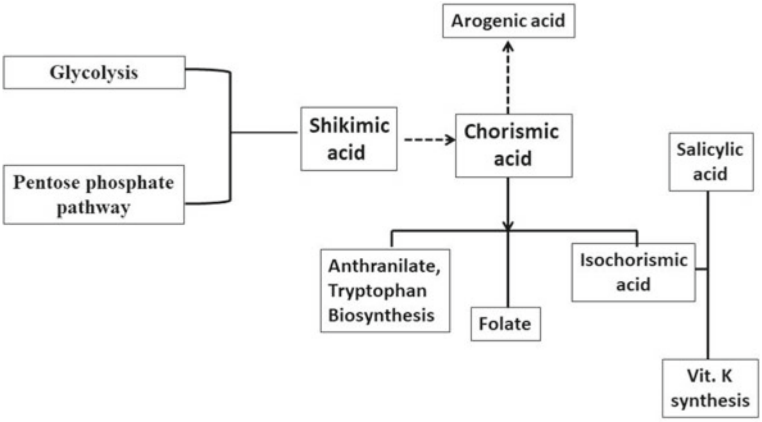

Fig. 3 Salicylic acid synthesis pathway in plants

for the biosynthesis of aromatic amino acids, thus, it acts as regulatory links between primary and secondary metabolic pathways in plants.

Dean and Delaney (2008) reported many SA derivatives from plants like (1) SA O-β-glucoside (SAG), (2) salicyloyl glucose ester (SGE), (3) methyl salicylate (MeSA), (4) methyl salicylate O-β-glucoside (MeSAG) and (5) 2.5-dehydroxybenzoic acid (gentisic acid). Gentisic acid is necessary for the activation of specific PR genes (Belles et al. 2007). SA accumulation and concomitant activation of PR genes are needed for the establishment of systemic acquired resistance (SAR) in tissues that are distant from the site of primary infection (Liu et al. 2016). Induction in the protein amounts of PR-3 and PR-5 under UV-B were observed in *Arabidopsis* (Fujibe et al. 2000). Surplus et al. (1998) also reported an aggregation of loose SA in the foliage of *Arabidopsis thaliana* under UV-B. PR-1 mRNA and protein levels increased in tobacco under UV-B irradiation.

Moreover, PR proteins are widely dispersed in the entire plant realm and are localized in all plant organs, being particularly higher in the foliage where it forms 5–10% of total proteins (van Loon et al. 1994). PR proteins are generally light proteins with molecular weight ranging between 6 and 43 kDa which are thermostable, resistant to protein degrading enzymes and soluble even at low pH (van Loon et al. 1994). PR proteins comprise of two parts (1) acidic PR protein discharged into the extracellular space, and (2) basic PR protein conveyed into the vacuole. PR protein activity is controlled by the signal sequence present at the C-terminal end (Takeda et al. 1991). Pathogenesis-related proteins otherwise are predominantly present in the apoplastic zone apart from being present in vacuoles (van Loon et al. 1994). SA pathway enhances the transcription of NPR1 (non-expression of pathogen-related gene 1), which further leads to the stimulation as well as aggregation of PR1, PR2, and PR5. Based on the amino acid sequences, serological and biological relations, these PR proteins are divided into 17 classes, (van Loon et al. 1994) but not all of PR is relevant under UV-B stress. NPR1 regulates PR gene expression through interaction with transcription factors like TGA (Kim and Delaney 2002; Zhou et al. 2000).

PR1 promoter analysis revealed it's regulation through positive and negative cis-elements (Lebel et al. 1998). NPR1 and TGA transcription factor interaction was discovered in multiple two-hybrid screens, which suggested that TGA factors might be accountable for gene expressions via NPR1 (Zhang et al. 1999). TGA factor expression is important for tolerance against UV-B stress (Herrera-Vásquez et al. 2020). Johnson and his team undertook a chromatin immunoprecipitation experiment, and they showed that TGA factors are recruited to the PR1 promoter in vivo in the SA and NPR1 dependent manner (Johnson et al. 2003). Transcriptomic analyses revealed that PR genes get significantly altered under both biotic and abiotic stresses and thus, are suitable for developing crop varieties tolerant to multiple stresses (Ali et al. 2018). Further, increased mRNA levels were noticed for PR1 (SAR marker gene) under abiotic stresses in pepper plants (Hong and Hwang 2005). Activation of dehydration-responsive element-binding protein (DREB), drought-induced protein 19 (Di19), and cup-shaped cotyledon (CUC) induces PR genes.

3.1 Fate of SA in Plants Under UV-B

SA can be transformed into many derivatives through processes including glycosylation, methylation, sulphonation, amino acid (AA) conjugation, and hydroxylation. These modifications might inactivate SA and help fine-tune the SA activity and facilitate its temporary storage. SA derivatives also play pivotal roles in plants under UV-B stress (Santisree et al. 2020).

3.1.1 Glycosylation

Two uridinediphosphate (UDP)-glucosyltransferases (UGTs), i.e., UGT74F1 and UGT74F2 are responsible for glycosylation of SA in *Arabidopsis* (Dean and Delaney 2008). UGT74F2, also termed as S-glycosyltransferase (SGT1) is involved in catalysing the conjugation of glucosyl with the carboxyl group of SA, thus producing salicylate glucose ester (SGE). Both UGT74F1 and UGT74F2 utilize glucosyl group from UDP-glucose and conjugate with the hydroxyl group of SA, generating SA2-O-β-D-glucoside (SAG) (Dean and Delaney 2008).

3.1.2 Methylation

Methyl group can be added with the carboxyl group (-RCOOH) of SA via S-adenosyl-L-methionine (SAM)-dependent methyltransferases (MTs) in plants. SAM-MT enzyme is encoded by BA/SA carboxyl methyltransferase 1 (BSMT1) gene in *Arabidopsis* from 24-gene family of SABATH MTs. These genes were named after the three genes which were discovered earliest in this family as: SA carboxyl methyltransferase (SAMT), benzoic acid carboxyl methyltransferase (BAMT) and theobromine synthase (THS) (D'Auria et al. 2003). Similar to other modifications, SA gets inactivated upon methylation and transformed into MeSA which can be transformed into active SA by the methylesterase (MESs) (Vlot et al. 2008; Park et al. 2007).

3.1.3 Sulfonation

Sulfonation is carried out by the sulfotransferases (ST or SOTB) which is composed of 21 members of gene family (Günal et al. 2019). The sulfonate group for ST functioning is donated by coenzyme 3'-phosphoadenosine-5'-phosphosulfate (PAPs) and the final product carries 3'-phosphoadenosine-5'-phosphate (PAP) (Klein and Papenbrock 2004).

3.1.4 Amino Acid Conjugation

SA is conjugated with amino acid, and this reaction is catalysed by GH3 enzyme. In plants specifically, SA-Asp (salicyloyl-L-aspartate) is the dominating one which is being added (Steffan et al. 1988). In Arabidopsis, both GH3.5/WES1 can catalyse conversion of SA into SA-Asp and its over-expression leads to SA-Asp aggregation in plants.

3.1.5 Hydroxylation

In vitro, SA can trap free hydroxyl (OH) radicals without any enzymes and form two DHBA (dihydroxybenzoic acids): 2,3-DHBA and 2,5-DHBA (commonly called as gentisic acid), and these reactions are highly reformable (Maskos et al. 1990; Chang et al. 2008). The pathogen-induced generation of ROS is challenged in the rboh (respiratory burst oxidase homolog) mutants of *Arabidopsis*.

4 Antagonistic/Complementary role of JA and SA in Plants Under UV-B Stress

SA accumulation in roots and leaves was observed under UV-B in wheat (Kovács et al. 2014) and barley (Bandurska and Cieślak 2013). A-H-Mackerness and Jordan (1999) observed an increased production of JA in *Arabidopsis*. Mendez-Bravo et al. (2019) observed that UV-B activated JA mediated defense signalling which suppressed the SA signalling. Antagonistic interaction between JA and SA signalling and the crosstalk is thoroughly characterized (Bostock 2005). SA accumulation is inhibited by JA signalling via., multiple NAC TFs modulations such as ANAC019/055/072. NACs transcription is increased by MYC2. The activated NAC TFs limit the expression of ISOCHORISMATE SYNTHASE 1 (ICS1) and induce BENZOIC expression ACID/SA CARBOXYL METHYLTRANSFERASE 1 involved in SA methylation (Zheng et al. 2012). In addition, many components are concerned during crosstalk of JA and SA signalling pathway through mitogen-activated protein kinase (MAPK) (Rodriguez et al. 2010), redox regulators glutathione (GRX) and thioredoxin (TRX) (Spoel and Loake 2011), MYC2, TGAs and PDF 1.2 (Gatz 2013) and WRKY70 (Shim et al. 2013).

Similarly, TRX monomerized NPR1 polymers via SA-induced redox changes and then monomers like GRX480 are transported to the nucleus, where it specifically bind to TGA, which also directly regulates the expression of PR1 (Gatz 2013). Interestingly, the induction of GRYs can block TGA-mediated JA response gene expression, such as ORA59; further suggesting SA-JA antagonism (Zander et al. 2012). MPK4 positively regulates GRX480 in the SA signalling pathway and negatively regulates MYC2 in the JA signalling pathway, which is essential for JA responsive genes (PDF 1.2 and THI 2.1) (Wasternack and Hause 2013). Choudhary and Agrawal (2014a, b) reported a concomitant increase in SA and JA under elevated UV-B. Liu et al. (2016) reported a higher accumulation of JA and SA, and showed that a high level of SA promoted NPR3 which mediated degradation of NPR1, thus alleviating its crosstalk inhibition on JA signalling by degrading JAZs and activating NPR3 and NPR4.

5 Conclusion

Under UV-B stress, higher accumulation of endogenous JA level and exogenously supplied JA has a beneficial role by improving the defense system of plants via enhancing enzymatic and non-enzymatic antioxidant metabolites, photosynthetic functions, and several other physiological parameters responsible for the maintenance of crop yield. Under UV-B radiation, one of the two pathways, i.e., ICS and PAL may be dominant for SA synthesis and mostly its ICS pathway. The synthesis is usually a trade-off between primary and secondary metabolism. SA is known to affect PR genes, and the regulation is through NPR1. Many of the PR genes get activated under UV-B. The role of SA derivatives under UV-B in plants need further investigation. SA and JA signalling cross-talk may be complementary or antagonistic but mostly antagonistic under UV-B stress.

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Plant Responses to Exogenous Salicylic and Jasmonic Acids Under Drought Stress

Kazem Ghassemi-Golezani and Salar Farhangi-Abriz

Abstract In a vast area of the farming lands in the world, drought stress is an important factor for limiting plant growth and productivity. Adjusting hormonal signaling of plants under drought stress is one of the main goals of plant physiologist to increase drought stress tolerance and productivity of plants. Salicylic (SA) and jasmonic acids (JA) are involved in plant defense mechanism against abiotic stress tolerance such as drought. These growth regulators considerably enhance antioxidative capacity (enzymatic and non-enzymatic) of plant cells, which largely reduce lipid peroxidation and maintain membrane integrity. Exogenous salicylic and jasmonic acids increase plant osmolytes such as proline and soluble carbohydrates in response to drought stress. The critical roles of these growth regulators in enhancing photosynthetic activities under drought stress have been confirmed. Moreover, salicylic and jasmonic acids can change the biosynthesis of secondary metabolites in drought subjected plants. In this chapter, the SA and JA mechanisms of actions in changing physiological and biochemical properties of plants favoring drought tolerance were discussed.

1 Introduction

Global plant production is affected by periodical drought stress. Drought is a long dry period, which happens in an area when it receives a below average precipitation (Ali et al. 2017; Farhangi-Abriz and Ghassemi-Golezani 2019). This stress has an extensive impact on physiological and biochemical aspects of plants. Various aspects of plant physiology such as photo-synthetical activities, source and sink relationships, hormonal signaling and plant growth are affected by drought stress (Li and Liu 2016; Anjum et al. 2017). Changes in hormonal signaling is one of the important responses in plant cells, which controls various aspects of plant growth and physiology under drought stress (Pandey et al. 2017). Plant hormones such as Salicylic acid (SA) and jasmonic acid (JA) are the natural groups of molecules, which have important roles

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in adjusting plant growth and reacting to environmental stresses such as drought and salinity (Ilyas et al. 2017; Ghassemi-Golezani and Farhangi-Abriz 2018).

SA is generally present in plants in the form of methylated, glycosylated, glucose-ester, and amino acid conjugates or in a free state (Zhang and Li 2019). This hormone can be detected in large amounts in plant leaves after pathogenic infection (Qi et al. 2018). SA controls different parameters of plant growth such as root and shoot growth and leaf expansion (Mimouni et al. 2016). Exogenous application of SA noticeably improves plant growth under drought (Sharma et al. 2017), salt (Farhangi-Abriz and Ghassemi-Golezani 2018), heat (Wassie et al. 2020) and heavy metal (Kohli et al. 2017) stresses. This growth regulator also increases antioxidative activities and osmolytes production of plants under adverse conditions such as drought (Rao et al. 2012). Endogenous SA is strongly correlated with enzymatic and non-enzymatic antioxidants and osmolytes under normal and stressful conditions (Farhangi-Abriz et al. 2020). The organic osmolytes in plant tissues, such as proline and soluble carbohydrates are increased in response to foliar application of SA (Moustafa-Farag et al. 2020). This treatment also enhances root development of plants under drought and consequently improves water uptake by plants (Hayat et al. 2010).

Jasmonates family include jasmonic acid, methyl jasmonate, and jasmonyl-isoleucine are involved in control of plant responses to different kinds of environmental stresses and play an important role in several aspects of growth and development (Farhangi-Abriz and Ghassemi-Golezani 2019; Ruan et al. 2019). Jasmonic acid adjusts growth and development of plants through diverse interconnections between various signaling molecules such as SA and abscisic acid (ABA) (Sasaki et al. 2001). Exogenous application of JA under drought stress improves drought tolerance in brassica species (Alam et al. 2014). Many reports show that exogenous JA increases antioxidative defense mechanisms in drought stressed plants (Alam et al. 2014). JA increases production of ABA which in turn controls stomata behavior and water status of plants under drought stress (Farhangi-Abriz and Ghassemi-Golezani 2019). de Ollas et al. (2013) found that accumulation of JA in root cells is required for ABA biosynthesis in rice plants. In this chapter, the responses of plants to SA and JA under drought stress are evaluated, in order to identify the possible mechanisms of SA and JA involvement in drought subjected plants. Some possible effects of SA and JA on changing plant response to drought stress are summarized in Fig. 1.

2 The Roles of Salicylic and Jasmonic Acids in Drought Sressed Plants

2.1 *Oxidative Stress Tolerance*

Reactive oxygen species (ROS), such as hydrogen peroxide, superoxide anion, hydroxyl radicals and singlet oxygen are generated at low levels in plant organelles, especially in peroxisomes, mitochondria, chloroplasts, plasma membrane and

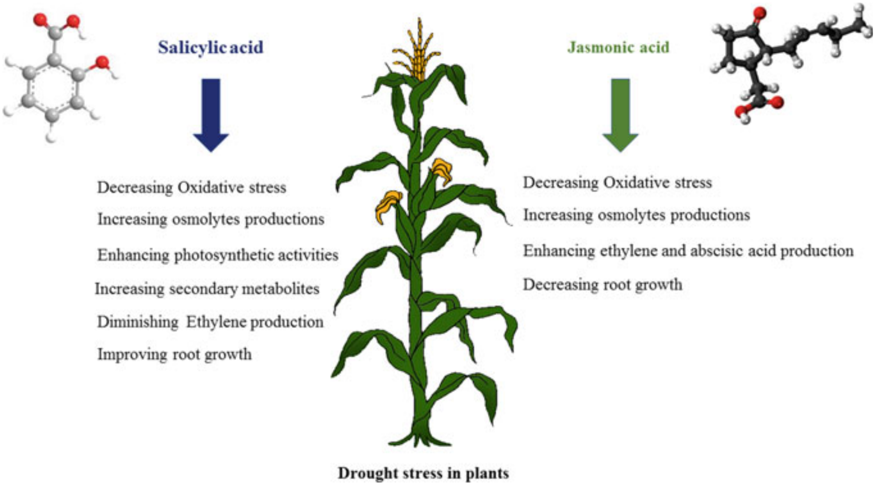

Fig. 1 Some important impacts of salicylic and jasmonic acids on plant response to drought stress

apoplast under normal water availability. However, generation of ROS is stimulated by drought condition (Kar 2011; Choudhury et al. 2017). Higher levels of ROSs act as noxious substances which can damage different molecules such as proteins, lipids and nucleotides (Banerjee and Roychoudhury 2018). Once the plant confront drought, the initial physiological response will be stomatal closure to evade water losses due to transpiration, but this response will have some harmful effects on photosynthesis and electron transportation system with limited CO2 fixation, altered photosynthetic activities and higher rate of photorespiration (Chaves et al. 2002; Osakabe et al. 2014). Plants have different antioxidative defense systems to control or detoxify ROSs in their cells. Different enzymatic (such as superoxide dismutase, catalase, peroxidases) and non-enzymatic antioxidant systems (such as proline, flavonoids, carotenoids, ascorbate, glutathione and α-tocopherol) have the capacity to scavenge ROSs in plant cells (Osakabe et al. 2014). Antioxidants and stress hormones are produced in a high amount under drought stress. According to available reports, there was a strong correlation between endogenous concentrations of stress hormones such as SA and JA with antioxidative activities in plant cells (Farhangi-Abriz et al. 2020).

The interaction of SA with ROSs was initially reported by Chen et al. (1993). Subsequent investigations revealed that SA activates different stress tolerance genes and transcription factors such as *TGA* factors from *bZip* family, bind to *cis*-elements containing *TGA* box and *WRKY* transcription factors, which control most of the antioxidative activities in plant cells (Singh et al. 2002; Johnson et al. 2003). It is confirmed that plants increase SA accumulation after being exposed to drought stress (Okuma et al. 2014). *ICS1* and *ICS2* are the two *Arabidopsis* genes coding for isochorismate, which is the key enzyme in adjusting SA biosynthesis. Environmental stresses such as drought upregulate *ICS1* and *ICS2* genes and consequently enhance

SA concentration in plant cells (Herrera-Vásquez et al. 2015). SA-deficient transgenic rice has lower antioxidant capacity and higher ROS levels (Yang et al. 2004). Durner and Klessig (1996) showed that SA detoxifies hydroxyl radicals and thus protects plants against catalase inactivation by hydrogen peroxide.

Exogenous application of SA is a practical way to increase SA concentration in plant cells (Farhangi-Abriz et al. 2020). Many reports showed that SA could be absorb by plant leaves, even in normal or stressful conditions (Nassef 2017; Ghassemi-Golezani et al. 2018a). Foliar application of SA increases antioxidative activities of plants under drought stress. Singh and Usha (2003) stated that irrespective of intensity of drought stress and SA concentration (1–3 mM), SA treated plants had the highest level of superoxide dismutase activity compared to untreated plants. In a pot experiment, Saruhan et al. (2012) investigated the role of SA in increasing antioxidative activities of different maize cultivars (*Zea mays* L.). The results of this study showed that SA treatment noticeably increased superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase and monodehydroascorbate reductase activities. Similar reports are available in tomato (Hayat et al. 2008), wheat (Sedaghat et al. 2017), barley (Torun 2019) and cotton (Hussain et al. 2020).

Kadioglu et al. (2011) reported that foliar application of SA significantly improved endogenous content of SA in *Ctenanthe setosa* plants and consequently improved the non-enzymatic antioxidants such as ascorbate, glutathione, α-tocopherol, and carotenoid contents under drought stress. In a field experiment, Ghassemi-Golezani et al. (2019) evaluated the possible effects of SA on promoting water stress tolerance of rapeseed and found that foliar spray of SA (1 mM) significantly enhanced peroxidase, catalase, superoxide dismutase, and ascorbate peroxidase activities, but reduced hydrogen peroxide generation under drought stress. These increments in antioxidative activities noticeably improved membrane integrity of plant cells under water deficit. In another field experiment, the drought-subjected ajowan (c*arum copticum* L.) plants produced more non-enzymatic compounds such as carotenoids and anthocyanins in response to foliar application of SA (Ghassemi et al. 2019).

JA is another stress hormone that has some important roles on decreasing oxidative stress of plants under different environmental conditions such as drought (Alam et al. 2014) and salt stress (Farhangi-Abriz and Ghassemi-Golezani 2018). Compared to research works showing a positive impact of jasmonic acid in response to pathogen attacks, less has been known about its' role on plants under abiotic stresses such as drought. Previous researches confirmed that water stress increases jasmonic acid production in leaves and roots of plants (Kiribuchi et al. 2005). Overexpression of some key genes in jasmonic acid biosynthesis pathway such as jasmonic acid carboxyl methyl transferase gene (*AtJMT*) in rice showed an increased level of jasmonic acid under drought condition (Kim et al. 2009a). Increasing endogenous content of JA has a positive effect on rising antioxidative activities in plant cells (Farhangi-Abriz et al. 2020). The JA may affect enzyme activities through changes in gene transcription and translation. The organ-specific nature of JA shows that the effects of this hormone are responsible for directing specific cellular and sub-cellular modifications in metabolism (Comparot et al. 2002).

Many reports showed positive effects of JA application on rising antioxidative activities in different plant species under water deficit (Farhangi-Abriz and Ghassemi-Golezani 2019). According to Alam et al. (2014) jasmonic acid stimulates the glyoxalase systems in plant cells and enhances antioxidative activities under drought stress. These researchers also found that foliar application of JA increases the activities of some important antioxidant enzymes such as ascorbate peroxidase, glutathione peroxidase, and catalase in *Brassica* species, leading to ROS detoxification under drought stress. Anjum et al. (2011) reported that foliar application of methyl-jasmonate enhances the superoxide dismutase, peroxidase, and catalase activities in soybean leaves and consequently reduces membrane lipid peroxidation under water stress. Priming with JA was also helpful in rising antioxidative activities of seedlings under water limitation. Abdelgawad et al. (2014) found that pretreatment of maize seeds with methyl-jasmonate increases the antioxidative activities of seedlings under drought condition. Foliar application of JA not only improves activities of antioxidants, but also increases the production of non-enzymatic antioxidants such as ascorbate and glutathione molecules (Shan and Liang 2010). The positive impacts of JA on increasing ascorbate–glutathione cycle have been confirmed by Shan et al. (2015) in wheat plants. Foliar spray of jasmonic acid alleviated oxidative stress in *Thymus vulgaris* by increasing antioxidative activities (Alavi-Samani et al. 2015). Ghaffari et al. (2020) showed that foliar applications of jasmonic acid increases the catalase, and peroxidase activities and reduces lipid peroxidation in sugar beet. The antioxidant activities of SA and JA treated plants are summarized in Table 1.

2.2 Osmotic Stress Tolerance

Water stress causes cell dehydration and changes cell metabolism. Production and accumulation of osmolytes such as proline, soluble carbohydrates, proteins and glycine betaine are the main changes in cell metabolism under drought (Kaur and Asthir 2017; Hussain et al. 2019). Drought-induced production and accumulation of osmolytes have been reported in various plant species. previous findings proved that production and accumulation of osmoprotectants can enhance drought tolerance of plants (Li et al. 2017; Shinde et al. 2018). Drought-induced limitation of water availability hinders cell expansion, cell division and growth of plants (Riboldi et al. 2016; Feng et al. 2016). Salehi-Lisar and Bakhshayeshan-Agdam (2016) reported that reduction of plant growth under drought stress is related to a decrement in cell water potential. Drought stress reduces some important plant-water related parameters such as relative water content, osmotic potential, leaf water potential, transpiration rate and pressure potential (Kirkham 2014). The other well-known mechanisms of osmolytes are detoxification of toxic compounds such as ROS, and protection of membrane and mitochondrial structures and photosynthetic system (Hayat et al. 2012). Furthermore, most of the osmolytes have signaling roles under drought stress. The concentration of natural osmoprotectants in cytoplasmic area can exceed 200 mM

Table 1 Salicylic acid and jasmonic acid impacts on antioxidative activities of different plant species under drought stress

Hormones	Plant species	Application method and dosage	Effects on plants	References
Salicylic acid	*Brassica napus* L	Foliar application—1 mM	Foliar sprays of salicylic acid increased the antioxidant enzymes activities such as peroxidase, catalase, superoxide dismutase, and ascorbate peroxidase and consequently reduced lipid peroxidation under drought stress	Ghassemi-Golezani et al. (2019)
Salicylic acid	*Oryza sativa*	Seed priming (0.5 and 1 mM)	Seed priming with salicylic acid noticeably improved seedling growth by increasing catalase, ascorbate peroxidase and guaiacol peroxidase activities under drought stress	Sohag et al. (2020)
Salicylic acid	*Brassica napus*	Foliar application—1.5 mM	Salicylic acid improves drought-stress tolerance by increasing the redox status and decreasing reactive oxygen species generation in *Brassica rapa*	Hien La et al. (2020)
Salicylic acid	*Phaseolus vulgaris*	Foliar application—1 mM	Foliar application of salicylic acid increased superoxide dismutase, catalase and ascorbate peroxidase activities, and reduced lipid peroxidation of plants under drought stress	Lopes et al. (2019)
Jasmonic acid	*Agropyron cristatum*	Protirement of plant—1 µM	Jasmonic acid enhanced the ascorbate and glutathione metabolisms in plant tissues and induced the water stress tolerance	Shan and Liang (2010)

(continued)

Table 1 (continued)

Hormones	Plant species	Application method and dosage	Effects on plants	References
Jasmonic acid	*Triticum aestivum*	Protirement of plant—10 µM	Exogenous jasmonic acid enhanced the nitric oxide production and antioxidative systems such as ascorbate–glutathione cycle under water stress	Shan et al. (2015)
Jasmonic acid	*Triticum aestivum*	Foliar application—100 µM	Jasmonic acid significantly enhanced antioxidative activities in wheat seedlings and improved drought stress tolerance	Abeed et al. (2020)
Jasmonic acid	*Thymus vulgaris*	Foliar application—200 µM	Foliar application of JA decreased the harmful effects of water stress on thymus plants by enhancing antioxidative activates and root growth	Alavi-Samani et al. (2015)

which is osmotically important in preserving cell turgor for water uptake under water stress condition (Sharma et al. 2019). Foliar application of SA and JA can enhance the drought stress tolerance of plants by increasing osmolytes production.

SA is an important signal molecule participating in defensive responses to abiotic stress (Khan et al. 2015). This hormone can enhance biosynthesis of osmolytes such as proline, glycine betaine and sugars under osmotic stress. Previous works have demonstrated that SA is involved in stimulating synthesis of proline under drought stress (Lee et al. 2019; de Andrade et al. 2020). Misra and Saxena (2009) reported that the activity of proline biosynthetic enzymes viz. γ-glutamyl kinase and pyrroline-5-carboxylate were enhanced in 0.5 mM SA-treated *Lens esculenta* plants. Three years later, Misra and Misra (2012) stated that SA reduces the activity of proline oxidase and consequently prevents proline degradation, which was later supported by Khan and Khan (2013) in wheat plants. Enhancing proline biosynthesis by SA is related to better nitrogen assimilation and photosynthetic activities (Sharma et al. 2019). SA stimulates glycine betaine synthesis in the range of 0.5–2.5 mM in plants exposed to various kinds of abiotic stresses such as drought and salinity (Sharma et al. 2019). Aldesuquy et al. (2012) reported that foliar application SA (0.05 M) in two cultivars of wheat (resistant Sakha 93 and sensitive Sakha 94) had a meaningful impact on rising growth and metabolism of drought stressed wheat cultivars by enhancing glycine and proline biosynthesis. Kareem et al. (2017) showed that foliar application of SA (1.44 and 2.88 mM) stimulates proline and glycine betaine biosynthesis. and enhances drought tolerance of wheat plants. Similar report is available for *Helianthus annuus* plants under drought stress (Hussain et al. 2009).

Soluble carbohydrates as important osmolytes in plant cells could be increased by SA treatment under drought stress (Fayez and Bazaid 2014). SA enhances soluble sugars in plant leaves by diminishing polysaccharide hydrolyzing enzymes (Khodary 2004). According to Sharma et al. (2019), soluble carbohydrates act as membrane stabilizers, ROS scavengers and Osmoprotectants under abiotic stresses. Beside the proline, glycine betaine and carbohydrates, free amino acids have imperative participation in regulating osmotic homeostasis in plant cells. Yadav et al. (2005) and Sankar et al. (2007) reported that SA enhances amino acids production in *Sorghum bicolor* and *Abelmoschus esculentus* and improves plant growth under water deficit condition. In another report, Abdallah et al. (2016) showed similar increment of amino acid content in quinoa plants in response to different concentrations of SA application (i.e., 200 and 400 mg L^{-1}) under drought stress. These researchers suggested that the elevation of amino acid biosynthesis in response to SA might be related to enhanced protein degradation.

The JA has a significant role in osmotic adjustment of plant cells. Foliar application of JA improves osmotic adjustment of plants via increasing the production of osmolytes such as proline and soluble carbohydrates (Farhangi-Abriz and Ghassemi-Golezani 2019). Shan et al. (2015) and Anjum et al. (2011) identified the helpful impacts of JA in reducing drought stress through the production of osmolytes such as proline. Endogenous JA up-regulates various important genes playing critical roles in water stress adaptation by stimulating different encoding stress responsive proteins and osmolytes such as proline (Per et al. 2018).

JA-induced increment of proline contents in drought stressed plants has been reported in wheat (Ilyas et al. 2017), barley (Bandurska et al. 2003) and rapeseed (Alam et al. 2014) plants. Increasing proline content is a good sign of drought tolerance in plants due to its role in the activation of Kreb's cycle and renewal of chlorophylls (Ashraf and Foolad 2007). Foliar application of JA also increases the production and accumulation of organic acids of Kreb's cycle such as citrate and malate, that enhance resistance to environmental stresses such as drought. In a study, foliar application of JA increased the GB content in pear leaves and consequently improved overall plant growth under water stress (Gao et al. 2004). Ilyas et al. (2017) found that exogenously applied jasmonic acid under water stress modulated the drought induced harmful effects through increasing the level of soluble carbohydrates in wheat plants. Soluble carbohydrates act as osmolytes and osmoprotectants and improve relative water content of plants under abiotic stress. Similarly, Farhangi-Abriz and Ghassemi-Golezani (2018) reported that foliar application of JA modulates the salt induced osmotic stress in soybean plants through increased contents of glycine betaine, soluble sugars as well as proline. The impacts of SA and JA on rising osmolytes of plants are summarized in Table 2.

Table 2 Salicylic acid and jasmonic acid impacts on osmolytes production in different plant species under drought stress

Hormones	Plant species	Application method and dosage	Effects on plants	References
Salicylic acid	*Brassica rapa*	Foliar application—1.5 mM	Salicylic acid increased proline and drought stress tolerance of plants by up-regulating the expression of genes encoding pyrroline-5-carboxylate synthase (*P5CSA* and *P5CSB*) and down-regulating the expression of the gene encoding proline dehydrogenase (*PDH*) compared to non-SA pretreated plants	Hien La et al. (2020)
Salicylic acid	*Zea mays*	Root pretreatment—10 µM	Salicylic acid increased the biosynthesis of proline, soluble sugar and soluble protein contents under drought stress	Shan and Wang (2017)
Salicylic acid	*Triticum aestivum*	Seed priming—10 Mm	Seed priming with salicylic acid noticeably reduced drought stress effects on wheat plants by rising proline and soluble sugar contents in plant tissues	Ilyas et al. (2017)
Salicylic acid	*Zea mays*	Seed priming—2 mM	Salicylic acid increased the biosynthesis of proline, soluble sugar and total carbohydrate in maize seedlings and consequently improved water content of plants under drought stress	Tayyab et al. (2020)
Jasmonic acid	*Triticum aestivum*	Seed priming—100 µM	Seed priming with jasmonic acid increased the germination percentage, proline, and soluble carbohydrate accumulation and shoot growth of wheat plants under water stress	Ilyas et al. (2017)

(continued)

Table 2 (continued)

Hormones	Plant species	Application method and dosage	Effects on plants	References
Jasmonic acid	*Triticum aestivum*	Foliar application—100 μM	Jasmonic acid improved total osmotic potential of plant cells by rising the contents of osmoregulatory component such as soluble carbohydrates, soluble proteins and proline under drought stress	Abeed et al. (2020)
Jasmonic acid	*Fragaria* × *ananassaDuch*	Root treatment—0.05 mM	Jasmonic acid improved water stress tolerance of strawberry plants by increasing proline and protein contents	Yosefi et al. (2020)
Jasmonic acid	*Pyrus communis* L.	Foliar application—50 mM	Jasmonic acid increased betaine accumulation in pear leaves and enhanced drought stress tolerance of plants	Gao et al. (2004)

2.3 Photosynthetic Activities

Crops are exposed to water stress when there is not adequate water accessible, or the water present cannot be taken up by the plants. Water stress diminishes photosynthetic activities for some reasons: (1) stomatal closure decreases the carbon fixation in leaves, and (2) water shortage damages the cell membrane and inhibits electron transportation systems (Lavergne et al. 2020). Some stress tolerance hormones such as SA and JA can have positive impacts on improving photosynthetic activities of plants under water deficit. Singh and Usha (2003) reported that foliar application of SA (1–3 mM) enhances total chlorophyll content of wheat seedlings under water stress. These researchers, also showed that SA improves carboxylase activity of Rubisco enzyme in stressed plants. High values of leaf chlorophyll in response to SA could be related to preserving chlorophyll structure from degradation by antioxidative enzymes. Moreover, SA enhances chlorophyll stability index by elevating nitrogen metabolism in plant cells (Farhangi-Abriz and Ghassemi-Golezani 2016). Hayat et al. (2008) stated that SA increases net photosynthetic rate of tomato plants under water stress by enhancing internal CO_2 concentration, stomatal conductance, transpiration and photosynthetic rates. According to these researchers, the beneficial effect of SA on increasing photosynthetic activities of tomato leaves could be related to high activities of some important enzymes such as carbonic anhydrase. The increment of carbonic anhydrase activity by SA treatment has been also reported in lemongrass (Idrees et al. 2010). Tang et al. (2017) exanimated the possible effects of

SA on gas exchange, pigment contents and chlorophyll fluorescence in water stressed soybean plants. The results showed that SA significantly improves gas exchange rate, chlorophyll content and chlorophyll fluorescence parameters of soybean leaves under water stress. This report revealed that SA-induced increment of PSII efficiency (ΦPSII) under water stress is related to strengthening photochemical quenching. SA not only improves photosynthetic activities in C3 plants, but also enhances photosynthetic performance in C4 plants. Idrees et al. (2010) reported a positive effect of SA on promoting the phosphoenolpyruvate carboxylase activities in lemongrass under drought stress. Similar impacts of SA application are shown in maize plants under cadmium toxicity (Krantev et al. 2008).

Foliar treatments of jasmonic acid and methyl-jasmonates are useful strategies for alleviating the harmful effects of drought on plant photosynthesis. Some researchers indicated that exogenous treatment of jasmonic acid could be useful for increasing photosynthetic activities in different plant species. Wu et al. (2012) reported that application of methyl-jasmonate improved drought tolerance of *Brassica oleracea* through enhancing the synthesis of chlorophyll and net photosynthetic rate. Sheteiwy et al. (2018) stated that Priming with methyl jasmonate reduces the negative effects of water stress in rice seedlings by improving photosynthetic activities and photochemical efficiency of PSII (Fv/Fm). Ma et al. (2014) investigated the photosynthetic responses of wheat to combined effects of water stress and exogenous methyl jasmonate and found that 0.25 μM MeJA increases the photosynthesis under water stress mainly through improving the water status and antioxidant capacity of wheat plants. Moreover, they showed that exogenous MeJA induces stomatal closure, that maintains water status and delays plant senescence under drought stress. Mahabub Alam et al. (2014) showed that application of 0.5 mM JA on *Brassica* species seedlings increases the biosynthesis of chlorophyll under water stress. A similar report is available for soybean (Mohamed and Latif 2017). In another study, Abbaspour and Rezaei (2014) found that foliar application of JA enhances hill reaction in *Dracocephalum moldavica* plants under water limitation.

2.4 Biosynthesis of Secondary Metabolites

SA as an endogenous signaling molecule plays an important role in plant defense mechanisms (Ahmad et al. 2019). This phytohormone has been used as a potential enhancer of some secondary metabolites such as alkaloids (Pitta-Alvarez et al. 2000), glucosinolates (Kiddle et al. 1994) and anthraquinones (Bulgakov et al. 2002). SA has also some positive roles in biosynthesis of terpenoids such as sesquiterpenoids (Aftab et al. 2010), diterpenoids (Wang et al. 2007) and triterpenoids (Shabani et al. 2009). Production and accumulation of secondary metabolites has an important role on rising water stress tolerance of plants. Foliar application of SA stimulated the biosynthesis of secondary metabolites such as phenolic compounds in plant leaves (Ali et al. 2007). Latif et al. (2016) showed that the accumulation of total soluble and cell wall-bound compounds and total soluble proteins in *Zea mays* plants were increased in response to foliar application of SA under water stress. Since SA is a plant produced phenolic compound, it can enhance phenolic compounds and also can produce new polyphenols (Yao and Tian 2005). Ghassemi-Golezani et al. (2018b) reported that foliar application of SA noticeably enhanced phenolic compounds such as thymol and carvacrol in ajowan (*Carum copticum* L.) plants under drought stress. These researchers also showed that foliar application of SA increased essential oil production of ajowan under drought stress.

JA is a signal molecule with great ability in changing biosynthesis of secondary metabolites in plant cells. JA by enhancing *ORCA* gene expression in plant cells enhances alkaloid metabolism in plant cells (Memelink et al. 2001). Exogenous application of JA on drought stressed *Agropyron cristatum* plants considerably enhanced ascorbate and glutathione metabolism and consequently improved water stress tolerance of plants (Shan and Liang 2010). Alavi-Samani et al. (2015) found that foliar treatment of JA under drought stress significantly increased carvacrol and thymol contents in the oils of two thyme species (*Thymus vulgaris* and *T. daenensis*), but reduced the essential oil yield and amount of γ-terpinene in the oil. These researchers indicated that foliar application of JA reduces the negative effects of water stress on thymol amount in *T. daenensis*, and γ-terpinene content in *T. vuglaris*. Farhangi-Abriz and Ghassemi-Golezani (2019) reported that exogenous JA enhances phenolic components of plants under water stress and consequently increases antioxidative activities and water stress tolerance of plants.

2.5 Plant Growth and Productivity

Improving crop production under unfavorable conditions is one of the main goals of agricultural scientists (Farooq et al. 2012). Changing hormonal signaling of plants is a practical strategy for enhancing plant growth and productivity under normal and stressful conditions (Bari and Jones 2009). SA changes various aspects of plant growth and development such as root and shoot growth, flowering time and grain production. This natural regulator increases root growth of plants by stimulating cell growth and division (Hayat and Ahmad 2007). In a study carried out in 2018, foliar application of SA in chickpea plants significantly increased the size of the root and improved water status of plants under drought stress (Khan et al. 2018). Quiroga et al. (2018) reported that exogenous SA noticeably improved aquaporins and root hydraulic properties in drought stressed maize plants. Foliar application of SA also manipulated the root proteome of plants and consequently increased plant adaptation to drought (Sharma et al. 2017). In a recent study, Pasternak et al. (2019) showed that salicylic acid affects root meristem patterning via auxin distribution in a concentration-dependent manner. These researchers stated that a wide range of SA concentrations activated auxin synthesis, but the effect of SA on auxin transport was rate dependent. SA-induced auxin production and accumulation were led to the formation of more layers of columella initials and extra layers of epidermis, cortex, and endodermis cells.

Flowering process is so important for successful grain production under normal or drought conditions. The effect of SA on the flowering process of plants was assessed since it is a parameter closely related to the productivity (Martínez et al. 2004). The SA treatment enhanced number of flowers in various kind of plant species (Martínez et al. 2004; Wada et al. 2010). Yildirim and Dursun (2008) showed that foliar application of SA increased the tomato yield. Sharafizad et al. (2012) reported that the highest grain yield of wheat was obtained with application of 0.07 mM SA. It is believed that increasing crop yield might be due to delayed senescence of plant leaves and flowers in response to exogenous SA (Imran et al. 2007) that will automatically help the plant in extending the duration of photosynthetically active sites and also prevent the premature loss of bulbs and flowers. Plants treated with salicylic acid in the field or greenhouse conditions had higher shoot growth and grain yield under drought. These responses could be related to the physiological and biochemical modifications in SA treated plants. For example, SA inhibited ABA and ethylene biosynthesis in plants and improved shoot growth (Meguro and Sato 2014; Li et al. 2019). Ullah et al. (2018) found that foliar application of SA significantly improved rapeseed growth and productivity under drought stress. Similar reports are available in maize (Rao et al. 2012), rice (Sohag et al. 2020), tomato (Hayat et al. 2008), ajowan (Ghassemi-Golezani et al. 2018b) and rapeseed (Ghassemi-Golezani et al. 2019) plants.

JA is an important natural plant growth regulator, which regulates a wide variety of physiological and developmental responses. This hormone has been shown to enhance stomatal closure, abscisic acid and ethylene synthesis, respiration, and carotenoid and anthocyanin formation in plants. JA is in charge for the activation of a number of defensive mechanisms against different biotic and abiotic stresses (Wang et al. 2020). This phytohormone significantly changes plant growth and productivity under normal and stressful conditions such as salt and drought stresses (Raza et al. 2020). Although there are various reports that show positive effects of JA on rising plant growth and productivity under various conditions (Anjum et al. 2011, 2016; Javadipour et al. 2019), some of the JA impacts on plant growth and productivity are negative. The JA treatment reduces growth of explants in tissue culture, and seed germination, chlorophyll synthesis and photosynthesis rate in plants (Creelman and Mullet 1997). Staswick (2009) showed that JA decreases plant growth by decreasing auxin production in plant cells. Investigations by Adams and Turner (2010) showed that inhibition of root growth of plants in response to JA treatment is related to increasing ethylene production in this organ. These researchers reported that COI1 as a jasmonate receptor in plant roots is responsible for ethylene production in plant cells. Ghassemi-Golezani and Farhangi-Abriz (2018) reported that foliar application of JA under osmotic stress caused by salinity decreases root growth of soybean plants. However, the inhibition of root growth in JA treated plants did not significantly affect the grain yield, compared to untreated plants. The JA treatment may also reduce the expansion of leaves and cotyledons (Ananieva et al. 2007). This hormone inhibits leaf expansion by reducing cell division and the activity of the mitotic cyclin CycB1;2, but the cell size is not changed by this hormone (Swiątek et al. 2004). Foliar application of JA reduces cotyledon expansion in plants by increasing ABA concentration in shoot tissues (Aleman et al. 2016). In a study by Kim et al. (2009b), jasmonates reduced grain yield by mediating stress signals to alter spikelet development in rice. Similarly, Kraus and Stout (2019) reported that seed pretreatment with jasmonates induces resistance to biotic stress, but reduces plant growth in rice.

3 Conclusions and Future Perspectives

The SA and JA as natural regulators can stimulate various defense mechanisms of plants under drought stress. These growth regulators considerably enhance antioxidants activities and osmolytes production in plant cells and consequently improve drought tolerance in plants. SA in comparison with JA has reliable results on improving crop growth and productivity under drought stress. However, JA shows various impacts on growth and productivity of drought subjected plants, depending on species. Future investigations could be focused on the impacts of different natural regulators on plant growth and productivity under normal and stressful conditions.

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Role of Jasmonic Acid and Salicylic Acid Signaling in Secondary Metabolite Production

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Abstract Secondary metabolite synthesis takes place from primary metabolites. Secondary metabolites have no role in the development of plant growth, reproduction, and physiological procedures but they are needed for competitive weapons against a wide range of plant pathogens. Natural products as bioactive compounds derived from plants are mainly produced by the secondary metabolism. These metabolites are known for their wide therapeutic values. Plants are utilized for the isolation of various bioactive compounds; so they are sometimes overexploited and are getting threatened. Therefore, this problem can be overcome by enhancement of secondary metabolite production with various in vitro culture procedures. Elicitation by different molecules upscales the secondary metabolites production in a number of plants with varied potential for bioactive metabolite accumulation. Jasmonic acid (JA) and salicylic acid (SA) are significant molecules involved in the regulation of plant growth, immunity to pathogens, and abiotic stresses. The present review categorizes synthesis and enhancement of various bioactive compounds by JA and SA as elicitation using in vitro cultures. We also discuss the inception of JA and SA signaling with a focus on gene expression in relation to secondary metabolite biosynthesis.

Abbreviations

12-OH-JA	12-hydroxyjasmonic acid
APX	Ascorbate peroxidase
CAT	Catalase
cDNA-AFLP	cDNA-amplified fragment length polymorphism
CJ	cis-jasmone

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CHI	Chalcone isomerase
CS	Chalcone synthase
F3′H	Flavonoid 3′-hydroxylase
FH	Fumarate hydratase
GP	Guaiacol peroxidase
GR	Glutathione reductase
H_2O_2	Hydrogen peroxide
h6h	Hyoscyamine-6-beta-hydroxylase
JA-Ile	Isoleucine conjugate
IS	Isochorismate synthase
JA	Jasmonic acid
JAV1	Jasmonate-associated vq-motif gene1
JAM1, JAM2	JA-associated MYC2-like proteins
LOX	Lipoxygenase
MeJA	Methyl jasmonate
MYC2, MYC3, MYC4	MYC-related transcriptional activator
NMT	N-methyltransferase
NO	Nitric oxide
NPR1	Nonexpresser of pathogenesis-related protein 1
POD	Peroxidase
PCC	Phenolic compound content
PAL	Phenylalanine ammonia lyase
SDH	Succinate dehydrogenase
SA	Salicylic acid
SABPs	SA-binding proteins
SAR	Systemic acquired resistance
TPC	Total phenolic content
TFC	Total flavonoid content
US	Ultrasound
YUCCA	YUCCA monooxygenase

1 Introduction

JA is the product of linolenic acid and octadecanoic acid-based metabolic pathways. Salicylic acid is a lipophilic monohydroxybenzoic acid. Compounds such as jasmonic acid (JA) and salicylic acid (SA) and their derivatives play an important role in the growth and development of plants and in signal transduction and formation of secondary metabolites. Their signaling systems have an immense effect on biological activity, mitigation of ambient stress, and plant longevity. Plant hormones, transcription factors (TFs) and enzymes linked to different biological pathways, main molecules, cell compartmentalization and ion exchange play crucial roles in the development of a signal transduction network. JA. Methyl jasmonate (MeJA) and its isoleucine conjugate (JA-Ile) are the most active jasmonates. They monitor closure of stomata, lead to expression of stress induced genes, solute transport, absorption of nutrients, RuBisCO biosynthesis, as well as induces plant defense reactions and incurs pathogen resistance reducing physiological damage (Mur et al. 2006; Clarke et al. 2009; Wasternack and Hause 2013). A variety of compounds, genetic switches, molecular causes and enzymatic regulation of biosynthetic pathways have been revealed in studies that specifically influence JA signaling, but the overall mechanism is complex and overlapping. Calcium efflux and potassium channels are also involved in signal transduction and various cell receptors, TFs, and kinases also control the interlinked signaling pathways (Campos et al. 2014; Gupta et al. 2017). The use of natural products in various applications has been increased by advanced biotechnological and industrial manufacturing techniques. Industrial processing of various metabolites, however, has faced persistent developmental blockades along with economic constraints.

There are several derivative compounds that are collectively called jasmonates and they have a distinct role in plant physiology and biochemistry. Mainly, JA and SA and their metabolites are functional against the reversal of biotic and abiotic stresses, in the introduction of systemic acquired resistance and in facilitating plant growth and development. These play important roles in flowering, fruit ripening, wounding and pathogenesis prevention, seed germination regulation, ion channel and transport of solvents. As an essential part of plant protection, SA signaling is a plant response to different abiotic stresses (Pedranzani and Vigliocco 2017).

2 Signaling at a Glance

2.1 Jasmonic Acid (JA) Signaling

In several monocotyledonous and dicotyledonous plants, JA biosynthesis has been investigated for decades in transgenic tomato and *Arabidopsis* sp. The involvement and interlinking of several JA biosynthesis enzymatic networks, such as octadecane and hexadecane pathways, has been revealed. In the cytoplasm and organelles, including chloroplast and peroxisome, these pathways are localized. At first, from unsaturated fatty acid, 12-oxo-phytodienoic acid (12-OPDA) and deoxymethylated vegetable dienic acid (dn-OPDA) were produced and then in the peroxisome they were converted to JA and finally, in the cytoplasm JA derivatives such as JA-Ile, MeJA, cis-jasmone (CJ), and 12-hydroxyjasmonic acid (12-OH-JA) were formed.

The initial phase of JA signaling includes a number of biochemical switches to be turned on. Generally, accumulation of polypeptides or generation of free radicals indicates the introduction of stress; both biotic and abiotic. The response of cell receptors, protein molecules, and over-activity of transporters also depict a stressed condition. Under pathogen attack, oligosaccharide signals were noted in the apoplastic and symplastic pathways which also indicates that the plant is undergoing a stress reversal mechanism. However, for JA biosynthesis and signaling to take place, activation of phospholipase enzyme is critical. Phospholipases (PLAs) release linoleic acid from the plasma membrane which acts as a precursor for JAs. The activities of PLAs have been studied in many mutant and transgenic plants (Liechti and Farmer 2002; Ellinger et al. 2010; Hind et al. 2010; Yan et al. 2013). The defense response introduces the systemic acquired resistance (SAR) in adjacent areas of the plant wound. In JA related short and long-distance transport of signaling, different plant growth regulators and hormones like SA, auxin, abscisic acid, and ethylene also play important roles in complex regulatory network building that in turn affect various metabolic processes and secondary metabolite production (Chini et al. 2018; Farmer and Ryan 1990). It has been noted that insect feeding and other forms of mechanical damage cause the accumulation of JA and JA-Ile. This phenomenon triggers defense gene expression and modulates symplastic and apoplastic transport (Truman et al. 2007). On the other hand, the specific localization of different JA synthetases helps in the systemic transmission of JAs. Interestingly, the genetic and physiological responses are detected in a large area surrounding the wound site. Sometimes, the involvement of highly volatile MeJA triggers the airborne transmission of defense signaling in adjacent stresses against a particular type of attack or infestation (Farmer and Ryan 1990). The 'internal regulation' of JA signaling is carried out by transferring JAs to the nuclear membrane's plasma membrane. The response of plants under stress is determined by the involvement of JAs, JA transporters, and intracellular and intercellular JA transport. The higher concentration of JA within a single cell activates JA intercellular transport and switches on the defense response genes. However, quick activation of transporters and their sensitized mode of action prevent inhibition of normal growth and developmental processes. Over accumulation of JAs activates the transporter function which prevents cell damage (Karban et al. 2000; Kost and Heil 2008; Li et al. 2017).

Several transcription factors (TFs) like NAC, ERF, and WRKY are involved in the JA signaling process. Recent studies have shown, JA-Ile binds with JAZ, causes degradation of JAZ, COI1, and activates the MYC. These JA-responsive TFs further regulate other gene cascades, involved in the growth and development, defense, and adaptation of plants. JA signaling induces the MAP kinase cascade pathway, regulates calcium channel, and interacts with functional molecules and plant growth regulators such as SA, ethylene, abscisic acid, gibberellic acid which in turn monitors a large network of plant physiological and biochemical processes. Plants are always exposed to vast array of environmental stresses. Their stress reversing defense mechanism involves the active participation of a number of secondary metabolites. The exposure of plant cells to various kinds of stress factors, the primary and secondary defense response, enhanced or localized production of secondary metabolites, multicomponent signaling, enzymatic regulation, and altered physiological and biochemical processes, genetic expression, and involvement of different transcription factors all are in sync with JA and SA signaling in many ways. The biosynthesis, storage, and transport of various metabolites are regulated via a precise signaling procedure. Plants do involve regulated expression of transcription factors to monitor signaling cascades that could reverse oxidative stress stimuli. The study of JA and SA signaling, specifically in transgenic plants has highlighted the role of many transcription factors and gene networks that work together to fight stress-induced anomalies and improves secondary metabolite production (Khare et al. 2020).

2.2 Salicylic Acid (SA) Signaling

SA functions as a mediator in the development of plant immunity to pathogens. SA helps to develop local resistance, systemic resistance, and gene-mediated defense of resistance. Due to elicitor therapy, stress conditions and pathogenic attacks, SA levels differ in plants (Lu 2009). In the presence of stress factors, SA plays a significant role and binds to a variety of metabolic compounds that control the entire signaling procedure. It is highly involved in endoplasmic reticulum (ER) stress regulation (Kørner et al. 2015), heavy metal generated toxicity (Ahmad and Prasad 2012) and antioxidant mechanisms (El-Esawi et al. 2017). The application of exogenous SA could protect plants from Cd toxicity; which play critical role in the plant defense. However, mutant or transgenic A*rabidopsis* plant-based studies have indicated facilitation of efficient defense processes involving SA. SA may increase the cell wall-based accumulation of Cd and prevents its translocation into other cell organelles. The cell wall functions as the first line of defense against a number of biotic stress factors and may cause the enhancement of the internal glutathione transport thus ameliorating oxidative stress and metal toxicity. The key transcriptional regulators of SA signaling are NPR1 (nonexpresser of pathogenesis-related protein 1) and SA-binding proteins (SABPs), catalase, etc. (Guo et al. 2019). The endoplasmic reticulum (ER) regulates protein synthesis. The disruption of ER homeostasis causes ER that leads to the accumulation of unfolded or misfolded proteins which induces stress stimuli (Poór et al. 2019). SA probably regulates the redox homeostasis and triggers the functioning of specific transcription factors (Mateo et al. 2006). At present, different environmental factors are causing cumulative food scarcity all over the globe. Under the changing environmental state, exogenous application of biologically active compounds like SA may enhance the agricultural output. The release of volatile SA-based derivatives may also reduce herbivore populations. Polyamine pretreatment may improve overall SA functioning. Cross talk between SA and JA signaling is schematically presented in Fig. 1.

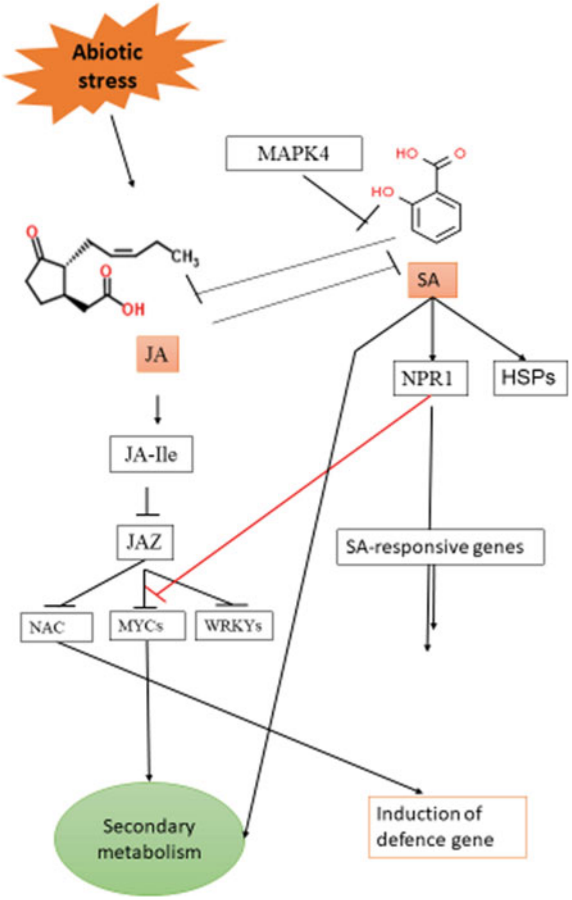

Fig. 1 Cross talk between salicylic acid and jasmonic acid signaling

3 Signaling and Effect on Secondary Metabolite Production

3.1 Effect of Jasmonic Acid (JA) on Biosynthesis of Secondary Metabolites

By altering secondary metabolite biosynthesis and gene expression, the application of JA actually induces the reversal of lead (Pb) toxicity in tomatoes. The reversal of sodium chloride toxicity has been recorded in *Solanum lycopersicum* L. induced by JA and nitric oxide supplementation (NO). Salt stress may cause electrolyte leakage, increased lipid peroxidation, and hydrogen peroxide (H_2O_2) production, which may get ameliorated by exogenous application of JA and NO (Ahmad et al. 2018). The activation of the JA signaling pathway reportedly increases the secondary metabolites production in tomato. Exogenous MeJA triggers the caffeoylputrescine accumulation in leaves of tomato plants. It has been detected that the enzymatic up-regulation of the phenylpropanoid and polyamine biosynthesis pathways was mediated by JA. JA induces copper chloride elicited phytoalexin production in rice. Phytoalexins are antimicrobial secondary metabolites that act against fungal invasion (Tamogami et al. 1997). In addition, JA elicited the production of phytoalexin under the control of ascorbic acid and cytokinins as observed in rice (*Oryza sativa* L.) leaves (Tamogami et al. 1997). Same feature has been shown by coronatine that also elicits phytoalexin production in rice leaves (*O. sativa* L.) (Tamogami and Kodama 2000). Higher level of JA actually antagonizes gibberellin biosynthesis and this phenomenon plays an inhibitory role in the growth of *Nicotiana attenuata* Torr. ex St Watson stems (Heinrich et al. 2013). JA signaling has been studied extensively for its elicitation effects and it was found that in the adventitious root culture of *Panax ginseng* C.A. Mey., it improves the ginsenoside content (Yu et al. 2002). However, SA and yeast extract may act together to enhance JA and sesquiterpenoids content in adventitious roots of *P. ginseng* (Rahimi et al. 2014). It also alters the ginsenoside content in elicited cell cultures of *P. ginseng* (Hu and Zhong 2007). In cell suspension cultures of *Artemisia absinthium* L., the elicitation of different antioxidant secondary metabolites was accomplished with jasmonates and gibberellic acid and it has substantially improved radical scavenging activity (RSA) of suspension cultures (Ali et al. 2015). Actually, in many plant species (cell and organ cultures) MeJa induced the accumulation of secondary metabolites (Ho et al. 2020). The production of phenylpropanoids and naphtodianthrones can also be induced by JA elicitation in cell suspension culture of *Hypericum perforatum* L. (Gadzovska et al. 2007). The effects of JA and MeJa were studied in *Mentha* × *piperita* cell suspension cultures where these two were effective on accumulation of rosmarinic acid (Krzyzanowska et al. 2012). In Sweet Basil (*Ocimum basilicum* L.) MeJa has improved aromatic secondary metabolite content (Kim et al. 2006). Under in vitro conditions, JA induced the accumulation of bioactive chemicals in *Hypericum* species (Cirak et al. 2020). It induces hypericin production in cell suspension cultures of *Hypericum perforatum* L. (Walker et al. 2002). JA induces even the fungal endophyte (*Gilmaniella* sp. AL12)-induced volatile oil accumulation in *Atractylodes lancea* (Thunb.) DC. plantlets (Ren and Dai. 2012). JA acts in the signaling of Lacl 3-induced baicalin production in *Scutellaria baicalensis* Georgi seedlings (Zhou et al. 2012). Similarly, in *Salvia miltiorrhiza* Bunge hairy root culture, it triggers the signaling mechanism of tanshinones biosynthesis (Zhou et al. 2019).

3.2 *Effect of Salicylic Acid (SA) on Biosynthesis of Secondary Metabolites*

Combination treatment with SA (2.0 mg/L) and chitosan (50 mg/L) increased dicentrine content and biomass production in cell suspension culture of *Stephania venosa* (Blume) Spreng (Kitisripanya et al. 2013). Increased benzophenanthridines alkaloids production was correlated with low concentrations of SA elicitation in *Eschscholzia californica* Cham. in vitro cultures. SA (4 mg/L) induces benzophenanthridine alkaloid, macarpine production in the suspension culture of *E. californica.* Another compound Sanguinarine, a type of phytoalexins was also accumulated by SA elicitation in *E. californica* (Balažová et al. 2020). Kollárová et al. 2014 also reported that improvement of sanguinarine production in suspension culture of *E. californica* was mediated by low concentration of SA (1.5 mg/L) elicitation (Kollárová et al. 2014). Sequential elicitation with MJ, SA, and yeast extract also supported that low concentration of SA treatment linked with the improved formation of sanguinarine and dihydrosanguinarine (Cho et al. 2008). Cho et al. 2007 also assessed benzophenanthridine alkaloids in *E. californica* suspension cells and concluded that benzophenanthridine alkaloids production was enhanced by combination treatment of elicitors rather than single elicitor treatment (Cho et al. 2007). In the root suspension culture of *Plumbago indica* L., the enhancement of plumbagin was accomplished with SA and ME. Additionally, the levels of antioxidant activity, total phenol, flavonoid, and tannin were substantially improved following the treatment (Roy and Bharadvaja 2019). The production of plumbagin was also increased in the elicited root cultures in *P. indica* L. treated with SA and naphthalene (Jaisi and Panichayupakaranant 2016).

SA elicitation moderately enhanced dopamine production in *Portulaca oleracea* L. hairy root culture. However, elicitation with MeJA showed a higher enhancement effect in dopamine production than SA elicitation (Moghadam and Habibi 2013). Similarly, *Gymnema sylvestre* (Retz.) R.Br. ex Sm. cell suspension culture elicited with SA showed a moderate elevation of gymnemic acid (4.9-fold) production (Chodisetti et al. 2015). SA elicitation improved the production of hypericin and pseudohyperian in elicited cell suspension culture of *Hypericum perforatum* L. (Gadzovska et al. 2013). Mahalakshmi et al. 2013 reported the production of alkanes and fatty acids using inoculation of SA in in vitro callus culture of *Jatropha Curcas* L. in which lower concentration of SA elicitation increased the alkanes and fatty acid content (Mahalakshmi et al. 2013). Lower concentration of 200 μM SA was used to increase anthocyanin production in both callus culture of *Rosa hybrida* L and *Daucus carota* L. (Sudha and Ravishankar 2003). Ram et al. 2013 assessed the roles of SA and MeJA in caffeine biosynthesis in endosperm and they have concluded that crosstalk between SA and MeJA is responsible for caffeine accumulation. Theobromine content was also increased by low concentration of SA treatment in in vitro cultures (Kumar and Giridhar 2015). Presence of SA in the root cultures of *Cichorium intybus* L. enhanced the concentration of sonchuside A by two-fold as compared to the control (Malarz et al. 2007). *Catharanthus roseus* (L.) G. Don treated with foliar application of SA showed an increase in the vincristine and vinblastine under salt stress conditions. Additionally, this treatment improved the growth conditions and reversed salinity. This study also revealed that plant growth promotion influenced by SA is associated with alkaloid production under stress conditions (Idrees et al. 2011).

SA (5 and 20 μM) significantly enhanced total alkaloids in marine microalgae *Arthrospira platensis*. The total alkaloid content was increased by 1.7 and 1.4 times as compared to control (Hadizadeh et al. 2019). SA to the callus cultures of *Digitalis trojana* Ivanina plant exposed to high temperature stress, additively improved the accumulation of the cardenolide, proline, phenolic, and flavonoid content (Cingoz and Gurel 2016). Cell suspension cultures of *Ginkgo biloba* L. induced by SA enhanced the concentration of bilobalide, ginkgolide A, and ginkgolide B (Kang et al. 2006). SA treatment in post-harvest *G. biloba* leaves showed an increase in the flavonoid concentration under light conditions and decreased flavonoid content under dark conditions (Ni et al. 2018). Hairy root culture of *Hyoscyamus reticulatus* L. using *Agrobacterium rhizogenes* supplemented with SA (0.01, 0.1 and, 1 μM) showed an elevation in the concentrations of tropane alkaloids, hyoscyamine, and scopolamine (Norozi et al. 2019). In *Withania somnifera* L., adventitious root cultures treated with 150 μM SA for 4 h duration, stimulated the synthesis of withanolides (Sivanandhan et al. 2012). Applications of JA, SA and MeJA for enhancement of secondary metabolites are listed in Table 1. Chemical structure of the elicited secondary metabolites is presented in Fig. 2 (Chemical structures retrieved from www.Chemspider.com). in Fig. 3 we have illustrated the mode of action of these signalling molecule.

4 Jasmonic Acid (JA) and Salicylic Acid Signaling in Alteration of Gene Expression

JA signaling triggers alteration in carbohydrate transport, storage organs partitioning that leads to better resistance against herbivore attack and induces resistance (Babst et al. 2005). Epigallocatechin-3-gallate is one of the most abundant polyphenols, which has significant signaling function and could promote JA signaling in *A. thaliana* (Hong et al. 2015). In *Polygonum minus*, cDNA-amplified fragment length polymorphism (cDNA-AFLP) transcript profiling study revealed SA and MeJA elicitation involved in regulating oxidative stress related genes like zeaxanthin epoxidase, cytosolic ascorbate peroxidase 1, and peroxidase. (+)-delta cadinene synthase and cinnamoyl-CoA reductase were also involved in secondary metabolite production (Ee et al. 2013). MYC is one of the major transcription factors involved in JA signaling. However, JA promotes de-greening via the regulation of MYC2/3/4 and ANAC019/055/072, major chlorophyll catabolic genes (Zhu et al. 2015). The protein expression study conducted on *Arabidopsis* sp. revealed P450 protein CYP82C2 modulates jasmonate-induced inhibition of root growth, upgrades defense gene expression, and promotes indole glucosinolate biosynthesis (Liu et al. 2010). It was noted that both JA and SA signaling pathways could alter gene expression of

Table 1 Effects of JA, MeJA, and SA on elicitation of bioactive secondary metabolites

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
Ajuga bracteosa Wall ex Benth	MeJA	TPC, TFC	adventitious root suspension	biomass ↑, antioxidant activity ↑	Saeed et al. (2017)
Artemisia absinthium L	JA, MeJA	TPC	suspension	radical scavenging activity ↑	Ali et al. (2015)
Artemisia amygdalina D	MeJA	TPC, TFC, essential oil	adventitious roots	PAL ↑	Taj et al. (2019)
Artemisia dubia L. ex B.D.Jacks	SA	artemisinin	hairy root	growth rate ↑	Ali M (2012)
Azadirachta indica A. Juss	JA, SA	azadirachtin	hairy root	–	Satdive et al. (2007)
Bacopa monnieri (L.)	SA	bacoside A, bacoside A3, bacopaside II	shoot	biomass ↑	Largia et al. (2015)
Calendula officinalis L	JA	oleanolic acid	cell suspension	metabolites biosynthesis ↑	Wiktorowska et al. (2010)
Catharanthus roseus (L.) G. Don	SA	vincristine, vinblastine	–	plant growth ↑ reversed salinity↑	Idrees et al. (2011)
Carthamus tinctorius (L.)	chitosan, SA	TPC, TFC	callus	antioxidant activity ↑	Golkar et al. (2019)
Centella asiatica (L.) Urban	SA	phytosterol, triterpene	suspension	–	Loc et al. (2016)
Cichorium intybus L	SA	sonchuside A	hairy root	no affect-on growth	Malarz et al. (2007)
Citrullus colocynthis (L.) Schard	MeJA	cucurbitacin E	root subculture	–	Dasari et al. (2020)
Codonopsis pilosula (Franch.) Nannf	MeJA	lobetyolinin	root	biomass ↑, polysaccharide ↓, sucrose ↓	Ji et al. (2019)
Coffea canephora Pierre ex A.Froehner	SA	theobromine, caffine	–	dry weight ↑	Kumar and Giridhar (2015)
	MeJA	caffine	–		

(continued)

Table 1 (continued)

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
Daucus carota L	SA	anthocyanin	callus	ethylene production ↓	Sudha and Ravishankar (2003)
Digitalis lanata Ehrh	MeJA	lanatoside C	shoot	length and shoot number ↓	Pérez-Alonso et al. (2012)
Digitalis trojana Ivanina	SA	cardenolide, proline, TPC, flavonoid	callus	stress protection ↑ antioxidants synthesis ↑	Cingoz and Gurel (2016)
Eschscholtzia californica Cham	MeJA, SA	sanguinarine	cell suspension	metabolite accumulation ↑	Cho et al. (2007)
	MeA, SA, YE	dihydrosanguinarine, sanguinarine	cell suspension	–	Cho et al. (2008)
	SA	sanguinarine	cell suspension	LOX ↑	Kollárová et al. (2014)
	SA	macarpine, sanguinarine	cell suspension	–	Balažová et al. (2020)
Fagonia indica Burm.f	Chitosan, SA	phenol, flavonoid	callus	biomass ↑, SOD ↑, POD ↑	Khan et al. (2019)
Fagopyrum esculentum Moench	SA, JA	phenylpropanoid	–	metabolite synthesis ↑	Park et al. (2019)
Ginkgo biloba L	SA, MeJA	bilobalide, ginkgolide A, ginkgolide B	cell suspension	biomass ↑	Kang et al. (2006)
Glycyrrhiza glabra L	JA	glycyrrhizin	root	metabolites biosynthesis ↑	Shabani et al. (2009)
Gymnema sylvestre (Retz.) R.Br. ex Sm	MeJA, SA	gymnemic acid	cell suspension	radical scavenging activity ↑	Chodisetti et al. (2015)
	MeJA	gymnemic acid	cell suspension	biomass ↑	Veerashree et al. (2012)
Hyoscyamus reticulatus L	SA	hyoscyamine, scopolamine	hairy root	Biomass ↓, catalase ↑, GP ↑, APX ↑	Norozi et al. (2019)
Hypericum perforatum L	JA	hypericin	cell suspension	metabolites biosynthesis ↑	Walker et al. (2002)

(continued)

Table 1 (continued)

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
	SA	hypericin, pseudo hypericin	cell suspension	PAL ↑, CHI ↑	Gadzovska et al. (2013)
Isatis tinctoria L	SA	alkaloids, flavonoids	hairy root	–	Gai et al. (2019)
Jatropha curcas L	SA	alkanes, fatty acid	cell suspension	percentage compounds↑	Mahalakshmi et al. (2013)
Linum album Kotschy ex Boiss	MeJA	podophyllotoxin, 6-methoxypodophyllotoxin	cell suspension	PAL ↑	Van Fürden et al. (2005)
Lycopersicon esculentum Mill	JA	caffeoylputrescine	–	phenylpropanoid pathway ↑ polyamine pathway ↑	Chen et al. (2006)
		TPC, polyphenols, flavonoids, anthocyanin	–	chlorophyll content ↑, CS ↑, FH ↑, PAL ↑, SDH ↑, in vitro polyamine accumulation ↑	Bali et al. (2019)
Momordica charantia L	SA, JA	PCC	hairy Root	biomass ↑, antioxidant activity ↑	Chung et al. (2016)
Momordica dioica Roxb. ex. Willd	JA, SA	carotenoid, flavonols, hydroxycinnamic acid, hydroxybenzoic acid	cell suspension	biomass ↑, antioxidant activity ↑	Chung et al. (2017)
Ocimum basilicum L	JA	essential oil	–	antioxidant activity ↑	Złotek et al. (2016)
Ophiorrhiza mungos L	JA	camptothecin	cell suspension	biomass ↑	Deepthi and Satheeshkumar (2017)
Panax ginseng C.A. Mey	JA	saponin	cell	metabolite accumulation ↑	Hu et al. (2003)
Papaver armeniacum L	MeJA	hebaine, codeine, morphine	hairy root	–	Sharifzadeh Naeini et al. (2020)
	SA	papaverine and noscapine			

(continued)

Table 1 (continued)

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
Plumbago indica L	SA	plumbagin	root	metabolite production ↑ root biomass ↑	Jaisi and Panichayupakaranant (2016)
	MeJA, SA	plumbagin, total phenol, flavonoid, tannin	–	antioxidant activity ↑	Roy and Bharadvaja (2019)
Podophyllum hexandrum Royle	MeJA	podophyllotoxin	cell suspension	phenylpropanoid pathway ↑, monolignol pathway ↑	Bhattacharyya et al. (2012)
Polygonum multiflorum Thunb	JA and SA	anthraquinones, PCC	cell suspension	biomass ↑	Thiruvengadam et al. (2016)
Portulaca oleracea L	SA, MeJA	dopamine	hairy root	–	Moghadam and Habibi (2013)
Rauvolfia serpentina Benth. Ex Kurz.,	MeJA SA	TPC, TFC	root	antioxidant activity ↑, APX ↑, CAT ↓	Dey et al. (2020)
Rehmannia glutinosa (Gaertn.) DC	SA	acteoside	hairy roots	LOX ↑	Wang et al. (2017)
Rosa hybrida L	SA	anthocyanin	callus	pigment content ↓, pigment production ↓	Ram et al. (2013)
Rumex vesicarius L	SA	flavonoids	callus	PAL ↑, H_2O_2 ↑	Sayed et al. (2017)
Salvia miltiorrhiza Bunge	JA, brassinolide	salvianolic acid B	–	antioxidant metabolism↑	Chen and Chen. (1999)
Satureja khuzistanica Jamzad	MeJA	rosmarinic acid	cell suspension	no affect on biomass	Khojasteh et al. (2016)
Scrophularia kakudensis Franch	JA	TPC, flavonoids, acacetin	cell suspension	antioxidant metabolism ↑	Manivannan et al. (2016)

(continued)

Table 1 (continued)

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
Stemona sp.	SA, MeJA	1′,2′-didehydrostemo-foline, stemofoline	shoot tips and auxiliary buds	–	Chaichana and Dheeranupattana (2012)
Stemona curtisii Hook. F	SA	oxyprotostemonine, stemocurtisine, stemocurtisinol	root	–	Chotikadachanarong (2011)
Stephania venosa (Blume) Spreng	chitosan, SA	dicentrine	cell suspension	biomass ↑	Kitisripanya et al. (2013)
Stevia rebaudiana Bertoni	MeJA	stevioside rebaudioside A	adventitious roots	antioxidant compounds ↑	Kazmi et al. (2019)
Swertia paniculata Wall	SA	amarogentin, swertiamarin, mangiferin	shoot	–	Kaur et al. (2020)
Tanacetum parthenium (L.) Sch.Bip	SA	parthenolide	–	–	Majdi et al. (2015)
Taxus baccata L	US, SA	taxol	cell suspension culture	H_2O_2 ↑, lipid peroxidation ↑	Rezaei et al. (2011)
	SA	taxol, total taxanes	callus	biomass ↑, free radicals ↑	Sarmadi et al. (2018)
Thevetia peruviana (Pers.) K. Schum	JA	cis-9, cis-12-octadecadienoic acid, cis-9-octadecenoic acid, PCC	callus	–	Rincón-Pérez et al. (2016)
Thevetia peruviana Dary	MeJA	PCC, flavonoid	cell suspension	antioxidant activity ↑	Mendoza et al. (2018)
Valeriana jatamansi Jones	MeJA, JAs, SA	valtrate	hairy root	*Agrobacterium rhizogenes* induced root formation ↑	Shuang and Hong (2020)
Vitis vinifera L. cv. Cabernet Sauvignon	MeJA	stilbene	cell suspension	–	Xu et al. (2015)
	UV-C, SA	stilbene, trans-resveratrol			

(continued)

Table 1 (continued)

Plants	Elicitor	Metabolite	Culture type	Up or downregulation	References
Uncaria tomentosa (Willd. ex Schult.) DC	JA	monoterpenoid oxindole, glucoindole alkaloids	root	H_2O_2 ↑, GP ↑, glutathione content ↓, GR ↓	Vera-Reyes et al. (2015)
Withania somnifera (L.) Dunal	SA	withanolide A, withanolide B, withaferin A, withanone, 12-deoxy withastramonolid, withanoside V, withanoside IV	hairy root	root biomass ↑	Sivanandhan et al. (2012)
	JA	withaferin A, withanolide A	–	–	Singh et al. (2020)

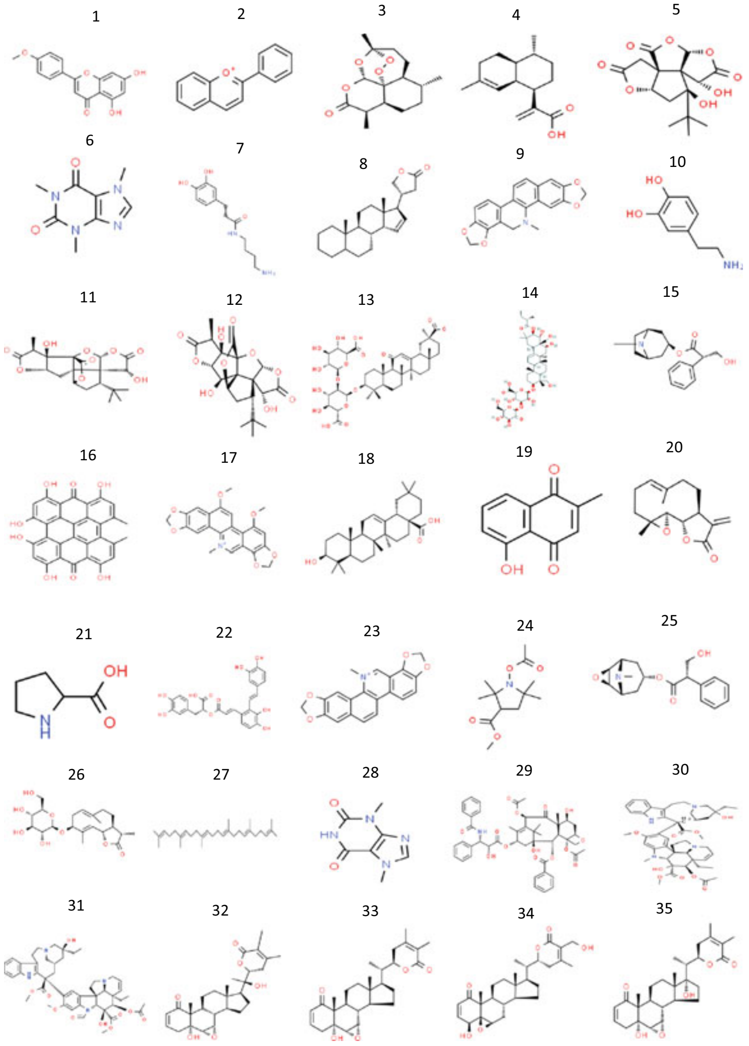

Fig. 2 Chemical structures of secondary metabolites enhanced by JA, MeJA and SA elicitation. All the chemical structures are retrieved from https://www.Chemspider.com 1. Acacetin $C_{16}H_{12}O_5$, 2. Anthocyanin $C_{15}H_{11}O$, 3. Artemisinin $C_{15}H_{22}O_5$, 4. Artemisinic acid $C_{15}H_{22}O_2$, 5. Bilobalide $C_{15}H_{18}O_8$, 6. Caffeine $C_8H_{10}N_4O_2$, 7. Caffeoylputrescine $C_{13}H_{18}N_2O_3$, 8. Cardenolide $C_{23}H_{34}O_2$ 9. Dihydrosanguinarine $C_{20}H_{15}NO_4$, 10. Dopamine $C_8H_{11}NO_2$, 11. Ginkgolide A $C_{20}H_{24}O_9$, 12. Ginkgolide B $C_{20}H_{24}O_{10}$, 13. Glycyrrhizin $C_{42}H_{62}O_{16}$, 14. Gymnemic acid $C_{36}H5_8O_{11}$, 15. Hyoscyamine $C_{17}H_{23}NO_3$, 16. Hypericin $C_{30}H_{16}O_8$, 17. Macarpine $C_{22}H_{18}NO_6$, 18. Oleanolic acid $C_{30}H_{48}O_3$, 19. Plumbagin $C_{11}H_8O_3$, 20. Parthenolide $C_{15}H_{20}O_3$, 21. Proline $C_5H_9NO_2$, 22. Salvianolic acid B $C_{36}H_{30}O_{16}$, 23. Sanguinarine $C_{20}H_{14}NO_4$, 24. Saponin $C_{12}H_{21}NO_4$, 25. Scopolamine $C_{17}H_{21}NO_4$, 26. Sonchuside A $C_{21}H_{32}O_8$, 27. Squalene $C_{30}H_{50}$, 28. Theobromine $C_7H_8N_4O_2$, 29. Taxol $C_{47}H_{51}NO_{14}$, 30. Vinblastine $C_{46}H_{58}N_4O_9$, 31. Vincristine $C_{46}H_{56}N_4O_{10}$, 32. Withanolide A $C_{28}H_{38}O_6$, 33. Withanolide B $C_{28}H_{38}O_5$, 34. Withaferin A $C_{28}H_{38}O_6$, 35.

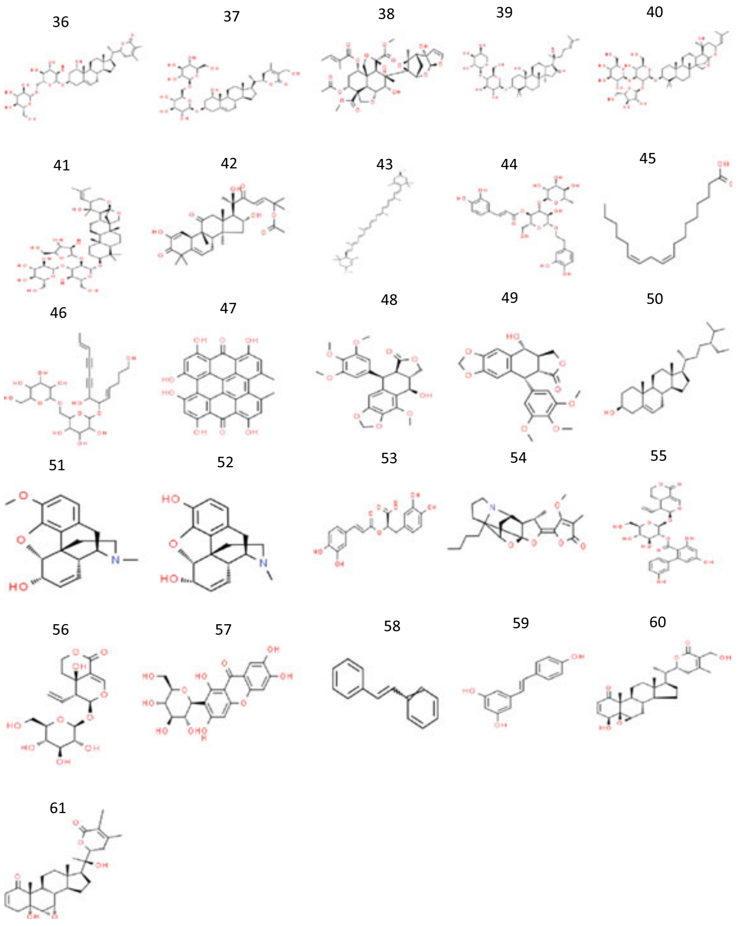

Fig. 2 (continued) Withanone $C_{46}H_{58}N_4O_9$, 36. Withanoside V $C_{40}H_{62}O_{14}$, 37. Withanoside IV $C_{40}H_{62}O_{15}$, 38. Azadirachtin $C_{35}H_{44}O_{16}$, 39. Bacoside A $C_{41}H_{68}O_{13}$, 40. Bacoside A3 $C_{47}H_{76}O_{18}$, 41. Bacopaside II $C_{47}H_{76}O_{18}$, 42. Cucurbitacin E $C_{32}H_{44}O_8$, 43. Carotenoid $C_{40}H_{56}O_2$, 44. Acteoside $C_{29}H_{36}O_{15}$, 45. cis-12-octadecadienoic acid $C_{18}H_{32}O_2$, 46. lobetyolinin $C_{26}H_{38}O_{13}$, 47. Hypericin $C_{30}H_{16}O_8$, 48. 6-methoxypodophyllotoxin $C_{23}H_{24}O_9$, 49. Podophyllotoxin $C_{28}H_{32}O_{13}$, 50. Phytosterol $C_{29}H_{50}O$, 51. Codeine $C_{18}H_{21}NO_3$, 52. Morphine $C_{17}H_{19}NO_3$, 53. Rosmarinic acid $C_{18}H_{16}O_8$, 54. Stemofoline $C_{22}H_{29}NO_5$, 55. Amarogentin $C_{29}H_{30}O_{13}$, 56. Swertiamarin $C_{16}H_{22}O_{10}$, 57. Mangiferin $C_{19}H_{18}O_{11}$, 58. Stilbene $C_{14}H_{12}$, 59. trans-resveratrol $C_{14}H_{12}O_3$, 60. Withaferin A $C_{28}H_{38}O_6$, 61. Withanolide A $C_{28}H_{38}O_6$

glutathione reductase1 as it plays a critical role in leaf responses under intracellular hydrogen peroxide-induced stress (Mhamdi et al. 2010). In cultured *Lycopersicon esculentum,* application of triacontanol and JA improves root induction mechanism (Soundararajan et al. 2018).

The regulation of plant defense via JA and SA signaling may alter bacterial community structure on rhizosphere as observed in some *Arabidopsis* sp. which

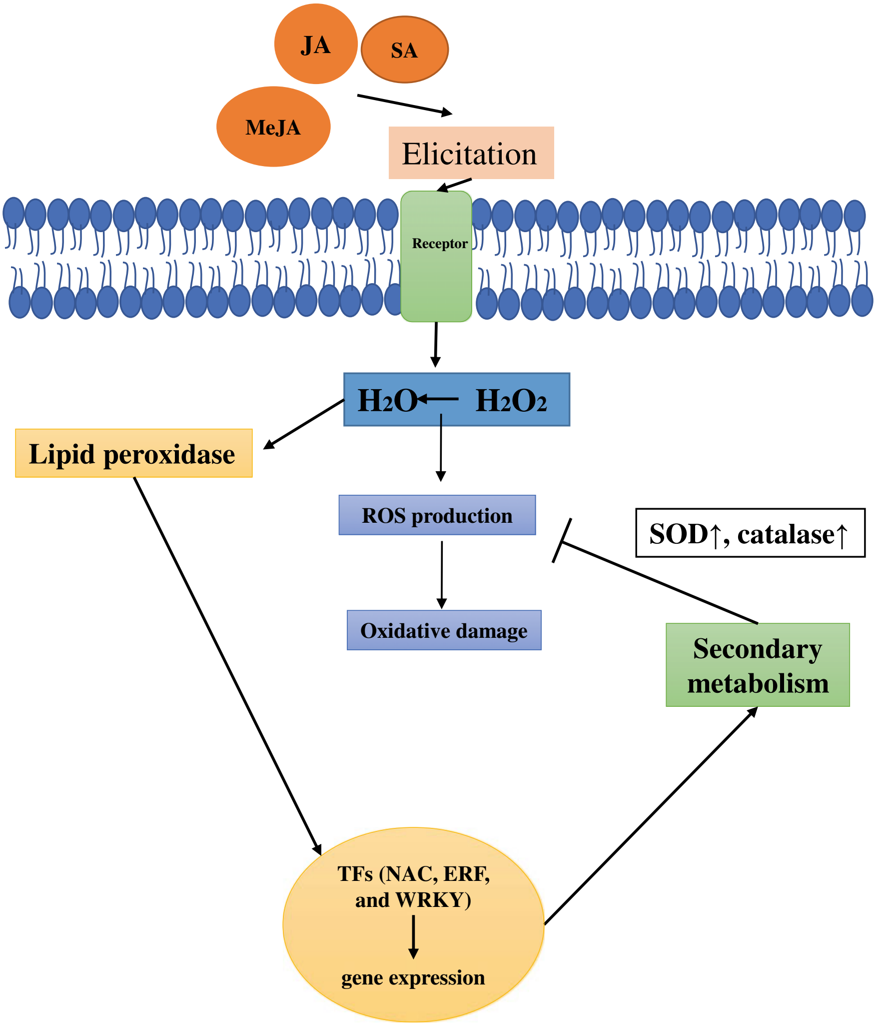

Fig. 3 SA, JA, MeJA elicitation and secondary metabolite production mechanism

indicates the elicitation of SAR may negatively affect bacterial microflora present in soil (Doornbos et al. 2011). In *Arabidopsis thaliana* MYC2 along with MYC3 and MYC4, functions additively. They regulate wounding-induced JA accumulation, alters JA biosynthesis, catabolism and promote transcription. MYC2 influences other genes like *JAV1* and *JAM1*, and it could bind to the *MYC2* promoter to inhibit its self-expression (Zhang et al. 2020). Silencing brassinosteroid receptor *bri1* gene expression impairs the herbivory-elicited accumulation of JA-Ile and diterpene glycosides in *Nicotiana attenuata* (Yang et al. 2013). Caffeine accumulation revealed an understanding of the interplay between SA and MeJA stress signaling. MeJA elicitation on fruits of coffee restores the transcription activity of N-methyltransferase (NMT) gene expression (Kumar and Giridhar 2015). Exogenous application of SA or MJ can produce secondary signals that can initiate defense response via transducer cascades which are further involved in gene activation associated with phytoalexin biosynthesis. Alkaloids and flavonoids in the hairy root cultures of *Isatis tinctoria* L. elicited by SA and MeJA, activates 11 genes that involved in alkaloid and flavonoid biosynthesis. Elicitation treatments upregulates YUCCA monooxygenase (YUCCA), chalcone isomerase (CHI), and flavonoid 3′-hydroxylase (F3′H) genes that trigger the production of many phytochemicals. YUCCA is responsible for alkaloid production in hairy root culture of *I. tinctoria*, while, CHI improves flavonoids synthesis, and F3′H genes initiates quercetin biosynthesis (Gai et al. 2019). Elicitation with acetylsalicylic acid alters hyoscyamine-6-beta-hydroxylase (h6h) gene expression which is involved in tropane alkaloids production. Transcriptional study revealed that h6h gene expression level is correlated with hyoscyamine and scopolamin accumulation in hairy root cultures of *H. reticulatus* L (Norozi et al. 2019).

5 Future Prospects

The JA signaling pathway has been enumerated extensively in the recent few years; however, detailed insight on JA signaling response in relation to environmental stimuli is yet to be fully deciphered. Environmental stimuli bring complex responses that are managed by different signaling pathways. The mode of action of JA signaling is not fully understood, but signal transduction pathways linked to JA signaling are more or less well known. Cell membrane carries different types of receptors which further activate different enzymes and other reactions like Ca^{2+} and K^+ channel opening. Details on JA receptors and JA signal transduction pathway have already been known, but regulatory process-related questions are yet to be answered. SA is found in all plants but differs between species. The primary metabolite for SA synthesis is chorismite. Chorismate derivative, 1-phenylalanine also has the efficiency to convert into SA. Precursors for phenylalanine to SA conversion are free benzoic acid, benzoyl glucose, or ortho-hydroxy-cinnamic acid. SA play important role in physiological processes related to plant growth, seed germination, thermogenesis, and plant response regulation under both biotic and abiotic stress conditions. SA signalling can alter gene expression. It is also involved in antioxidative metabolism and maintaining redox homeostasis. Plant defense hormones are also involved with SA crosstalk. Though wide studies have already been done on SA-related signalling processes, its complete mechanism of signalling is not yet known. Therefore, much work is needed to decipher the details of signalling mechanisms involving JA and SA and their role in cross talk in relation to modulate and upscale of valuable secondary metabolites of biomedical and industrial significance.

6 Conclusion

In the biosynthesis of secondary metabolites by elicitor-induced signaling in plants, JA and SA are considered among the major molecules. As elicitors, MeJA, JA, and SA stimulate bioactive compounds production to meet the large-scale requirements of pharmaceuticals. So, out of the various strategies developed by researchers, elicitation to enhance their production at commercial scale has also been studied in different in vitro cultures. JA, SA and MeJA supplementation in the culture medium and direct application on leaves (foliar spray) have been used in this regard. SA elicitation and metabolite production was found to be concentration-dependent. Low concentrations of SA application generally enhanced secondary metabolite production in *R. hybrida, D. carota, E. californica* and *J. Curcas.* Additionally, SA mediated expression of zeaxanthin epoxidase, cytosolic ascorbate peroxidase 1, and peroxidase related genes through biosynthesis of key enzymes; phenylalanine ammonia-lyase (PAL), chalcone isomerase (CHI), and isochorismate synthase (IS). SA and JA also responds to the abiotic stresses such as temperature and salinity stress which initiates stimulation of secondary metabolite productions. Similarly, JA modulates MYC2/3/4- and ANAC019/055/072, *JAV1* and *JAM1* gene expression, and biosynthesis of the key enzymes chalcone synthase (CS), PAL, succinate dehydrogenase (SDH), fumarate hydratase (FH). Hence these elicitors are biodegradable, cost-effective, and quick in action. The elicitation by JA, MeJA, and SA is therefore a potent solution for large-scale secondary metabolite production to meet the ever-expanding industrial demands.

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Role of Jasmonates and Salicylates in Plant Allelopathy

Anam Asif, Mohd Affan Baig, and M. Badruzzaman Siddiqui

Abstract Phytohormones reported to be the most important category of hormones playing key role in the plant growth and developmental processes. Most of these hormones are considered to be strongly communicative in nature. Among the diversified forms of phytohormones the jasmonates and salicylates have profound role in plant defense process. These phytohormones act as signaling molecules in secondary metabolite production for plant defense responses which is mainly due to their methylated products. These vital chemical messengers of the plant system cause wide range of morphological and physiological changes. The Biological encroachment has found its way into the flashes of Allelopathy, the mechanism that by its defensive nature influences the native plant species, by the continuous production of chemical exudates thereby hindering the growth of the plant. Allelopathy provides an insight for herbicide and weed control. The exogenous application of phytohormones can upraise allelopathic potential in plants. The plants acquire a wide radius of mechanisms to combat invasion of other plants which include physical, chemical barriers and defense responses that get started off upon exogenous application of communicating molecules, in which rhizosphere being the utmost sink for allelochemicals. This chapter describes the role of jasmonates and salicylates in plant allelopathy and different pathways of signal transduction involved.

1 Introduction

The commencement of Allelopathy was written under the name of Molisch (Molisch 1937), "allelopathy" the root word has a Greek origin, meaning the counter effect of native plant over another. Rice demonstrated allelopathy in terms of neighboring plants and their direct or indirect positive as well as negative impact of them on

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other plant via the release of chemical exudates (Rice 1984). It is an intervention process, in which the physiologically active or inactive parts of the plant release chemicals, which are known. as allelochemicals. It is also defined as direct or indirect communication, via the released chemicals from one organism which thereby counteract the physiological activity of neighboring organism (Molisch 1937; Rice 1984). Plants and microbiota associated with them simultaneously produce varied compounds of different chemical nature, with most of the does not involved in primary metabolism which is pre-requisite for the plant growth and development. These compounds having low organic weight are commonly called plant secondary metabolites. Allelochemicals are secondary metabolites which can affect behavior of neighboring plants through stimulatory and/or inhibitory effects on their growth and health (Rice 1974). This phenomenon is termed as allelopathy which was first coined by Molisch (1937). Some researchers defined it as counter effect of plants on other plants through indirect biochemical interactions, and microorganisms mediated release of allelochemicals by plants (Weston and Duke 2003) Infact, proposition of allelopathy as a result of evolution within existent plant patches may have detrimental effect on the newly inhabiting plants (Mallik and Pellissier 2000).

The International Society of Allelopathy (IAS) has eliminated the effect and impact of herbivores from the definition of allelopathy (Weir et al. 2004). Most of the researchers have focused only upon plant mediated interactions. Upon encountering stress prone conditions, chemicals released from the plants deal with their enemies. The plant defense mechanism is pervasive, empirical, and activate through a circuitous network of communicating molecules like jasmonic acid and salicylic acid. Jasmonates and salicylates directs the defence mechanism in plants (Kessler and Baldwin 2002) and induce resistivity in plants against insects and pathogens (Creelman and Mullet 1997). Most of the times jasmonic acid (JA) and salicylic acid (SA) are involved in activating the genes which control resistance and defense mechanism (Reinbothe et al. 1994; Thomma et al. 1998; Turner et al. 2002). Plant tissues including leaves, stem, roots, flowers, seed, rhizomes, pollen, bark, and buds release allelochemicals which are ubiquitous in nature and can be released over time (Weston and Duke 2003). Several mechanisms are involved in release of allelochemicals from plants over time in the environment which include volatilization or leaching from aerial parts, exudation from roots and decomposition of plant residues in soil (Cheng and Cheng 2015).

The reports from above studies have created a doubt regarding the importance and role of allelopathic interactions as well as methods demonstrating them (Harper 1977) Such studies provides more rigorous standard of proof for allelopathic interactions than any other plant-plant interactions (Harper 1977). A reasonable allelopathic interaction involve ecologically relevant species that interact in nature. The chemical mediated interaction must undergo identification and the amount of chemical released into the environment and can be simulated and quantified for experimental studies (Williamson 1990). Bioassays describing the allelopathic interaction in plants can be considered as unambiguous proof of allelopathy which might get attributed to the quantity of chemicals released under natural circumstances (Newman and Rovira 1978; Putnam and Tang 1986; Inderjit 1996). Induction of seed germination via allelopathy is attributed to inhibition or toxicity or both during seed to seed or plant to seed interactions. Delaying or slowing growth can also significantly inhibit the competitive abilities of the affected plant and have large fitness effect thus complete inhibition is not mandatory.

Several case studies were reported which demonstrated the presence of MeJA as signalling molecule in plants. In sage brushes, MeJA is a highly active compound which is present in massive quantities (Karban et al. 2000; Preston et al. 2001). MeJA released by sagebrush into its surrounding environment as a volatile compound as well as in aqueous form (Karban et al. 2000; Preston et al. 2001). Small concentration of MeJA released by sagebrush via volatilization and leaching in the environment is enough for inhibition of seed germination. The plant must become desensitized to the compound itself before release of an active compound or any effective toxin into its surrounding environment. This case study has made the fact crystal clear that MeJA is an active compound with allelopathic properties. The final and the most crucial step in demonstration of allelopathy and the chemical species mediating the interaction is compared with the applicational criteria postulated by Koch (Harper 1977). These postulates, basically focuses on understanding the nature and symptoms of the disease, and it was very difficult to apply for allelopathic research as there is a difference between how disease spreads in a body and the activity of active allelopathic compounds in the environment. Synergism between different chemical compounds that do not have one to one relationship and having allelopathic response provide a framework to carry out test for proposed allelopathic substances (Williamson 1990).

2 Allelopathy in Plants

Allelopathy is an event which effects the morphology,etiology,anatomy and developmental patterns of other plant existing in the same vicinity via release of growth inhibitory compounds (Hussain et al. 2011; Farooq et al. 2011; Pan et al. 2015). The allelochemicals sinked into the surroundings are ecologically stable (Duke et al. 2002), thus they are ecofriendly, shield agronomic products (Sodaeizadeh et al. 2010), along with edging off the community health issues (Khanh 2007) and therefore are a better alternative of herbicide for haulting the vigorous growth of weeds. About 240 weed species is reported to intercess with the progress and replenishment of new crops (Qasem and Foy 2001). The allelopathy is a sole effective technique in certain cropping patterns and also in controlling the weed invasion. The allelopathic nature of about 240 weed species has been found to interfere with the growth and production of crops (Qasem and Foy 2001). Whittaker and Feeny (1971) coined the term allelochemical. Secondary metabolites sometimes act as allelo-chemical. At a particular concentration allelochemicals retards the growth of some species or they might accelerate the growth of same or different species at lower concentration (Narwal 1994). With the help of allelopathy, the interaction between weed-crop, crop-crop, cropweed and weed-weed can be easily demonstrated. Allelopathic compounds show selectivity towards different plant species and can change the composition of plant populations. Allelochemicals can be discharged in the soil by decomposition, root exudation and volatilization of compounds. Allelopathy can be potentially utilized for weed control by releasing allelochemicals from leaves, flowers, seeds, stems, and roots of living or decomposing plant materials (Weston 1996).

Plants are always being the hotspot for most of the herbivorous attacks, pathogenic attacks and strongly competing nearby plants. In response to which they have expanded an array of chemicals that defend against pathogens, herbivores and provide compounds with allelopathic traits. The JA and SA signaling pathways induce and regulate the defense against herbivorous and pathogenic attack. Exogenous application of JA elevates the resistivity of widely ranging plants against pathogens in the workfield (Baldwin et al. 1998). Bioactivity and structure of several bioactive compounds extracted from plants have been studied so far but the information on mechanism of action of allelochemicals is limited (Vyvyan 2002). Benzoxazinones (BOA), sarmentine, citral, momilactones and sorgoleone are the allelochemicals which serve as sources for the discovery of new herbicides. Various cultivated grasses exude benzoxazinones from their roots and exerts multiple physiological effects on plants. The mechanism of action of BOA in plants include production of ROS against oxidative stress (Schulz et al. 2013). Competitive allelopathy occurs between one or more plant species when they exist together in the same vicinity. Several studies reported this phenomenon where different plant species existing together retaliate to allelochemicals which can affect their growth and biomass allocation (Rutherford and Powrie 1993; Ninkovic 2003; Kong et al. 2006).

In Agroecosystems allelopathic plants have some positive impacts through their effects on herbicides. Various classes of allelochemicals such as alkaloids, flavonoids, benzoxazines, ethylene, cyanogenic compounds, cinnamic acid derivatives, and some other stimulants, were extracted from the seed germination of varied terrestrial and aquatic plants. These allelochemicals are strongly phytotoxic to many plants. A great recognition to an agroecosystem is due to preexisting crops as allelopathic plants. Allelopathic potential of a selective crop plant can be used as a companion crop therefore, weeds will selectively out number certain plants but will not hinder the growth of the main crop plant, like oats, beets, rye, barley, corn, wheat, peas, millet etc. Many companion crops were found to be influential in hampering the growth of number of weeds. Plant hormone ethylene has powerful ability to initiate seed germination. Therefore, ethylene can be used to initiate seed germination in the absence of a host plant. The germination of seeds of weed plants stimulates the release of suicidal allelochemicals that results in the reduction of dormant seeds in the soil. Allelopathic interactions have important role of microorganisms because of their ability to easily alter the released allelochemicals. Allelopathic potential of plants can be enhanced owing to their weed suppressing ability and their genetic modification has been suggested as a possibility.

Allelopathy has emerged as a leading trend in agricultural ecosystems when it comes to collective or successive cultivation of a variety of plants (Scognamiglio et al. 2013). However, allelochemicals are widely used as a potent substitute for natural herbicides. Owing to its natural origin researchers proposed its incentive in the face of the chemical compounds being less polluting contrasting to the traditional herbicides, and inkling towards the suppression of weeds resistance to earlier used synthetic compounds (Reigosa et al. 1999).

3 Phytohormones in Plant Allelopathy

The allelochemicals hinders the growth and development of nearby plants by bringing on the secondary oxidative stress displaying enlarged production of ROS which act as a trigger (Weir et al. 2004) regulating response to biotic and abiotic havoc (Foyer CH and Noctor G, 2005). Hormonal signaling transduction depends on ROS production sites which is implicated as secondary messenger (Kwak et al. 2006). Secondary compounds must favor the establishment of a plant, leading to high reproduction rate in stressful environment. Even now it is not clear, whether the release of these potential exudates is active or passive. In last few years various articles related to allelopathic interactions were published however very few researchers have orchestrated on specific phytohormones and their mechanism of action.

JA and SA are well known signaling molecules and knowledge of their involvement in defense against predators and microbes is ever increasing but there is less information about their interactions and behavior with other plant competitors. Number of studies were carried out for interaction of JA and SA to allelochemicals. The relation of JA and SA in a rice -barnyard grass coexistence systems to the rice allelochemicals were quantified. Endogenous JA was released from the grass roots leading to the production of rice allelochemicals. SA was not detected as an exogenous signaling molecule in the coexistence system. Production of defensive metabolites in plants is elicited by JA and SA signaling compounds (Beckers and Spoel 2006; Bari and Jones 2009; Pieterse et al. 2009). Certain allelopathic crops grown in the presence of competing weeds can elicit the production of allelochemicals (Dayan 2006; Kong et al. 2006; Chen et al. 2010). Barnyard grass is a common paddy weed which usually coexists with rice crop. Several studies reported effect of rice allelochemicals on barnyard grass (Koeduka et al. 2005; Zhao et al. 2005). Rice yields can drastically reduce due to barnyard grass infestation of paddy fields which might be due to allelopathic interactions between these plants (Kong et al. 2006; Xuan et al. 2006). Alternatively, few rice varieties can cease germination and growth of barnyard grass through release of allelochemicals (Gealy 2013; Kong et al. 2008). Root interactions between allelopathic rice variety and competing barnyard grass can elicit the release of allelochemicals by rice (Kong et al. 2006; Gealy and Fischer 2010). Very little data is available which calls for further studies on the role of chemicals and other hormones in stress signaling.

4 Jasmonates

An endogenetic growth regulatory substance before all else recognized as a stress regulator in higher plants. JA are derived from fatty acids including components such as methyl jasmonates, jasmonate isoleucine conjugates and jasmonic acid (Ruan et al. 2019). The core of the JA consists of 3-oxo-2-2'-cis-pentenyl-cyclopentane-1-acetic acid a remote signalling molecule involved in diverse developmental process that was originally considered as stress related hormone in upper class plants (Campos et al. 2014; Llanes et al. 2016). Similarly, the exogenous application of JA also has a regulatory effect on plants. JA does not counter independently it works in unison with complicated signalling cascades of other phytohormones. JA has synergistic and antagonistic effects with ABA, ET, SA and other plant hormones in order to resist environmental stress. Over the last decades numerous genes and TFs involved in the JA biosynthesis and the signal transduction pathway have been identified including various inhibitors and activators involved in environmental signalling (Howe et al. 2018; Wasternack 2007). This plant signalling molecule is closely associated with physiological and molecular response. Physiological responses often include activation of the anti-oxidant system (peroxidase, superoxide anion radical, and NADPH oxidase), regulation of stomatal opening and closing, accumulation of amino acids (isoleucine and methionine) and soluble sugars (Karpets et al. 2014; Wasternack 2014; Acharya and Assmann 2009). Molecular responses often involve the expression of JA associated genes (JAZ, AOS1, AOC, LOX2, and COI1) (Hu et al. 2017; Robson et al. 2010), interactions with other plant hormones (ABA, ET, SA, GA, IAA, and BR) (Ku et al. 2018; Yang et al. 2019) and interactions with TFs (MYC2, bHLH148) (Zhao et al. 2013; Seo et al. 2011). This chapter basically focuses on the allelopathic effects of JAs and SAs that mediate environmental response. The growth of Nicotiana attenuata is inhibited, due to allelopathic activity of methyl jasmonates (MeJ) which is released in excess by the aerial parts of sagebrush. To recognize the typification of secondary metabolites different extracts of roots in growth bioassays with naturally existing tobacco were refined for test of volatiles by various researchers. The fractions depicting volatile compounds were rich in phytotoxins. The allelopathic potential of methyl jasmonates is then compared with these root volatiles.

The roots of the allelopathic crop plants release an astounding several different types of compounds such as alkaloids, flavonoids, terpenoids, and most of them are specific to roots only and play major part in plant armor system (Field et al. 2006). Roots can dominate over the soil microbial community by releasing a broad range of chemical exudates, which can affect the physical and chemical properties of the soil, inhibition of plant growth, interaction with herbivores, communication with other plant species and stimulating beneficial symbiosis (Walker et al. 2003; Bais et al. 2006). Volatiles emitted from the roots having allelopathic potential still needs to be taken into serious consideration (Lin et al. 2007; Ens et al. 2009). Few volatile organic compounds (VOCs) such as 1,8-cineol is emitted by the roots of *Arabidopsis thaliana* (Steeghs et al. 2004).

Currently, monoterpenes a class of volatile terpenoids extracted from roots and the rhizosphere of Pinus spp. were identified by solvent and dynamic headspace. (Lin et al. 2007). The bitou bush (*Chrysanthemoides monilifera*) is an invasive plant which release volatiles from the roots. Ens et al. (2009) analyzed these volatiles using gas chromatography and mass spectrometry and demonstrated the allelopathic impacts of the sesquiterpenes.

An important shrub *A. tridentata* emits volatile terpenoids from its aerial parts. These terpenoids such as 1,8-cineol, alpha-pinene, and camphor has inhibitory effect on the establishment of competitors which is due to their allelopathic properties (Weaver et al. 1977). The shoots of *A. tridentata* release non-volatile sesquiterpene lactones namely achillin, desacetoxymatricarin, arbusculin-A, viscidulin-B and viscidulin-C have the growth inhibitory effects on cucumber (*C.sativus*) radicles and hypocotyls in and also cause increase in rate of respiration in plants (McCahon et al. 1973).

The methyl jasmonate (MeJA) is an endogenous plant hormone having volatile nature and allelopathic potential. Aerial parts of *A.tridentata* emits MeJA as allelopathic aggregates (Preston et al. 2002) which can activate the formation of shielding compounds released from *N. attenuata* and the surrounding plants growing in their vicinity (Preston et al. 2002; Karban et al. 2000; Kessler et al. 2006). Airborne MeJA released by *A. tridentata* can arrest seed germination in *N. attenuata* (Preston et al. 2004). Furthermore, the seed germination of *N. attenuata* was restricted when sown in the same soil as that of A. tridentata, or when the seeds were sown in the soil used to germinate *A. tridentata* (Preston et al. 2002). MeJA is responsible for the maximum inhibitory action of original litter extract of sagebrush (Preston et al. 2002). MeJA released from the shoots of sagebrush and other compounds display pronounce allelopathic properties in the soil around the plant (Preston et al. 2002).

Several studies reported that rice is allelopathic and release allelochemicals into its environment. Various compounds have been identified as potential rice allelochemicals such as terpenes, fatty acids, phenylalkanoic acid, phenolic acids, hydroxamic acids, and indoles. Different studies revealed that the labdane related diterpenoid momilactones are important allelochemicals specifically, momilactone B which is released by rice plants from their roots into the native environment. Momilactone B seems to account for maximum observed allelopathy in rice. Exogenous application of JA leads to the production of momilactone A, potential allelochemicals in rice and a major phytoalexin (Nojiri et al. 1996). Poplar leaves have increased levels of phenolic acids when exogenously treated with methyl jasmonate (MeJA) (An et al. 2006). Two acyclic homoterpenes 4,8,12-trimethyl-1,3E,7E,11-tridecatetraene (homoterpene I), 4,8-dimethyl-1,3E,7-dimethylnonatriene (homoterpene II), which are of diterpenoid and sesquiterpenoid origin, can be induced by 0.1–10 mM of JA on leaves of and Zea mays and Phaseolus lunatus (Jorn et al. 1994). MeJA also induce indole glucosinolate biosynthesis in Arabidopsis (Brader et al. 2001) and oilseed rape (Loivamäki et al. 2004). Thus, allelopathic interactions may play vital role in natural ecosystem. However, this area has been rather controversial and the evidence for allelochemical mediated plant allelopathy is mostly correlative (Field et al. 2006). It is hypothesized that the JA and SA signaling pathways triggers the release of chemicals which are reported to exhibit allelopathic properties.

5 Salicylates

Salicylic acid is a monohydroxy benzoic acid i.e., benzene ring containing carboxylic acid and a hydroxy group at the ortho position. It is generally obtained from the bark of the white willow and wintergreen leaves, it has a role as an inhibitor, a plant metabolite, an algal metabolite and a plant hormone which is a conjugate acid of salicylate (Green et al. 2017). It is one of many phenolic compounds that are synthesized by the plants. Plant phenolics were shown to be involved in many important biological processes, including allelopathy. SA is a critical hormone that regulate many aspects of plant growth and development as well as thermogenesis and disease resistance.

Biosynthesis of SA in plants utilize the isochorismate and the phenylalanine ammonia lyase pathways and many other important compounds.

In plant pathogen interactions, salicylic acid is the most popular inducer of systematically acquired resistance in plants as a result of which the defense-related genes were expressed and phytoalexins, phenylpropanoids and pathogenesis-related proteins were synthesized (Metraux 2001; Durrant and Dong 2004; De Vos et al. 2005). The biosynthesis of secondary metabolites in plants was also initiated by SA (Taguchi et al. 2001). Methylsalicylate treatment has increased levels of u-tropine, and tropine in jimsonweed (Datura stramonium) seedlings (Fan 2005) and induced triterpenoid synthesis in both Galphimia glauca and Centella asiatica plantlets (Mangas et al. 2006).

SA is a natural phenolic compound that plays a role in the regulation of physiological and biochemical processes it contains aromatic ring bearing a hydroxyl group which is synthesized by the plant (Santner and Estelle 2009). These hydroxyl groups are involved in lignin biosynthesis; others serve as allelopathic compounds, regulate plant responses to abiotic stress and disease resistance by inducing antimicrobial defense compounds termed phytoalexins or by signalling defense activation (Raskin 1992; Yusuf et al. 2013; Wiesel 2015). The exogenous application of SA act as potential antioxidant capacity inducers, and also increase the levels of hydrogen peroxide in plants. These pathways also regulate many physiological processes in plants, such as increased germination rate, cell growth, stomatal opening, photosynthesis and ion uptake (Vazirimehr et al. 2014). Methyl salicylates is a volatile organic compound which is synthesized from SA. MeSA is associated with induced resistance plant defense which has been used in effective disease control methods (Tavares et al. 2014; Tang et al. 2005; Kauffman et al. 1973).

Treatment of seeds with MeSA accelerate the rate of germination and growth of rice. MeSA influences seed germination, cell growth, seedling establishment, stomatal closure, respiration, senescence associated gene expression, fruit yield, basal thermotolerance, as well as nodulation in legumes (Yusuf et al. 2013; Vlot et al. 2009). The allelopathic potential of the root and shoot of rice thus gets increased after treatment with MeSA.

6 Conclusion

This chapter concludes the allelopathic potentiality of strongly active secondary metabolites, plant hormones as well as transcription factors i.e. JA and SA. The above- mentioned theories has clearly described the impact of the chemicals released from different parts of the plants which are coincidently components of JA and SA having strong indulgence in the growth and development of native plant community.

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Jasmonate: A Versatile Messenger in Plants

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Abstract Jasmonic acid (JA) and its methyl ester, methyl jasmonates (MeJAs), is categorized under phytohormones. It is ubiquitously found all over the plant kingdom but varies in concentration from species to species. Chemically, it is known as derivatives of the fatty acid metabolism. JAs are synthesized from α-linolenic acid (α-LeA/18:3) via the octadecanoid pathway. JAs attached to its receptor, CORONATINE INSENSITIVE1 (COI1) triggers the signaling cascade and enables the expression of genes and generate various responses under stress and stress-free conditions. Moreover, JAs are known to regulate a wide range of physiological processes in plants such as plant growth, reproductive development and senescence. It also induces plant defense responses against various biotic stresses such as herbivore attack or pathogen infection. In this chapter, a summary of recent advances in our understanding of JA synthesis and signaling along with its role in regulating physiology of plant in presence or absence of biotic stress.

Abbreviations

JA	Jasmonic acid
MeJA	Methyl jasmonates
α-LeA	α-linolenic acid
JA-Ile	Jasmonic Acid Isoleucine Conjugate
SA	Salicylic acid
ABA	Abscisic acid
OPDA	12-Oxophytodienoic Acid
LOX	Lipoxygenase
AOS	Allen oxide synthase
AOC	Allen oxide cyclase
OPC	3-Oxo-2-(2-Pentenyl)-Cyclopentane

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COT1	CORONATINE INTENSITIVE1
OPR3	OPDA Reductase

1 Introduction

Plants are autotrophic-self sustaining organisms capable of fulfilling the requirements of humans as well as other organisms. The sessile-nature of plant makes them more susceptible to various environmental cues such as temperature, salinity and other biotic stresses (Farrant and Ruelland 2015). Plants evolve the special internal machinery that check the stress-induced damages through different mechanism. In response to environmental stresses, plants regulate the production of volatile and non-volatile compounds such as phytohormones that help plants to cope with stressed situation (Javid et al. 2011). The Phytohormones are foremost compounds allied to growth, physiology and provide stress resilience to plants (Ashraf et al. 2010). An imperative phytohormone, Jasmonates or Jasmonic acids (JAs) is far and wide in plant kingdom (Pirbalouti et al. 2014), is lipid derived signaling molecule that governs physiology, metabolism and defensive mechanisms of plants. Earlier, the oil extracted from *Jasminum grandiflorum* (Jasmine) was used to segregate the MeJA (Avanci et al. 2010). Firstly, it was extracted from *Lasiodiplodia theobromae* (a fungus) culture (Tsukada et al. 2010). JAs are present in different forms and some of them are cis-jasmone, methyl-jasmonate, jasmonyl isoleucine, and jasmonyl ACC (JA-ACC) that perform important biological functions (Wasternack and Kombrink 2010; Koo and Howe 2012) in the life of different plants. JAs content in the tissue might be responsible for altering growth, seed germination, embryo development, stamen/pollen growth, glandular trichome formation, adventitious and lateral root formation (Ahmad et al. 2016). Other JA mediated processes are oxidative defense, sex determination, fertility, reproductive process; storage organ formation and their communication with additional phytohormones (Browse 2009a; Avanci et al. 2010). JAs are specifically active against the biotic stresses caused by necrotic pathogens, bacteria, symbiotic fungi, nematodes and the herbivores. JA biosynthesis is a multi-step biochemical reaction involving fatty acid (lipid derivatives) oxygenation, cyclization, reduction and also the beta-oxidation. The synthesis of JA is completed through seven types of branches of lipoxygenase pathways (Wasternack and Feussner 2018), while other branches gives leaf aldehydes, epoxy-, divinylether-, keto-hydroxy-, epoxy hydroxyl-polyunsaturated and different volatile compounds. The α-linolenic acid (18:3) liberation from galactolipids positioned on the chloroplast is the preliminary step of the JA synthesis.

Synthesized JAs released from their site of synthesis and localized via xylem/phloem, act as signaling compound and regulate the plant's defensive mechanism (Thorpe et al. 2007). JA and its isoleucine conjugate (JA-Ile) are the signaling molecules responding to these stresses and other growth processes (Wasternack and Strnad 2018). JA and their derivatives originated from the lipids (preferentially α-linolenic acid) of cellular chloroplast membranes. Most of the researches related to JA signaling were performed on *Arabidopsis* and tomato that revealed many important clues such as involvement of different genes and their respective transcriptional factors (Turner et al. 2002; Browse and Howe 2008). Several researches on JA signaling are still in progress because of their tremendous role against environmental stresses (Fonseca et al. 2009; Koo et al. 2009) and their integration with other signaling plant hormones, for instance ethylene, ABA and SA.

JA, MeJA and their other derivatives are known to alter the physiology of plants. They can actively participate in senescence process (Ahmad et al. 2016). Till date, a couple of JA-induced growth, development and physiological changes have been reported from different plants (Ahmad et al. 2016). The major noticeable JA-induced changes that occurred in the plants are during the biotic/abiotic stresses, causing oxidative argument, affecting reproductive practices, fertility/sex determination, storage organ (tuber) formation, fruit ripening, fruit senescence and hormone interaction (Ahmad et al. 2016). JA also promotes seed and flower maturity (Wasternack et al. 2012), germination in dormant seeds, chlorosis (Creelman and Mullet 1997), floral-nectar synthesis (Radhika et al. 2010), tuber formation and increase storage proteins (Pelacho and Mingo-Castel 1991), boost activity of antioxidant enzymes (Soares et al. 2010), systemic resistance (Pieterse et al. 2012), allelopathy (Baldwin 2010), wounding and herbivory (Ballaré 2011; Erb et al. 2012a). JAs have been reported to manipulate expression of several defense related genes in different plants such as *A. thaliana* (Sasaki et al. 2001), *Oryza sativa* (Liu et al. 2012), *Saccharum officinarum* (De Rosa et al. 2005), *Solanum lycopersicum* (Boter et al. 2004).

Plants cannot move, so, they are in direct contact with the changing environment. The environmental stresses and biotic agents could affect the vegetation inadequately; to cope with these plant evolved signaling molecules like JA that can guide the plants to shield against these artifacts. JA and its derivatives along with other phytohormones such as ethylene, salicylic acid (SA) are the primary signaling molecules for regulating plant defense (Santino et al. 2013). Here, we will discuss about JA biosynthesis, signaling, JA-mediated physiological changes and its role in plant defense.

In this review chapter, focus will be on occurrence, biosynthesis of JA and its reaction in several cellular compartments such as chloroplast, peroxisome and cytoplasm; and regulation of JA biosynthesis. Based on recent researches, present chapter focuses on JA signaling and genes involved in it. Furthermore, this chapter highlights physiological modulations done by JA including seed germination, root growth inhibition, trichome formation, senescence, reproduction, tuber formation and nodulation. Present chapter also appraises role of JA in ameliorating biotic stress induced by biotic agents such as insects and pathogen.

2 Occurrence

In this world, only some prokaryotes, lower and higher autotrophic organisms are responsible for successfully conducting the biosynthesis and signaling of the JA and its various components. The first ever discovered JA complex was the famous methyl ester of JA (JA-Me); present in the aroma of flowering plants (Demole et al. 1962) and also in the fugal (*Lasiodiplodia theobromae*) culture media (Aldridge et al. 1971). Additional research on the same fungus (*Lasiodiplodia* species) resulted in breakthrough of lasio-jasmonates (Andolfi et al. 2014). Another JA component, JA furanoyl ester LasA was exposed from a grapevine pathogen (L. mediterannea), and could be altered into the active JA-Ile (act like a non-active JA pool) (Chini et al. 2018a). Famous fungus, *Fusarium oxysporum* has been detailed to hold several JA derivatives (Miersch et al. 1999) including allen oxide 12,13(S)-epoxy-octadecatrienoic acid and the 12-Oxophytodienoic Acid (OPDA) as sole intermediates (Oliw and Hamberg 2017), which grant a hint that both fungi and plants form JA in a comparable manner. As a substitute of JA, its precursor OPDA have been investigated in bryophyte *Marchantia polymorpha* (Yamamoto et al. 2015), in moss *Physcomitrella patens* (Stumpe et al. 2010), and in spikemoss *Selaginella martensii* (oldest vascular plant) (Ogorodnikova et al. 2015), while in *S. moellendorffii* both OPDA and JA were brought into being (Pratiwi et al. 2017). Although total absence of JA was observed in *M. polymorpha*, essential ingredients of JA signaling are still persistent indicating the involvement of another ligand than the JA-Ile (Bowman et al. 2017). Indeed, identification of two isomers of dinor-OPDA (JA-Ile precursor) viz., dinor-cis-OPDA and dinor-iso-OPDA indicated co-evolution in JA-Ile perception and receptor/ligand specificity (Monte et al. 2018). JA compounds occur universally in the higher plants. Even the conjugate of OPDA with amino acid isoluecine was detected in *A. thaliana* (Floková et al. 2016). In vitro enzymatic technique shows its formation from Ile conjugates of the αLeA (Uchiyama et al. 2018).

3 Biosynthesis of JA

3.1 Biosynthesis Overview

JAs are the lipid-derived signaling compounds, active against both the biotic stresses (such as pathogen attacks and wounds by herbivores) and the abiotic stresses (salt, heavy metals, or thermal stresses). JA also modulates germination of seeds, growth of roots, stamen development, and season of flowering, their senescence and other developmental activities (Wasternack and Hause 2013). Biosynthesis of JA is completed through several steps that includes oxygenation of the lipid-derived fatty acids and their cyclization, reduction, and beta-oxidation (Vick and Zimmerman 1983). However, since the last two and a half decades, no new path for JA biosynthesis has been exposed. JA biosynthesis occurs via one of the seven kinds of branches of so called LOX or lipoxygenase pathway (Wasternack and Feussner 2018), while the other branches lead in leaf aldehydes, epoxy-, divinylether-, keto-hydroxy-, epoxy hydroxyl-polyunsaturated and several volatile compounds. All the enzymes required for JA-biosynthesis have already been well characterized and their regulation and gene expression has also been studied (Wasternack and Hause 2013).

Initially, chloroplast membrane librates α-linolenic acid (18:3) from galactolipids to initiate JA biosynthesis (Wasternack and Strnad 2018). This biosynthesis also involves an enzymatic conversion in which allen oxide synthase (AOS) and allen oxide cyclase (AOC) form cis-(+)-12-oxo-phytodienoic acid (OPDA) where 13-LOX engaged with oxygenation within the chloroplast. Similar kind of reaction occurs with the hexadecatrienoic acid (16:3) giving dinor OPDA (dnOPDA), one among the JA precursors. dnOPDA and OPDA were translocated from the chloroplast to the peroxisome. This translocation was supported by ATP-binding cassette transporter (also named as COMATOSE, CTS), peroxisomal ABC transporter1 (PXA1) and also via passive transport. Peroxisome carried out the ultimate steps of JA biosynthesis. Here, the OPDA reductase (OPR) reduces the cyclopentenone ring of dnOPDA and OPDA giving OPC-6 and 8-(3-oxo-2-(pent-2-enyl) cyclopentenyl)octanoic acid (OPC-8), respectively (Wasternack and Hause 2013). The fatty acid b-oxidation performs the conversion of OPC-8 to OPC-4 and OPC-6 derivatives and ultimately, the JA. Synthesized JA is released into cytosolic region and here, JA-Ile-conjugate synthetase (JASMONATE RESITANT JAR1) carries the JA conjugation with isoleucine (JA-Ile) or with other amino acids. JA-Ile functions as ligand of JA co-receptor complex containing CORONATINE INTENSITIVE1 (COT1, Fbox protein) as the key component (Pauwels and Goossens 2011).

Like other plant growth regulators, synthesis and activity of JAs can also be influenced by its stereochemistry, especially pentenyl and carboxylic acid side chain at 3 and 7 position, respectively, of pentanone ring.

3.2 Detailed Process of JA Biosynthesis

Vick and Zimmerman (1984) were the first to describe the JA biosynthetic pathway, followed by deep evaluation in the *Arabidopsis* and tomato. Basically, pathway of JA synthesis includes the oxygenation of lipid-derived fatty acids (FA) where OPDA is an active intermediate. Here we will discuss JA biosynthesis in the organelle-based reactions manner which starts from chloroplast and ends with the release of JA in the cytoplasm.

4 Chloroplast-Based Reactions

Ω-3 (Omega-3) fatty acid, ALA; dominant lipid component of leaf, are generally situated in galactolipids, mono (MGDG)- and digalactosyldiacyl glycerol (DGDG) of chloroplast. The pioneer substrate for the pathway is still not clear, and the esterification of ALA to galactolipid may be subject to oxygenation (Nilsson et al. 2016) by the 13-LOX (13-lipoxygenase, non-haem iron-sulphur protein). It is possible that initially lipase hydrolysed the ALA from the parent lipid, followed by conversion into the 13-HPL (18:3-OOH) (Wang et al. 2018). Variant of JA i.e., dinor-JA (dinor-oxo-phytodienoic acid (dOPDA); analogous reactions can also be operated on the trienoic acid. It was investigated that the extra-plastidic ALA enhanced the JA defensive response raising questions regarding origination of acyl-substrate and indicating the involvement of ER-based phospholipids like phosphatidylethanolamine and/or phosphotidylcholine (Zhang et al. 2019).

Allene oxide synthase (AOS), a cytochrome P450 enzyme (from CYP74A family) is the next enzyme in this pathway that transforms 18:3-OOH into the 12, 13-epoxylinolenic acid, which is a transient intermediate and is cyclised very fast to cis (+)-12-oxo-phytodienoic acid (OPDA) with the help of allen oxide cyclase (*AOC*) (Wasternack and Feussner 2018) (Fig. 1). There are four genes responsible for cyclase (*AOC1-4*) except *A. thaliana* (single gene is responsible) and seems

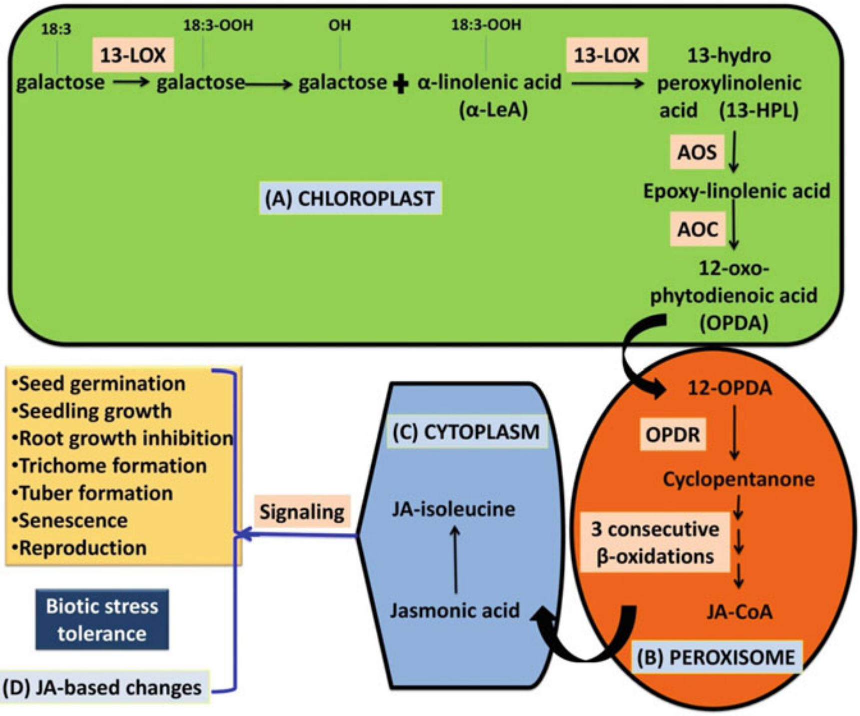

Fig. 1 **a** Release of galactolipids (from chloroplast membrane) and their metabolization gave α-linolenic acid (α-LeA; JA precursor). 13-LOX mediated action over α-LeA produce the 13-hydro peroxylinolenic acid (13-HPL). A transient epoxy intermediate is developed by allene oxide synthase (AOS) activity and this further face allen oxide cyclase (AOC) mediated cyclisation to provide 12-oxo-phytodienoic acid (12-OPDA). **b** 12-OPDA transferred to peroxisome and here it experience reduction of its cyclopentenone ring followed by three consecutive β-oxidations to produce JA. **c** The conjugation of JA with isoleuciene is conducted in the cytoplasmic zone. **d** Any exogenous trigger excites the JA signaling to perform various physio-biochemical functions and it also has an important role in counter-acting the consequence of biotic stress

to regulate various functions. Possible heteromerization of these four AOCs and their differential expression are partially responsible for JA formation (Stenzel et al. 2012). Both OPDA and dnOPDA (7s, 11s)-10-oxo dinor phytodienoic acid) have been recognized acylated at sn-1 and sn-2 positions of the galactolipids. It was observed that in Arabidopsis, cyclo-oxylipin galactolipids level enhances following the wounding. In the case of MGDG, OPDA was initially indentified at sn-1 position, and 16:3 was at sn-2. Around 167 molecular species of galactolipids have been discovered from Arabidopsis, About of which 63% are prokaryotic in origin (i.e., synthesized within chloroplast) while remaining are eukaryotic in origin, so imported into organelle (Griffiths 2020). External triggers further stimulate oxidation, the lipoxygenase does the oxidation of 16:3 and results in dnOPDA whereas 18:3 gives OPDA. In Arabidopsis, availability of both dOPDA and OPDA in galactolipids at relatively higher levels may be responsible for race-specific bacterial resistance (Andersson et al. 2006). The OPDA itself is a strong anti-microbial compound having α, β-unsaturated carbonyl group. Studies on structural basis have been and it was observed that arm of C8 chain combined to a cyclopentene ring was raised as highly effective molecule in antimicrobial tests (Zhou et al. 2011). OPDA synthesized in chloroplast is further exported to the peroxisome using the transporters (Nguyen et al. 2017).

5 Peroxisomal Reactions

The transported OPDA undergoes sets of reactions and starts with the reduction of cyclopentenone ring of OPDA to form cyclopentanone by the activity of OPDA reductase (OPDR, Fig. 1). (9S,13S)-OPDA [cis-(+)-OPDA] is the only naturally occurring diastereomer among other possible diastereomers and this structure is stabilized by AOC, undergoing subsequent reactions (Griffiths 2020). The ultimate product of the subsequent reactions is one among four of the diastereomers, viz. (3R, 7S)-JA [(+)-7-iso-JA] and considered to be in equilibrium with (3R, 7R)-JA [(-)-JA]. (3S, 7R)-JA and (3S, 7S)-JA are the diastereomers that are not found in nature (Wasternack and Feussner 2018). OPDA (being converted into JA), can regulate the gene transcription similar to the signaling molecule (Taki et al. 2005). The four OPR genes recognized in Arabidopsis show variable activities towards OPDA dia-stereoisomers. Among these, OPR2 can reduce natural 9S,13S-OPDA (cis-[+]-OPDA) as well as other isomers. In an Arabidopsis mutant, the OPDA reductase 3 (OPR3) shows a different pathway that utilizes the 4,5-didehydrojasmonate for β-oxidation and JA-biosynthesis (Chini et al. 2018b). It is observed in OPR mutants of maize that they are also important for immunity development against insects and pathogen and in *Arabidopsis* it might be involved in seed germination (Dave et al. 2011).

The cyclopentanone faces three β-oxidation reactions and cuts six carbons of the carboxy-terminal carbon chain to produce JA (Fig. 1). The by-product of β-oxidation (i.e., acetyl CoA) can be utilized in the Krebs cycle for generating energy or as a precursor of several metabolic pathways such as synthesis of terpenoid and fatty acids. Synthesized JA are then translocated via xylem and phloem for being there for plant defense. The synthesized JA moves outside of the peroxisome to the cytoplasm and faces further modifications.

5.1 Cytoplasm-Based Modifications

To be in the active state, JA follows the conjugation reaction with an amino acid, specifically with the isoleucine. Cytoplasm facilitates the conjugation of isoleucine with JA and results in JA-isoleucine (JA-Ile). A study carried out on Arabidopsis transgenic *jar1-1* showed that wild-type *JAR1* restored to JA and to high JA-Ile content was just equal to the wild type (Staswick and Tiryaki 2004). JAR1 enzyme forms the JA-amido conjugates with various amino acids, such as leucine, phenylalanine and valine but in very much lower amount than with the isoleucine.

Wounding triggers the instant accumulation of JA-Ile at the affected portion and regulates the early transcriptional responses related to degradation of JAZ (JA Zim domain) protein. Synthesis of JA-Ile during wounding needs the OPR3 in healthy un-damaged active leaves rather than in wounded leaves and it relies on JAR1, a JA-conjugating enzyme.

6 Regulation of JA Biosynthesis

According to Browse (2009b, c), JA biosynthesis regulation is checked by substrate availability, tissue specificity, and the positive feedback loop. Apart from these, the activity of branches present in LOX pathway regulates the same; specifically, HYDROPEROXIDE LYASE (HPL) and AOS branches that work simultaneously on a substrate i.e., the product of a 13-LOX. The HPL branch results in either volatile or non-volatile oxylipins such as leaf alcohols and aldehydes (Andreou et al. 2009). One among the three known HPLs in rice up regulates the green leafy volatiles (GLVs) but due to substrate competition it suppresses the JA biosynthesis (Tong et al. 2012). Further, the JA-related transcription factors (TFs), MAPKs, Ca^{2+} related signaling and JAZ proteins also regulate JA biosynthesis. The SCFCOI1-JAZ regulatory module can be used to elaborate the positive feed-back loop mediated JA biosynthesis regulation as it is activated during expression of LOX, ACX, OPR3, AOC and AOS. Formations of JA/JA-Ile cause the JAZ degradation, which further evokes MYC2 genes to up-regulate JA-responsive promoters involved in JA biosynthetic genes (Chung et al. 2008). An investigation using Arabidopsis microarray datasets revealed that both transcriptional and post translation can mediate the regulation (van Verk et al. 2011). According to the Arabidopsis co-expression analysis of van Verk et al. (2011), MYC2 and MKK3/MPK6 cascades are linked to the JA-synthesis. In Arabidopsis, JA content causes the activation of MAPKs like MKK3 and MPK6, which negatively regulate MYC2, thus repressing the JA biosynthetic genes (Takahashi et al. 2007). Similarly, for exogenous stimulation-induced JA accumulation, the Ca^{2+} dependent protein kinases (CDPK4 and CDPK5) of Nicotiana attenuate acts as off-putting regulators (D. H. Yang et al. 2012). In contrast to CDPK4/CDPK5, a wound induced protein kinase (WIPK) is immediately activated in the vicinity of wound, thus enhancing JA synthesis (Wu et al. 2007). Another investigation on tomato, revealed the participation of MPK1, MPK2 and MPK3 in expressing the JA biosynthetic genes (Kandoth et al. 2007). The CONSTITUTIVE PHOTOMORPHOGENESIS 9 (COP9) signalosome (CSN), which is a CULLIN-RING E3 ubiquitin ligases regulating multiprotein unit, interestingly reported to altering the biosynthesis of JA. This CSN is not only essential for proper plant development but also needed for guarding the plant against the pathogens and herbivores; as it modulate the JA levels in plants (Hind et al. 2011). Role of Ca^{2+} as secondary messenger for several biotic/abiotic triggers is well understood (Kudla et al. 2010), though most of these triggers are linked with improved JA synthesis but the actual mechanism of Ca^{2+} mediated upregulation of JA biosynthesis is not fully revealed.

7 JA Signaling

The JA is responsible for defending plants against necrotic pathogens and herbivores; they can be leaf-eating insects (ex-beetles, caterpillar), sucking-piercing insects (ex-leaf hoppers, spider mites, thrips, mired bugs, fungal gnats), soft-tissue feeding insects (ex-leaf miners), and can be stylet-mediated phloem feeding whiteflies and aphids (Howe and Jander 2008; Campos et al. 2014; Goossens et al. 2016). JA-signaling is also prone to bacterial attack (Plectobacterium atrosepticum), fungal infestation (ex-Alternaria brassicicola, Fusarium oxysporum, Plectosphaerella cucumerina, Botrytis cinerea) and infection with oomycetes such as Pythium spp. (Campos et al. 2014; Yan and Xie 2015). It also mediates the defense against the detritivorous crustaceans (Farmer and Dubugnon 2009), molluscan (Falk et al. 2014) and vertebrate herbivores (Mafli et al. 2012). JA-content initiates the resin-duct, nectarines and glandular trichome production that further check the primary protection of plants or for acting against biotic agents (Wasternack and Hause 2013; Campos et al. 2014; Wasternack and Strnad 2016). JA-induced plant defense mechanism starts with any kind of pathogen or herbivore attack, and results in activation of signaling pathway and JA production.

Herbivores/pathogens attacks generate various kinds of pathogen/microbe associated molecular pattern (PAMPs/MAMPs), such as systemin/systemin like peptides, plant cell derived oligogalacturonides, damage associated molecular patterns (DAMPs), herbivore associated molecular patterns (HAMPs), flagellin etc. (Felton and Tumlinson 2008; Mithöfer and Boland 2008; Campos et al. 2014; Heil and Land 2014). They are the attacker associated pattern identified by plant pattern recognition receptors (PPRs) situated at the plasma membrane of plant cells (Choi et al. 2014);

furthermore, they regulate the gene expression, specifically those genes that are associated with defense hormone signaling (Campos et al. 2014). In response to MAMPs, DAMP and HAMPs, JA accumulates in prone areas (Yamaguchi and Huffaker 2011; Huffaker et al. 2013; Kim et al. 2014). In addition to wounds, plants sense the pressure developed by landing, walking and other mechanical damage caused by insects (Erb et al. 2012b) also upregulating the JA production and its signaling (Glauser et al. 2009; Farmer et al. 2014). Actual mechanism causing MAMP/DAMP/HAMP signaling and JA production remains elusive. Various intracellular signals such as ROS, calcium ion, calcium dependent protein kinases (CDPKs), mitogen activated protein kinase (MAPK) cascades are involved in signal perception of these conserved patterns, their transduction and initiation of JA biosynthesis (Zhang et al. 2017).

JA signaling starts with the plant pattern-recognition receptors (PRRs) based perception of the molecular patterns (PAMPs/DAMPs/HAMPs) from biotic agents, JA biosynthesis and their subsequent action (Wu and Baldwin 2010). The signal perception, calcium flux and MAPK cascades in cells further support the signal amplification from local leaves to systemic leaves and from cytosol to the nuclear region, JA and their derivatives reprogram the expression of defense related genes. The main dependency of JA signaling is basically on the CORONATINE INSENSITIVE1 (COI1), which is an F-box protein and takes the function of JA-Ile receptor in combination with a repressor protein viz., JASMONATE ZIM (JAZ), in E3 ubiquitin-ligase SKP1 Culin F-box complex (Sheard et al. 2010). In resting cells, JAZs with adaptor protein NOVEL INTERACTOR OF JAZ (NINJA) and co-repressor TOPLESS (TPL) may bind to basic helix-loop-helix MYCs (Fig. 2) and other such positive transcriptional factors (e.g., WRKY, ERF/AP2, MYB) to down regulate the JA pathway (Pauwels et al. 2010). The JA-Ile binding to COI1, triggers the JAZ to soon get degraded by proteosomic activity and thereby activates downstream gene expression and immunity (Lorenzo et al. 2004; Pauwels and Goossens 2011; Kazan and Manners 2013). The transcriptional regulators give a multilayer defense to exogenous stressing factors. Studies on Arabidopsis show two branches i.e., ERF and MYC branch of the JA signaling, where the bHLH controls the MYCs branch. Wounding and herbivore attacks induce toxic protein synthesis, such as VEGETATIVE STORAGE PROTEINs (VSPs; Howe and Jander 2008; Kazan and Manners 2012; Schweizer et al. 2013). The ERF branch is governed by two phytohormones i.e., JA and ethylene, they regulate expression of PLANT DEFENSIN1.2 (PDF1.2) against the necrotrophic pathogens (Berrocal-Lobo et al. 2002). The APETALA2 (AP2)/ETHYLENE RESPONSE FACTOR (ERF) family of TFs form the protein complexes, one of them is ERF1 + OCTADECANOID-RESPONSIVE ARABIDOPSIS59 (ORA59) complex (Pré et al. 2008; Li et al. 2018).

JA signaling causes the activation and regeneration o f cells, further supporting the role of JA in developmental processes (Pacheco et al. 2012; Zhou et al. 2019). JA-Ile level directly influences herbivore fitness. JA signaling stimulates the production of several alkaloid, terpenoids, and glucosinolates on herbivore attacks (Howe and Jander 2008; Chen et al. 2019). Synthesis of glucosinalates checks the infestation of chewing and phloem feeding insects (Mewis et al. 2005; Schweizer et al. 2013).

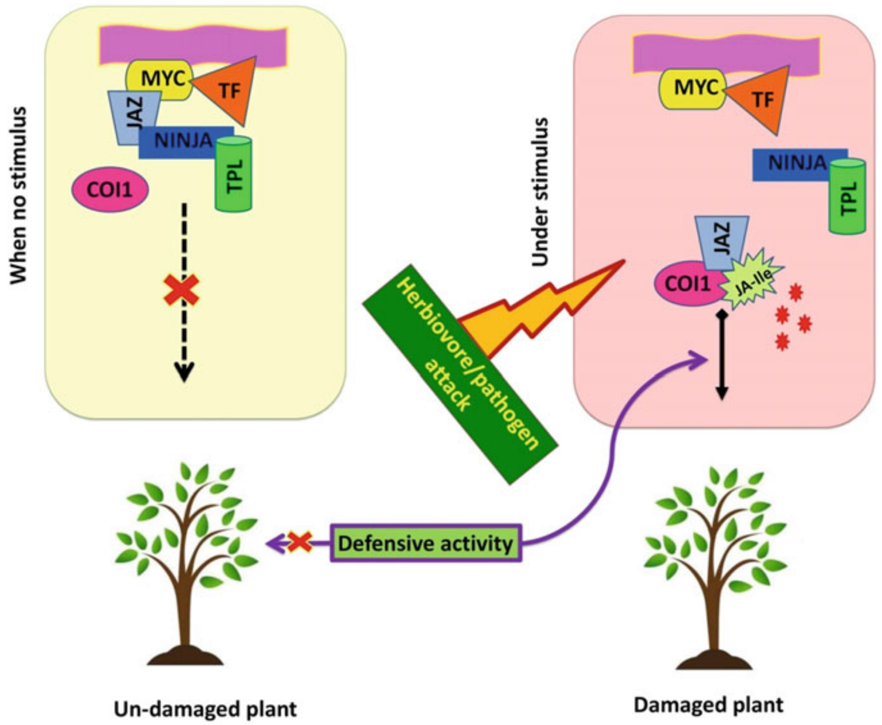

Fig. 2 Jasmonic acid (JA)-based security aligned with biotic stresses in plants. In un-damaged plants, repressor proteins JAZ (JASMONATE ZIM) unite with positive TFs like basic helix-loop-helix MYCs. Under normal conditions, JA pathway is suppressed by NINJA (NOVEL INTERACTOR OF JAZ) and their recruited co-repressor TPL (TOPLESS). In damaged or pathogen assaulted plants, JA signaling corridor become vigorous to contradict the biotic trauma. Under trigger state, F-box protein COI1 (CORONATINE INSENSITIVE) got stimulus from JA-Ile and results in JAZ deprivation. Meanwhile, protein MYC is liberated and JA-mediated defense system get activated

In response to biotic stress, JA initiates resin duct or trichome production which further induces JA synthesis and the respective signaling. Attack of biotic agents stimulate attacker associated molecular patterns (PAMPs/MAMPs) and in response to these patterns the JA gets accumulated to the prone region. The perception of induced signal and MAPKs further amplify the signals. JA signaling rely on COI1 that further work with JAZ protein. In resting cells, JA pathway is down-regulated by binding of JAZ, NINJA, and TPL with the positive transcription factors like basic helix-loop-helix MYCs, WRKY, ERF/AP2, MYB etc. whereas, binding of JA-Ile to COI1 triggers JAZ to get degraded and provides immunity to the plant.

8 Physiological Roles

The phytohormones are known for their tremendous power of directing morphology, physiology and other biochemical traits. Although, phytohormone JA is famous for its biotic stress resistant, but it is also capable of interfering with important physiological changes under abiotic stress as well (Ahmad et al. 2016). First demonstrated physiological change caused by JA was growth inhibition in Arabidopsis root (Adams and Turner 2010; Liu et al. 2010). While some insensitive mutants of Coi1, Jin1 or Jar1 have not showed any effect on root length after JA application and were just similar to the roots of wild typesome JA-sensitive mutants such as Joe2, Cet1, Cev1, and Cex1 were dwarfed with reduced roots as the mutant JA-induced genes were overexpressed (Pauwels et al. 2009). In apple seeds, high JA levels promote lipid peroxidation that cause the membrane damage, thereby inducing the germination (Ranjan and Lewak 1992). According to Creelman and Mullet (1995), the hypocotyls hook, plumule and axes like organs of soybean had high JA value than the un-elongated stems, roots and elongated cells of hypocotyls zones. Initially the JA was present in species of family solanaceae, but now it is present in several widely distinct genera (Gidda et al. 2003). Regulation of some proteins rely on the JA content, but it needs help from minerals such as nitrogen and phosphate, phytohormone like auxin and the sugars (Creelman and Mullet 1997). In *A. thaliana*, Sulfotransferase2a *(AtST2a)* checks the endogenous 12-OH-JA levels that is hydroxylated product of jasmonate (Gidda et al. 2003; Faraz 2006).

9 Seed Germination and Seedling Growth

JA doses were found to inhibit the seed germination. According to Dave et al. (2011), the biochemical and genetic studies suggested that inhibitory role of OPDA in combination with ABA but in a COI1-independent way. External JA supply was found to retard growth of seedlings, elongate hypocotyls, promote primary root and expand leaf (Wasternack et al. 2013). InsP5 promotes interaction of COI1 with the JAZ9 and cause JA induced root inhibition (Mosblech et al. 2011). JA inhibits expansion of leaves by repressing the activity of mitotic cyclin (CycB1; 2) and cellular multiplication (rather than influencing cell size). MYC2 and its homologs give both encouraging and discouraging things on hypocotyl under blue and red/far-red light conditions. In Arabidopsis, ERF109 bind and activate ASA1 (anthranilate synthase A1) and YUCCA2 that further enhance the lateral root formation (Sun et al. 2011).

10 Root Growth Inhibition

Screenings of different mutants predicted the importance of JA in inhibiting the root growth. cev1, a short root phenotype mutant inhibits the root growth under JA-elevated conditions (Ellis et al. 2002). For inhibiting the root growth the JA needs the COI1. However, ethylene and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) can inhibit the root growth, for this, they need day light and COI1 but not the JA (Adams and Turner 2010). On the other hand, several researchers are engaged in revealing the exact relationship of various factors governing complex root developmental process with the JA-induced inhibition. The earlier cell and tissue specific gene expression mapping concluded that the non-overlapping between JA, auxin and GA induced expression of genes (Birnbaum et al. 2003). JA responsive genes are generally expressed in outer layers of the roots. Mainly the GA, auxin and CK are key signaling molecules, but the cross-talk with several other hormones indicates the role of JA in root growth. The growth of root is a complex phenomenon involving hormonal and mechanic signaling, resulting in cell multiplication, membrane trafficking, cell wall synthesis and loosening, growth rate and turgor (Band et al. 2012). Some of these processes are directly under JA regulation, while some are indirectly regulated by JA through auxin. The Auxin synthesis in Arabidopsis further depends on a JA-induced ASA1 (Sun et al. 2009), endocytosis, PIN2 accumulation in plasma membrane (Sun et al. 2011), hence proving its indirect role in root growth. Mutant axr1, showing defective SCF-complex component (Mockaitis and Estelle 2008) is needed for auxin signaling. This mutant results in low inhibition of root growth by MeJA, suggesting AXR1 dependent alteration of CULLIN1, a subunit of SCFOI1 complex essential for JA signaling (Xu et al. 2002). Thus JA can inhibit root growth either solely or in combination of other phytohormones, specially auxin.

11 Trichome Formation

Trichomes are defence associated cellular structures. Glandular trichomes are the multicellular structures filled with different kinds of alkaloids, flavonoids, terpenoids and defense proteins (Tian et al. 2012). A tomato homologue of COI1 gave the clue of JA-induced trichome formation (Li et al. 2004). A female sterile tomato mutant jai1 is defective in spider mite resistance, trichome monoterpene and grandular trichome synthesis. Another recessive tomato mutant od-2 (odorless-2) having differential morphology, density and glandular trichomes with altered chemical composition suggests the connection of formation of trichome with the JA (Kang et al. 2010). In the field condition this od-2 mutant is extremely prone to solanaceous specialist Manduca sexta and Colardo potato beetle larvae; clearly indicating the role of trichome-borne chemical compounds in verifying the host-plant selection in natural environmental conditions (Kang et al. 2010; Meldau et al. 2012). A study based on trichome free jai1 mutant (JA-insensitive) and spr2 mutant (JA-deficient) clarified the effect of trichomes over the volatile release in tritrophic interaction (Wei et al. 2013). Not only glandular, but also non-glandular trichomes are associated with plant defense against pathogen/herbivores through these trichomes and JA-synthesized defense compounds including monoterpenes, sesquiterpenes and PI2 (Tian et al. 2012). Cotton fibre is a special kind of uni-celled seed trichome and it is well known that their initiation and elongation is under hormonal control including JA. Later Hao et al. (2012) showed the bHLH-mediated upregulation of JA biosynthesis in Gossypium barbadense. Consequently, the high JA content in the cotton fibre expresses the downstream of genes participating in ethylene biosynthesis and Ca2+ signaling. In A. thaliana, the TFs GL3, EGL3 and MYB75 are the accepted targets of JAZ and take part in trichome initiation as well as in anthocyanin biosynthesis (Qi et al. 2011). The JA-mediated trichome initiation depends on the endogenous JA-level through the interaction of JAZ with GL3 (Yoshida et al. 2009).

12 JA in Tuber Formation and Nodulation

Formation of tuber is also affected by JA level in several species including potato and A. thaliana. JA is responsible for manipulating the VSP (vegetative storage proteins) gene expression (Staswick 1994) and these genes were firstly characterized and purified from soybean (Wittenbach 1983). According to Staswick (1989), VSPs get accumulated in developing reproductive parts as well as in pods except the seeds, highlighting that the amino acids from disassembly of Rubisco and leaf proteins become active during formation of seeds. In developing fruits and flowers, VSP expressions were high in both Arabidopsis (*AtVSPs*) as well as in soybean (Bell et al. 1995). In the JA-insensitive mutant of Arabidopsis *Coi1*, AtVSP proteins were initially absent in flowers but they became visible after Me-JA application (Benedetti et al. 1995). Similarly, the two JA-deficient A. thaliana mutants, opr3 and dad1 showed reduction in filament length, associated with double mutant arf6/arf8 that have low JA in filaments. The following mutants cannot synthesize two ARFs (auxin response factors) that have important role in filament elongation, indicating the involvement of auxin in JA signaling (Wasternack 2007). Nodules, characteristic feature of legumes, contain nitrogenase (bacterial enzymes) that cause atmospheric nitrogen fixation. The rhizobial-bacteria secrete lipochito-oligosaccharide NOD factors that help in nodule initiation (Stougaard 2000) and the subsequent nodule development is under the supervision of cytokinin signaling pathway (Reid et al. 2016). Lipooxygenase genes (during JA-biosynthesis) were reported to be down-regulated in early nodules cells of *Lotus japonicas* (Kouchi et al. 2004) whereas in *Lotus japonicas* (Nakagawa and Kawaguchi 2006) and *Medicago truncatula* (Sun et al. 2006), JA induced nodule inhibition is noticed. According to EST analysis, during Lotus-Rhizobium interaction, genes responsible for enzymes of JA-synthesis (AOC and OPRs) and for pathogen defense response showed enhanced expression but it was suppressed during the late stages of nodule formation (Shigeyama et al. 2012; Bordenave et al. 2013).

13 Senescence

Ueda and Kato (1980) were the first to demonstrate physiological role of JA as the senescence in *Avena sativa* (Ahmad et al. 2016). They isolated and identified a senescence-promoting substrate from the *Artemisia absinthium.* After that Schommer et al. (2008), Reinbothe et al. (2009) and other researchers also reported the JA-induced senescence in several plants. The miR319 targets regulated the senescence and JA-biosynthetic process (Schommer et al. 2008). High JA-level promotes JA synthesis and this further activates SENESCENCE ASSOCIATED GENES (SAGs). Other senescence-related genes, such as SEN1, SEN4, SEN5, SAG12, SAG14, SAG15 and their expression are also under JA governance (He et al. 2002). In the transcription analysis of *Arabidopsis*, expression of two important genes, OPR3 and AOS in the JA synthesis pathway gave impression of JA-induced senescence (van der Graaff et al. 2006). Plants showed several phenotypical changes during senescence including yellowing.

14 JA in Plant Reproduction

JA production is impaired with nector-secretion processes in flowering plants. Radhika et al. (2010) predicted the floral-nector secretion in the Brassica species under JA-influence. Exogenous JA application significantly enhanced the floral nector production in *B. napus* (Bender et al. 2012). Presence of JA and MeJA was also diagnosed by Yamane et al. (1982) in the anthers and pollens of three different *Camellia* spp. Later, the Arabidopsis mutants clarified that JAs play an essential role in stamen elongation, pollen development and in pollen releasing period (Liechti and Farmer 2006). An Arabidopsis mutant, delayed dehiscence1 (dde1) showing delayed anther dehiscence, causes in-efficient fertilization. However, the JA treatment on this Arabidopsis mutant induces the phenotypes similar to the wild type and also helps in seed production. During the flower maturation process, except in stomium, accumulation of DDE1 have been observed in anther-filamental tissues, pistil and petals. From these observations, it is concluded that the process of dehiscence is controlled by the JA-signaling. Furthermore, the studies of Browse (2009d) on the Arabidopsis also predicted that JA induced and coordinated the filament elongation, stomium opening during anthesis as well as the production of functional pollens. Later, Mandaokar et al. (2006) did the transcription analysis and revealed that MYB21, MYB24 and other TFs (in total 13 TFs) are involved in the stamen maturation process. Avanci et al. (2010) showed that JA is responsible for the induction of TFs and stamen development.

15 JA in Growth Versus Defense

Apart from root inhibition, JA can reduce the growth of above-ground parts of the plants. The growth of a plant depends on a number of cellular activities such as cell cycle activity, ploidy dependent cell growth, cell division, cell expansion with the help of macromolecule synthesis, turgor pressure, cell wall elasticity and microtubule organization (Rymen and Sugimoto 2012). These cellular activities are governed by the phytohormones and also by the biotic and abiotic stresses. The unfavorable environmental conditions reduce the growth, while plant hormones such as auxin, GA and ethylene are capable of successfully rectifying the stress-induced loss (Murray et al. 2012; Petricka et al. 2012). JA is mainly associated with the mechanical and pathogenic/herbivorous wounding, these changes revert the plants from growth phase to defense phase (Zhang and Turner 2008). Internally synthesized JA (but not OPDA) has been reported to suppress mitotic division in *Arabidopsis* by influencing MYC2, JAZ or COI1, hence inhibiting plant growth. This clearly indicates the JA-mediated regulation of MYC2/JAZ/COI1 that leads the expression regulation of cell cycle genes (Pauwels et al. 2008). Similar observations are found in the case of *Medicago truncatula*, where mechano-stimulation by regularly touching leaves that give rise to high internal JA content concomitant with reduced growth (Tretner et al. 2008). Chehab et al. (2012) performed a similar experiment using Arabidopsis where they observed that touch-induced morphogenesis improves the resistivity of plants against B. cinerea in JA dependent manner. Analysis of mutants show that the JA also respond to thigmo-morphogenesis (Chehab et al. 2012). Contrary to the negative artifacts of JA and mechano-stimuation on plant longitudinal growth, Sehr et al. (2010) reported a boosting effect of mechano-activated MYC2/JAZ/COI1 during the secondary growth of plant in cambium formation. GA promoted the growth, hence reducing the activity of defense related genes. The inappropriate ratio of JA and GA is responsible for these antagonistic responses (Kazan and Manners 2012). When JA is not present, then GA promotes growth and defence containment; while in the absence of GA, the JA gives opposing responses. The GA-JA crass talk concludes the priority of JA in defence over the growth (D. L. Yang et al. 2012).

16 JA in Biotic Stress

Plants are natural dwellers and are prone to different kinds of environmental stresses. The environment is full of different microrganisms and other herbivores; sometimes these organisms behave as a threat to plants and damage the growth and development of plants. To overcome the biotic stress, hormonal regulatory system diverges its focus from growth to defense phase (Santino et al. 2013). The ethylene, salicylic acid (SA) and JAs generally function as primary defense signals. SA provides the systemic acquired resistance (SAR) against biotrophic pathogens (Durrant and Dong 2004), while ethylene and JAs give response to necrotrophs (Glazebrook 2005). However, this categorization is not rigid as several pathogens modifytheir pathogenic patterns during their life span.

16.1 Plant Response to Biotic Injury

Plants facing tissue injury show two types of responses i.e., local and systemic, JAs play a key role in managing these responses via signaling pathways. In local response, when tissue has been damaged, several attacker-derived and damage associated plant-derived signals are either physical or chemical in nature. These signals are identified by PRRs (pattern recognition receptors) situated on the cell surface. This signal identification by PPRs results in JA- and JA-Ile synthesis. JA-Ile resulted activation of SCF^{COI1}/26 proteasome degrades the JAZ proteins. These proteins suppress those TFs that participated in defense related traits. On the other side, the systemic responses are arbitrated by two distinctive pathways entailing JA. The cell-autonomous pathway is faster than the cell non-autonomous pathway. In the autonomous pathway, wounding induces the mobile signals (but not the JA) which start the biosynthesis of JA/JA-Ile and their consequent responses. On the other hand, in the cell non-autonomous pathway, leaf injury leads to JA production and its transportation in un-injured leaves where it generates JA responses in objective cells (Lalotra et al. 2020).

16.2 Plant JA to Insects

Signaling molecule JA respond to insect attack in a very specific manner. In Arabidopsis, attack of insect Pieris rapae initiates only one branch of down streaming JA signals controlled by MYC2 and this further activates the VEGETATIVE STORAGE PROTEIN2 (VSP2) gene. The necrotrophic pathogen attack induced ERF branch, was down-regulated with repression of marker gene PLANT DEFENSIN 1.2 (PDF1.2) and TF OCTADECANOID RESPONSIVE ARABIDOPSIS 59 (ORA59, Verhage et al. 2010). In jar1-1 (JA-Ile defective mutant) and myc2 mutants the MYC2 branch is repressed, this redirects the JA-dependent response to ERF branch against P. rapae (Verhage et al. 2011). Likewise, a series of experiments using jin1 and jar1 mutants showed high expression of ERF branch on P. rapae attack compared with Col-0 plants; this clearly indicates that MYC2 is the supreme branch for providing wouding-insect resistance in Arabidopsis (Verhage et al. 2010). Later, Verhagen and co-workers concluded that salivae of P. rapae elicited ERF branch which causes insect attractant secretion. An infestation of insects altered plant defense towards MYC2 branch and at the same time the ERF-controlled branch has been repressed. The under-ground parts of plant respond differently to the attackers; they can sense the attackers but actual mechanism is least understood (Erb et al. 2012a). It is well known about JA-mediation in insect-root interaction, but having low local JA level compared to systemic JA content found in the leaves makes some differences. High

JA levels in roots is connected as root can perceive other jasmonates (different to JA and JA-Ile) and can potentially modulate plant reaction to the wounding or insect actions (Erb et al. 2012a).

Apart from immediate response of plants to environmental cues, plants keep a memory of previously exposed biotic/abiotic stresses and this helps the plants to perform better in their second hazardous stress. This is commonly called priming, and is observed during the interaction of plant with pathogens (Pastor et al. 2013). Priming is mostly governed by SA mediated signals (Ahmad et al. 2011) whereas, JA and their conjugates are also reported as movable signals for providing long distance priming in plants having arthropod infestation (Frost et al. 2008). Engelberth et al. (2004) predicted that the priming is mediated through the GLVs. Later, in maize, with exposure of these volatiles showed high JA accumulation and subsequently more induction of the volatiles during wounding or caterpillar infestation (Frost et al. 2008). Priming is a multi-component horizontal phenomenon including several kinds of signaling pathways that depend on the type of stress to which plant is exposed (Pastor et al. 2013). In the SA-based priming, MAPKs and ROS participate as they are already active in defense processes against insects and sum-up with oxylipin accumulation and activation of JA-based signals. Further, Rasmann and co-workers (2012) also reported JA-mediated priming in insect-infested plants.

16.3 Plant JA to Pathogens

During plant pathogen interaction, JA may interact either synergistically or antagonistically with the SA (Durrant and Dong 2004). An interaction of rice with bacterium *Xanthomonas oryzae* pv. oryzae, MPK6 activation leads to SA and JA accumulation and then induction of JA and SA induce expression of responsive genes. In Arabidopsis, the infection of necrotrophic fungus Botrytis cinerea induces local resistance through SA and JA-based signaling (Ferrari et al. 2003). The systemic resistance is a quicker process, transient JA accumulation in the phloem exudates is essential for SAR initiation. In the case of *Pseudomonas syringae* avr Rpm 1, the systemic induction of genes responsible for JA-synthesis was activated before SA induction (Truman et al. 2007). JA can transmit information even at a long distance. In Arabidopsis, systematic MYC2 induction was found to repress the local-defense associated JA-responsive markers (Lorenzo et al. 2004). SA and JA work in tandem fashion; in which the JA induction is followed by SA-based defense response. Even sometimes, SA and JA amalgamate their action to defend a lone aggressor. For instance, plants infected with *Pseudomonas syringae* (hemi-biotrophic bacteria) cause SA-based defense induction; make plants more vulnerable to fungus *alternaria brassicola* by repressing the JA-signaling and is moderately reliant on NPR1 (NONEXPRESSOR OF PR GENES) genes. However, infection with a-virulent strain of *Pseudomonas* does not suppress the JA-based defense system (Spoel et al. 2007). The COI1 is considered as an essential component in JA-signaling for managing resistance against fungi and oomycetes (Adie et al. 2007). Ethylene is also supposed to sustain the JA-SA interaction. The contact of tomato to *Alternaria alternate* activates the pathways of ethylene and JA so they can perform synergistically. On the contrary, SA provides resistance to tomato tainted with Alternaria alternate f. sp. Lycopersici; meanwhile being antagonistic to ethylene signaling (Jia et al. 2013).

TFs are also the key players in developing immune response as large amount of genes are under transcriptional regulation. The ERF family members manipulate the expression of JA-responsive genes needed for pathogen defense. Mainly, ERF1, ERF2, ERF5, ERF6 and ORA59 impair with PDF1.2 expression, providing power to fight against *Alternaria brassicicola* and *Botrytis cinerea* i.e., against the necrotrophic fungi (Berrocal-Lobo et al. 2002; Brown et al. 2003; McGrath et al. 2005; Moffat et al. 2012) via ERF4 TF and mixing of JA and ethylene signals. VSP2 induction and PDF1.2 suppression are the two important functions of ERF4 (Memelink 2009). Interestingly, bZIP (basic leucine zipper) TFs of TGACC motif family are needed for the SAR establishment and arbitrated by hormone SA, and are also mandatory for stimulating ethylene and JA response for rectifying necrotrophic pathogens. It was observed that a triple i.e., tg2-tg5-tg6 mutant show no PDF1.2 expression during the infection of bacteria like *Pseudomonas syringae maculicola* ES4326 and *B. cinerea* (Zander et al. 2010). Here, ethylene signaling may be needed for TGA. TFs as the expression of PDF1.2 are not influenced by exogenous JA application (Ndamukong et al. 2007). One more TF, MYC2 is considered to be essential for JA (Lorenzo et al. 2004) and ABA signaling is capable of manupulating various genes responsive to the same hormones. In the nuclear region, MYC2 physically interacts with TIC (TIME FOR COFFEE) that subsequently inhibits root growth which is a MYC2 mediated JA responsive act and gives the resistance against Pseudomonas syrigae via off putting JA signaling which needs interaction with the MYC2. JA helps MYC2 to accumulate in a circadian manner. It was observed that the *P. syringae* infected Arabidopsis is more susceptible in the beginning as compared to the end of the cycle and the expression of MYC2 and JAZ5 genes is enhanced after exogenous JA treatment at starting of light cycle (Shin et al. 2012). COR, is a secretion of bacteria *P. syringae* pv tomato DC3000 and is also a phytotoxin that structurally mimics compound of JA-Ile (Fonseca et al. 2009). Their injection in host cells via type III effector system is done to repress the basal defense system. It is estimated that COR is 1,000 times more active than the JA-Ile (in vitro) and the same receptor is used to identify both compounds (Katsir et al. 2008). Uppalapati et al. (2007) demonstrated the COR contribution in virulence by reducing SA gathering through COI1 activation. However, in Arabidopsis the COR is reported to suppress both SA-dependent as well as SA-independent defense reactions (Geng et al. 2012). COR mediates the re-opening of stomata; hence supporting bacterial propagation via suppressing SA accumulation (Zheng et al. 2012).

The crass-talk of phytohormones furthers reveals the various aspects of plant growth and pathogen response (Kazan and Manners 2012). During the GA-JA crosstalk, protein DELLAs (GROWTH REPRESSOR of GAs) fight to MYC2 for JAZs binding, and likewise JAZ can fight for DELLA such as PHYTOCHROME INTERACTING FACTORs (PIF3, PIF4). Therefore, balance between JAZ-DELLA proteins is found to be participating in both, growth inhibition during pathogen infestation or defense repression when hazard of pathogen has been defeated (Navarro et al. 2008). Not only GA, but also ABA cross-talk with JA participated in pathogen-mediated defense in plants (Lackman et al. 2011).

17 Concluding Remarks and Future Prospective

JA is a plant hormone that is present diversely in the plant kingdom and plays a significant role in modulating plants physiological and metabolic responses under healthy and stressful biotic environment. This chapter gives a better understanding of JA occurrence in several plant parts and organs. This chapter further emphasized on JA biosynthesis and its regulation in several cellular compartments like chloroplast, cytoplasm and peroxisome. Furthermore, recent investigations on JA signaling are also explored. Particularly, a couple of genes/TF are engaged in regulating JA-synthesis. Signaling of JA involves suppression of a range of TFs, degradation of JAZ and also the transcriptional activation. MYCs share a critical job in arbitrating JAs responses, but the other JAZ-interrelating TFs give specificity and complexity to signaling outputs. JA remarkably emerges to be a novel hormone in increasing germination, root growth depletion, senescence, reproduction and tuberization. A major part of the chapter occupies role of JA in ameliorating biotic stresses via insects and pathogens and facilitating plant growth, development, cellular and metabolic responses. JAs mainly come in the role when a plant is in danger or when it has to alter physio-biochemistry. JA and oxypolins play a crucial role in providing resistance against a great amount of (a)biotic stresses. Apart from these compounds, several other components (such as phytohormones and induced TFs) also work in a co-ordinated way, participate and cross-talk with one another to mitigate wound/herbivory-induced damages.

During the course of time, accumulation of data by advanced techniques such as transcriptomic, proteomic, metabolomic and lipidomic help us to more clearly understand the JA-induced adjustments in plant life. However, some points are still required to be evaluated deeply and these are; revising protein interaction and gene activation/suppression during JA-based signaling that involves numerous TFs including JAZs. The crosstalks between JA and its derivatives with other phtyohormones including GA, auxin, ABA or SA; that may explore involvement of several other genes/proteins in JA-mediated responses. The JA-mediated translation/post translation control system (for ex-phosphorylation) could be explored.

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The Crucial Role of Jasmonates in Enhancing Heavy Metals Tolerance in Plants

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Abstract Climate change is the leading cause of crop yield losses worldwide. Recent progression in plant biology and ground-breaking molecular and biochemical procedures have increased our understanding of phytohormonal signaling in response to numerous abiotic stresses, including heavy metals (HMs) toxicity in plants. HMs toxicity owns numerous harmful effects on plant health, including growth inhibition, reduction in biomass production, leaves chlorosis, imbalance of nutrients, and water contents, ultimately causing leaf senescence and plant death. Jasmonates (JAs) are naturally occurring lipid-derived hormones that normalize global plant growth and development under HMs toxicity. Notably, JAs as vital growth controllers are involved in numerous physiological, biochemical, and molecular mechanisms in plants. JAs alone or occasionally in grouping with other phytohormones upgrade the stress tolerance system in plants. As a whole, JAs can secure plants from the harmful effects of HMs toxicity through the up-regulation of JA-associated gene expression and several physiological and biochemical mechanisms. Moreover, JAs can uphold the veracity of plant cells in response to different HMs by increasing the antioxidant defense systems and biosynthesis of some osmoprotectants. In this chapter, we have discussed the JA biosynthesis and metabolisms, its beneficial role in response

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to several HMs, its crucial role as antioxidant defense, and its cross-talk with other phytohormones have been explained.

1 Introduction

Plants cultivate in a changing climate that implements several environmental stresses, including heavy metals (HMs) toxicity, and the discrepancy of these stresses can hamper the standard physiological, biochemical, and molecular mechanisms (Raza et al. 2019a, 2020a, b; Raza 2020). Over the past few decades, fast-increasing industrial modernization and progress, modern agricultural operations, human activities, fiery, and throwing away fossil fuels, which have augmented the verge level of several HMs in the plant, soil, and water environment that triggering harmfulness to several living organisms (Hasanuzzaman et al. 2020a; Raza et al. 2020c, 2021).

Heavy metals cause several harmful effects on plants, including growth inhibition, reduction in biomass production, leaves chlorosis, imbalance of nutrients, and water contents, ultimately causing plant senescence (Raza et al. 2021; Rai et al. 2019). Nevertheless, apart from the harmful effects of HMs on plants, still HMs well-thought-out as an immense caution to human health because of their continued retentiveness in the environment (Mao et al. 2019; Rai et al. 2019; Raza et al. 2021). Henceforward, Fig. 1 demonstrating numerous possible direct and indirect effects of HMs on crop plants, which finally condensed the plant's overall productivity. Moreover, plants rising in polluted soils buildup high absorption of HMs, triggering their entry into the food system, ensuing in sign of numerous diseases (Mao et al. 2019; Rai et al. 2019; Adimalla 2020; Raza et al. 2021). Plants have multipurpose HM transport arrangements that transfer and collect the HMs inside the plant's body. Plant protein family ATP-binding cassette (ABS) elaborated in ion movement henceforth, its appearance can be altered to improve the conversion of HM ions (Zhang et al. 2020; Raza et al. 2021).

Heavy metals can interrupt gene expression, biosynthesis of diverse proteins and secondary metabolites, adjustments in hormonal signaling, and antioxidant defense activities (Raza et al. 2020c; Raza 2020; Hasanuzzaman et al. 2020a, b). Antioxidant enzymes and phytohormones play an essential role in defining the plant's gene expression at the molecular level, considered as a critical mechanism amongst other physiological progress (Hasanuzzaman et al. 2020b; Raza et al. 2019b). As a signaling molecule, phytohormones regulate the numerous plant responses under stressful environments (Raza et al. 2019a, b). Among different phytohormones, jasmonates or jasmonic acid (JA) is one of the best-investigated hormones. Jasmonates as endogenous signaling molecules are included in numerous evolving procedures and were formerly recognized as stress-related hormones in higher plants (Wasternack and Xie 2010; Wasternack and Strnad 2018). In plants, JA is elaborated on evolving purposes and triggers the defense responses against multiple abiotic stresses, including HMs (Raza et al. 2020d). In contrast, exogenous JA and methyl jasmonate (MeJA) have

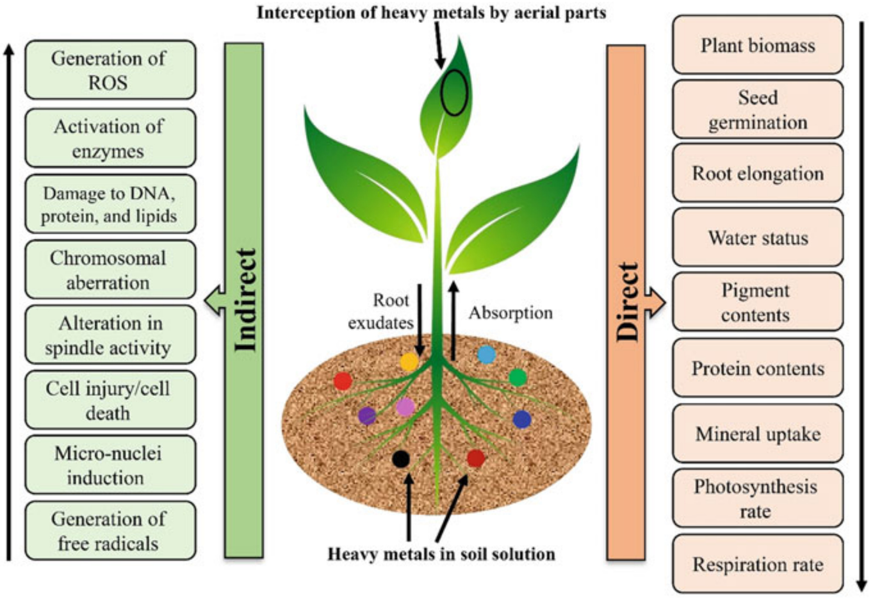

Fig. 1 Some probable direct and indirect effects of heavy metals on plants, which eventually reduced plant productivity. The upward arrow means to increase, and the downward arrow means a decrease. Adapted and modified from Raza et al. (2021a) with permission from Elsevier

been described to advance the antioxidant defense activities under HM toxicity (Raza et al. 2020d; Dai et al. 2020; Sarabandi et al. 2019). Therefore, this chapter underlined JA's vital role under HM toxicity for enhancing HM tolerance in plants. Additionally, JA-mediated antioxidant defense system and cross-talk with other phytohormones have been explained in several plant species.

2 Jasmonates Biosynthesis and Metabolism

Over the past decades, JA biosynthesis has been well categorized in several monocotyledonous and dicotyledonous plant species (Wasternack and Hause 2013; Huang et al. 2017; Ruan et al. 2019). In general, JAs are biosynthesized through the frequent success of numerous enzymes present in the chloroplast, peroxisome, and cytosol (Fig. 2) (Feussner and Wasternack 2002). Numerous environmental stresses, including HM toxicity, trigger phospholipases in the plastid membrane, helping the amalgamation of α-linolenic acid (α-LeA) in the plant (Wasternack and Hause 2013; Hou et al. 2016). Whereas, α-LeA, which acts as a precursor during the JA biosynthesis procedure, is changed to 12-oxo-phytodienoic acid (12-oxo-PDA) by oxygenation with lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase

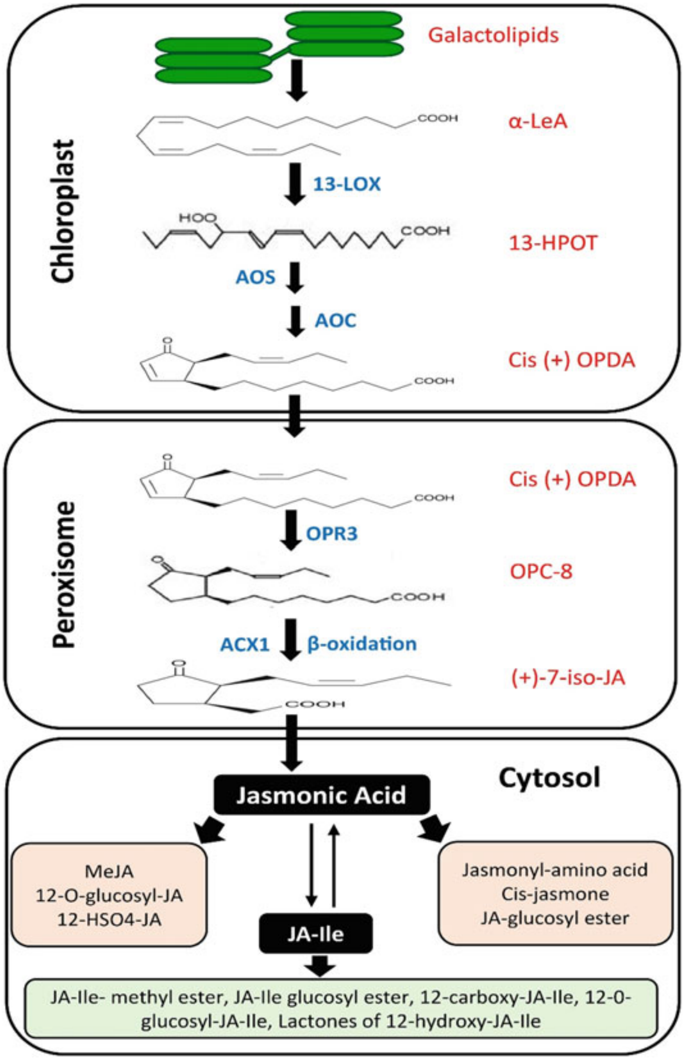

Fig. 2 Step-wise illustration of JAs biosynthesis and metabolism in plants. For more detail, read the text and review article published by Raza et al. (2020d). Adapted and modified from Raza et al. (2020d) with permission from Springer Nature

(AOC). JA is at that point produced from 12-oxo-PDA through the movement of 12-oxo-phytodienoic acid reductase (OPR) and 3 series of ß-oxidation. Consequently, the JA biosynthesis way is recognized as the octadecanoid pathways (Hou et al. 2016; Han 2017; Ruan et al. 2019).

The JA metabolic pathway changes the phytohormone into > 30 separate vigorous and indolent byproducts in the cytosol in the cytosol, reliant on the carboxylic acid group's chemical alteration pentenyl side chain and the pentanone ring (Wasternack and Strnad 2016). Amongst various metabolites, freely available JA, cis-jasmone, JA-Ile, and MeJA are well-thought-out to be the key types of bioactive JA in plant species (Fonseca et al. 2009; Wasternack and Hause 2013). However, cis-jasmone is formed by the decarboxylation of JA (Dąbrowska and Boland 2007; Matsui et al. 2019). The unpredictable MeJA is formed from JA by JA carboxyl methyltransferase (Li et al. 2018b). Moreover, JA-amino acid synthetase 1 (JAR1) catalyzes the changeable alteration among JA and JA-Ile (Fonseca et al. 2009). Findings recommend that JA-Ile is a vital molecule in the JA signaling pathway (Wasternack and Song 2017; Wasternack and Strnad 2018).

3 The Interplay of Jasmonates for Enhancing Heavy Metals Tolerance

Due to the known toxic impacts and high accumulation in several food crop plants, HMs have worldwide seemed like a matter of main fear (Raza et al. 2020c, 2021; Hasanuzzaman et al. 2020a). JA signaling pathways and plant physiological, biochemical, molecular, cellular, and metabolic influences have been described, which relate to plants grown under HM toxicity (Table 1). In the subsequent sections, we have re-reviewed JA's beneficial role in enhancing HM tolerance in several plant species (Table 1).

3.1 Cadmium Toxicity

Cadmium (Cd) has severe detrimental effects on plants like an imbalance of essential plant nutrients, chloroplast destruction, inhibition of photosynthetic pigments, and membrane damage (Raza et al. 2020c). Recently, 25 μmol L^{-1} JA was observed as a 'stress-ameliorating molecule' by improving the rapeseed plant's tolerance towards Cd toxicity. JA lowers the Cd uptake in leaves, reducing membrane damage and malondialdehyde (MDA) content, and improving the uptake of essential nutrients (Ali et al. 2018). Exogenous application of MeJA alleviates the Cd generated leaves chlorosis by lowering the Cd levels in the shoot, root cell sap, and decreasing the *AtIRT1*, *AtHMA2*, and *AtHMA4* gene expression and promoting the Cd uptake as well as long-distance translocation (Lei et al. 2020).

Under Cd-stress, MeJA effects on maize seedlings growth have been investigated. It was found that exogenous MeJA application induced the polyamines (PAs) accumulation and partially alleviated the Cd-generated inhibition of plant growth (Yan et al. 2020). In Cd-stress, spermidine (spd)- and MeJA-treated plant leaves contained low Cd than plant leaves not treated with spd or MeJA. Further, with the addition of spd synthesis inhibitor dicyclohexylamine and MeJA, Cd levels in leaves were

Table 1 A description of some recent discoveries on JA-mediated heavy metals stresses responses and tolerance in several plant species

Studied plant	Stress condition	Type and dose of JA	Beneficial outcomes	References
Cadmium				
Mentha arvensis	150 mg kg^{-1} $CdCl_2$; 30 d	1 μM MeJA	MeJA alleviates the Cd stress by regulating the ROS detoxification and physio-biochemical damages	Zaid and Mohammad (2018)
Brassica juncea	0 μM Cd; 15 d	0, 5, 10, and 20 μM MeJA	MeJA alleviates the Cd-induced photosynthetic destruction by increasing S-assimilation and glutathione production in mustard	Per et al. (2016)
Vicia faba	150 mg L^{-1} $CdSO_4.8H_2O$; 14 d	0.01 mM JA	JA alleviates the negative effects of Cd stress in faba beans plants by inhibiting the Cd, H_2O_2, and MDA and increasing the osmolyte and antioxidant activities that lower oxidative stress	Ahmad et al. (2017)

(continued)

Table 1 (continued)

Studied plant	Stress condition	Type and dose of JA	Beneficial outcomes	References
Copper				
Medicago sativa	100 µM Cu; 3 weeks	1, 5, or 10 mM JA	Alfalfa growth and biomass stressed by Cu relieved by JA. The antioxidant enzyme activities, MDA, Chl, and H_2O_2 levels increased accordingly with JA	Dai et al. (2020)
Phaseolus coccineus	50 µM $CuSO_4.5H_2O$; 5 h	10 µM MeJA	MeJA showed a time-dependent response to antioxidative enzyme activity In a long-term experiment, it elevated the concentration of anthocyanins mediating the Cu toxicity and ROS production	Hanaka et al. (2016)
Cajanus cajan	5 mM Cu; 12 d	1 µM, 1 nM, and 1 pM JA	Seed priming with JA help in alleviating the toxic effect of Cu^{2+}	Poonam et al. (2013)
Arsenic				
Oryza sativa	25 µM AsIII; 2 weeks	0.25 µM MeJA	MeJA provides tolerance to As and attenuates the damage caused by AsIII. MeJA alters the expression of AsIII transporters and promotes As detoxification by *OsNRAMP1*	Verma et al. (2020)

(continued)

Table 1 (continued)

Studied plant	Stress condition	Type and dose of JA	Beneficial outcomes	References
B. napus	0, 200 µM As; 14 d	0, 0.1, and 1 µM MeJA	MeJA enhanced the redox states of AsA and GSH and related enzymes. MeJA has a role in As-generated oxidative damage mitigation through AsA and GSH redox states' regulation by lowering As uptake	Farooq et al. (2018a)
Oryza sativa	0, 25, and 50 µM As; 65 d	0, 0.5, and 1 µM MeJA	MeJA improved the growth and yield of rice verities under As stress by alleviating the oxidative stress by improving antioxidant enzymes and the AsA-GSH cycle, lowering accumulation via modulating As transporters	Mousavi et al. (2020)
Boron				
Puccinellia tenuiflora	250 mg L^{-1} B; 2 weeks	0.1–1.0 mM JA	JA has an alleviatory effect on the germination inhibition caused by excess B. JA can help plants tolerate high B levels at both germination and seedling stages	Zhao et al. (2019)
Artemisia annua	0, 1, and 2 mM H_3BO_3; 60 d	300 µM MeJA	MeJA enhanced plant growth and photosynthetic efficiency, reduced the amount of lipid peroxidation, induced the synthesis of antioxidant enzymes, and improved the content and yield of artemisinin	Aftab et al. (2011)

(continued)

Table 1 (continued)

Studied plant	Stress condition	Type and dose of JA	Beneficial outcomes	References
Vitis vinifera	0, 10, and 20 mg B kg^{-1} soil; 48 h	0, and 100 μM MeJA	MeJA increased the antioxidant capacity and lowered the *VvBOR1* gene expression	Sarabandi et al. (2019)
Nickel				
Alyssum inflatum	0, 100, 200, and 400 μM Ni; 21 d	0, 5, and 10 μM JA	JA alleviates the Ni-induced oxidative effects by lowering H_2O_2 contents. Further JA treatment reversed the Ni detrimental effects on carotenoid content and decreased proline content in Ni exposed plants	Kakavand et al. (2019)
Zea mays	$NiSO_4.6H_2O$ 8 mM; 22 d	10–6, 10–8, and 10–10 M JA	Ni reduced the plant growth, but JA's co-application alleviated the Ni induced effects through antioxidant enzyme activities, biomass production, and protein content	Azeem (2018)
Glycine max	2 mM $NiCl_2.6H_2O$; 15 d	1 nM JA	Prevented the photo-inhibition and oxidative burst in plants by modulating compatible solute and antioxidant gene expression. JA co-application with Ni enhanced dry weight by 11.47%, 30.74% shoot length, and 70.06% root length than control plants	Sirhindi et al. (2016)
Daphne jasminea	0.05, 0.1, 0.5, and 1.0 mM $NiSO_4$; 8 weeks	0.5 μM	Exogenously provided JA to enhance Ni tolerance or improve metal toxicity in *D. jasminea*. JA ameliorates the plant growth and induces the defense system under unfavorable conditions	Wiszniewska et al. (2018)

(continued)

Table 1 (continued)

Studied plant	Stress condition	Type and dose of JA	Beneficial outcomes	References
Glycine max	4 mM $NiCl_2$; 4–8 d	1 pM JA	JA increased soybean Ni tolerance by regulating Ni uptake and accumulation and lowers Ni-induced membrane damage by reducing ROS levels, MDA, lipoxygenase activity, and electrolyte leakage	Mir et al. (2018)
Lead				
Lycopersicon esculentum	0, 0.25, 0.50, and 0.75 mM $Pb(NO_3)_2$; 30, 45, and 60 d	0, 0.01, 1, and 100 nM JA	JA treatment increased the roots and shoot length, carotenoid and Chl contents, improved gaseous exchange traits, and enhanced several antioxidant defense enzymes' activities. It also increases the contents of metal-chelating elements and osmolyte under Pb-toxicity	Bali et al. (2018)
Lycopersicon esculentum	0.25, 0.50, and 0.75 mM Pb; 15 d	100 nM JA	JA treatment modulated the concentrations of photosynthetic pigments, osmolytes, secondary metabolites, organic acids, metal ligation elements, and polyamine storage in response to Pb toxicity	Bali et al. (2019b)
Lycopersicon esculentum	0.25, 0.50, and 0.75 mM Pb; 15 d	100 nM JA	JA application reduced the Pb uptake and improved the growth; it also lessened the oxidative injury by dropping the expression of the RBO and P-type ATPase transporter genes and by modifying the activities of antioxidative defense enzymes	Bali et al. (2019a)

found higher compared to alone Cd-treatment. These findings suggest that spd has a vital role in JA-mediated improved Cd tolerance in maize seedlings by limiting Cd-transport from roots to leaves (Yan et al. 2020). Exposure of *Mentha arvensis* (mentholmint) plants to Cd stress resulted in enhanced endogenous root and leaf Cd content by 83.05% and 67.10%, respectively, 67.26% electrolyte leakage, 56.66% hydrogen peroxide (H_2O_2), and 53.97% MDA content compared to control plants. Notably, 1 μM MeJA supplementation to Cd-stressed plants moderately relieved the Cd-generated oxidative stress, while co-application of MeJA with nitrogen reversed the unfavorable effects (Zaid and Mohammad 2018).

Another study revealed that JA has an essential role in alleviating Cd stress in faba bean, improving the biomass yield and plant growth. JA consequently increased the chlorophyll (Chl) synthesis by lowering Cd-uptake by plants that formerly might have come from destruction or down-regulation of Chl biosynthesis enzymes. JA supplementation is also linked with the osmolyte production and enzyme antioxidant, which delivered resistance towards metal stress (Ahmad et al. 2017). Before Cd exposure, exogenous application of methyl-β-cyclodextrin (CD) and MeJA improve the *Arachis hypogaea's* hairy root culture that adversely affects Cd toxicity. After elicitation of 24 h, genes that encode main enzymes in phenylpropanoid biosynthesis pathway up-regulated to 3.2- and 5.4-fold, inducing stilbene production and pathogenesis-related (PR) genes expression. During prolonged Cd exposure, non-enzymatic antioxidants alleviated Cd stress (Pilaisangsuree et al. 2020). In rapeseed, oxidative stress was minimized by MeJA through the induction of the expression of genes encoding antioxidants and secondary metabolites. Therefore, the exogenous application of MeJA effectively alleviates HM damage by increasing antioxidative enzyme activities and secondary metabolites (Ali and Baek 2020). Some other examples have been briefly explained in Table 1.

3.2 Nickel Toxicity

Soil contaminated with nickel (Ni) is a persistent threat to crop production globally (Shahzad et al. 2018). Studies revealed that soybean seeds priming with JA considerably enhanced the soybean growth performance upon exposure to excessive Ni. The increased soybean Ni resistance resulting from JA could be credited to its ability to regulate the uptake and accumulation of Ni and lower the Ni-produced membrane damage, as shown by ROS levels lipoxygenase activity, MDA, and electrolyte leakage (Mir et al. 2018). Wiszniewska et al. (2018) studied the Ni-accumulation and toxicity in *Daphne jasminea* shoots in *in-vitro* culture with/without exogenous phytohormone supplementation, i.e., GA3, JA, and BL. Exogenously applied phytohormones differentially controlled the plant response by activating numerous defense pathways. Exogenous JA-induced active auxins and salicylic acid, contributing to improved mitotic activity in plants. These results suggest that phytohormones may improve Ni tolerance (Wiszniewska et al. 2018).

Under Ni stress, the JA effect on soybean physio-biochemical attributes, gene expression, and antioxidant enzyme activities have been evaluated (Sirhindi et al. 2016). As compared to control, Ni lowers the root and shoot length and Chl content by 37.23, 38.31, and 39.21%, respectively. JA application was found to improve the root and shoot length and Chl content of Ni fed seedlings. Further, JA supplementation lowers NADPH oxidase, H_2O_2, and MDA buildup, increasing ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) by 28.22, 40.04, 48.53, and 56.79%, respectively than control. Therefore, JA co-application helps soybean seedlings to combat the destructive effects of Ni by increased osmolytes, antioxidant enzyme activities, and gene expression (Sirhindi et al. 2016).

In another study, Azeem (2018) studied the effects of JA and Ni on the growth and antioxidant enzyme activities in maize plants. After giving pre-sowing treatment of $NiSO_46H_2O$ (8 mM), JA (10–6, 10–8 and 10–10 M) alone and JA (10–6, 10–8 and 10–10 M) in 1:1 combination with $NiSO_46H_2O$ (8 mM), maize seeds were sown in the field environment. The findings displayed reduced plant growth with Ni, but JA co-application alleviated the adverse Ni effects through the up-regulation of several antioxidant enzyme activities (Azeem 2018). Additionally, morphological, biochemical, and physiological changes in *Alyssum inflatum* Nyar have been assessed upon exposure to various concentrations of Ni (0, 100, 200, and 400 μM), SA (0, 50, and 200 μM), and JA (0, 5, and 10 μM). Results revealed that JA and SA treatment alleviated the adverse effects of Ni on carotenoid content and lowered the proline content in plants under Ni stress. These findings suggest that JA and SA confer Ni tolerance in *A. inflatum* by various mechanisms (Kakavand et al. 2019). Some other examples have been briefly explained in Table 1.

3.3 Arsenic Toxicity

Arsenic (As) is naturally found in the environment, considered a toxic metalloid for living things. Arsenic accumulation by plants triggers various adverse effects like protein function disruption (Li et al. 2018a; Vithanage et al. 2017). Recently, Coelho et al. (2020) examined exogenous JA's role in modulating As-generated oxidative stress in *Lemna valdiviana*. Plants were grown in a solution having As (4.0 mg L^{-1}) or As + JA (50, 100, 250, and 500 μM) for 24 h. Under As-stress, Chl-a/Chl-b content lowered, either with/without JA. In As exposed plants, the decreased Chl-a/Chl-b ratio recovered by 100 μM JA treatment. JA modulates the ROS homeostasis, pigment balance, antioxidant defense system, and letting high accumulation without showing significant damage (Coelho et al. 2020). In rice, exogenous MeJA alleviates the As toxicity through modulating As uptake and accumulation. 25 μM arsenite (AsIII) stress hampered the overall rice seedlings' growth and development. Interestingly, 25 μM AsIII + 0.25 μM MeJA co-application resulted in enhanced biomass, Chl content, increased antioxidant enzyme activities than AsIII treated plants. The co-application also modulated the genes expression intricate in downstream JA signaling mechanism, translocation, AsIII uptake, and detoxification that showed the possible adaptive response of rice seedlings to handle As stress (Verma et al. 2020).

Moreover, Mousavi et al. (2020) have studied the effects of 0, 0.5, and 1 μM MeJA on the biochemical, molecular traits, and yield of rice verities in 0, 25, 50 μM As treatments. Results suggest that As lowered the Chl content, biomass, and Chl fluorescence; while, MeJA enhanced the photosynthetic pigments as well as plant growth. MeJA improved the production of two rice verities in As toxicity by alleviating oxidative stress by improving the antioxidant enzyme activities and lowering accumulation via modulating the As transporters (Mousavi et al. 2020). Three doses of MeJA 0, 0.1, and 1 μM and two As levels 0, and 200 μM treatment were studied in rapeseed. Arsenic stress decreased the root growth by oxidative damage and increased ROS and lipid peroxidation. MeJA treatment lessened the H_2O_2 and $O_2.^-$ contents in roots and have high antioxidant enzyme activities. These results advise MeJA's role in alleviating the As-produced oxidative destruction by regulating AsA and GSH redox states and by dropping As uptake in both cultivars (Farooq et al. 2018a). In another study, rapeseed plants upon exposure to 200 μM As resulted in inhibited growth, high lipid peroxidation, and disrupted cellular ultra-structures. Exogenous MeJA application relieved the As induced oxidative stress and improved photosynthesis and plant growth (Farooq et al. 2018b). JA supplementation has reduced the destructive As stress effects on canola and lowered the ROS and lipid peroxidation (Farhangi-Abriz and Ghassemi-Golezani 2019). Some other examples have been briefly explained in Table 1.

3.4 Boron Toxicity

Boron (B) poses a severe threat to the plant's growth and development in both arid and semi-arid areas (Hua et al. 2020). JA improves the plant capacity to survive under harsh environments. Effect of exogenously supplied MeJA (0, and 100 μM) on the gene expression and biochemical response of two grape cultivars have been investigated under B toxicity 0, 10, and 20 mg kg^{-1} soil. Under B stress, 100 μM MeJA supplementation increased SOD activities, phenylalanine ammonia lyase, and CAT; lowered MDA and proline levels. Besides, MeJA increased grape leaves' antioxidant enzyme activities and decreased the *VvBOR1* gene expression (Sarabandi et al. 2019). B-generated toxicity causes an inhibitory effect in *Artemisia annua*, an essential artemisinin source, an antimalarial drug. Exogenous MeJA treatment was tested to alleviate the toxic B-induced impact and improve plant utility. The finding suggests that MeJA increased the antioxidant enzyme activities, plant growth, photosynthetic activity, and lowered lipid peroxidation by the ROS scavenging system (Aftab et al. 2011).

Moreover, MeJA considerably dropped the B toxicity in *A. annua* plants by increasing the antioxidant activities (Farhangi-Abriz and Ghassemi-Golezani 2019). Under 300 mg L^{-1} B stress and JA treatment, *P. tenuiflora* seeds germinated in Petri dishes. At 0.1- and 1.0-mM JA treatment, *P. tenuiflora* seedlings were grown under B

(250 mg L^{-1}) stress. The results showed that JA has a relieving effect on germination inhibition induced by excess B. Thus, exogenous JA supplementation helps plants cope with high B levels at both germination and seedling phases, indicating JA is a *P. tenuiflora* growth regulator under surplus B toxicity (Zhao et al. 2019). MeJA mitigated B toxicity in the sweet wormwood (*A. annua*) by reducing lipid peroxidation and stimulating antioxidative enzymes' synthesis (Ali and Baek 2020). Some other examples have been briefly explained in Table 1.

3.5 Copper Toxicity

Copper (Cu) is a vital element for plants and humans when available in minor quantities, while in extreme quantities, it employs damaging effects (Kumar et al. 2020). JA being an essential phytohormone involved in the regulation of Cu accumulation by plants. In a recent study, 1, 5, and 10 mM JA and Cu addition, Cu levels in the leaves and roots of alfalfa were found expressively lowered to some points than without JA treatment. In the treatment of JA additions, leaves, and roots, alfalfa biomass was increased significantly than Cu-stressed plants. Likewise, antioxidant enzyme activities, H_2O_2, MDA, and Chl contents were upgraded accordingly (Dai et al. 2020). JA provides self-defense against Cu's effects by activating the osmolyte proline accumulation and antioxidant enzymes like SOD and POX (Yu et al. 2019). Poonam et al. (2013) studied the effects of exogenous JA at seed levels that transduce throughout the seedling growth and regulate the antioxidant enzyme activities like guaiacol peroxidase and SOD in 12 days old pigeon pea seedlings with and without Cu. After seed priming with JA, the POD and SOD activities increased considerably in Cu's presence (Poonam et al. 2013).

On the other hand, MeJA and MeJA + Cu displayed a time plus organ dependent effect on antioxidant enzymes' activity. MeJA enhanced the anthocyanins and MDA levels in leaves from a long-term experiment. MeJA and MeJA + Cu did not amend the homoglutathione and proline content. After five days of Cu-incubation, MeJA triggered the tartrate and malate accumulation in roots. Thus, MeJA has an essential role in modifying plant response in a Cu-stressed environment (Hanaka et al. 2016). Combined toxicity of Cd and Cu was studied in *Avicennia marina* seedlings. The effects of exogenously applied JA were investigated on the lipid peroxidation, Chl contents, antioxidant capacity, Cu and Cd uptake, JA concentration type-2 metallothionein gene (*AmMT2*) expression. Low-dose of Cd 9 μmol L^{-1} and high-dose of Cu 900 μmol L^{-1} given to plants directed by the significant augmentation in leaf MDA and leaf Chl reduction. This combined metal toxicity alleviated by exogenous application of 1 μmol L^{-1} JA and MDA plus Chl content restored compared to control. Notably, 1 and 10 μmol L^{-1} JA significantly increased the activity of APX (Yan et al. 2015a). Some other examples have been briefly explained in Table 1.

3.6 Lead Toxicity

In contrast to other HMs, lead (Pb) is considered the second most lethal HMs after As, which badly affects the plant growth and developmental processes and has no contribution to biological systems (Zulfiqar et al. 2019). A recent study was performed to examine JA's beneficial role in tomato plants under Pb toxicity (0, 0.25, 0.50, and 0.75 mM) (Bali et al. 2018). They detected a reduction in shoot and root lengths with experience to Pb stress. In contrast, JA treatment amended the shoot and root lengths in the Pb-treated tomato plants. The Pb intake was augmented with Pb's increasing levels; nevertheless, JA treatment decreased the Pb intake. Overall, JA supplementation improves several processes such as increased carotenoid and Chl contents, improved gaseous exchange traits, enhanced the activities of several antioxidant defense enzymes involved in the AsA-GSH cycle. Moreover, JA treatment also increases the contents of metal-chelating elements and osmolytes under Pb-toxicity and helps plants cope with Pb toxicity (Bali et al. 2018).

In another study, 100 nM JA enhanced Chl contents by dropping chlorophyllase expression under Pb toxicity in tomato plants. At the same time, Pb treatment reduced pigment content, RWC, and HM tolerance catalog. Findings suggest that JA treatment minimize the toxic effect of Pb by modulating the concentrations of photosynthetic pigments, osmolytes, secondary metabolites, organic acids, metal ligation elements, and polyamine storage in JA-treated tomato plants (Bali et al. 2019b). The same authors extended their work on the protective role of JA (100 nM) under Pb (0.25, 0.50, and 0.75 mM) toxicity in tomato plants (Bali et al. 2019a). Results suggest that the JA application reduced the Pb uptake and improved the tomato growth under Pb. Furthermore, JA lessened the oxidative injury by dropping the expression of the RBO and P-type ATPase transporter genes and modifying antioxidative defense enzymes (Bali et al. 2019a). In *Brassica juncea*, JA application improved the plant growth under Pb stress. JA also certainly normalizes the photosynthesis, AsA-GSH cycle, and phytochelatins compounds (Agnihotri and Seth 2020). The combined application of JA, SA, and proline improved plant growth, persuaded pigment production, reduced electrolyte leakage, MDA content, and Pb level in maize plants. Their combined effect improved the proline and total soluble sugar accumulation and the activities of GSH, AsA, SOD, CAT, POD, and phenol, thus helping plants to withstand Pb toxicity (Sofy et al. 2020). Some other examples have been briefly explained in Table 1.

3.7 Aluminum Toxicity

Aluminum (Al) harmfulness in acid soils is a noteworthy restriction to crop invention globally (Kochian et al. 2015). The harmful effect of Al seems initially in roots, hindering their cell separation and growth. This stops water and nutrient captivation, vital for the cellular and plant metabolisms, which reduces plant quality and production (Kochian et al. 2015). The protective role of MeJA under Al toxicity has been evaluated in highbush blueberry cultivars [Legacy (Al-resistant) and Bluegold (Al-sensitive)] cultivars (Ulloa-Inostroza et al. 2019). Results show that Al toxicity augmented the Al level (15-fold) and oxidative injury (5.5-fold) than control plants. The photosynthetic routine was sturdily condensed in the Al-sensitive cultivar, whereas the Al-resistant cultivar was extra steady throughout the research. Nevertheless, with experience in Al + MeJA, the Al-gathering and oxidative injury was remarkably reduced by augmenting the antioxidant enzyme activities such as SOD and CAT. The MeJA treatment reduced Al storage and modulated the antioxidant defense pathways, minimizing Al toxicity's negative effects (Ulloa-Inostroza et al. 2019). In another study, JA improved Al-induced root growth reduction in Al-stressed tomato plants. Further, Al-induced the transcript level of genes (*WRKY* and *ALMT*) linked with the JA biosynthesis and signaling under stress conditions (Wang et al. 2020b). The *WRKY* genes act as controllers of Al-activated malate transporter (ALMT) proteins by straight attaching to their promoters and varying malate efflux, thus modifying Al ion harmfulness in tomato plant roots (Wang et al. 2020b).

4 Potential of JA-Mediated Antioxidant Defense for Heavy Metal Tolerance

Jasmonates can excellently improve the plant stress resistance to HMs by increasing the antioxidant defense systems (Fig. 3; Table 2) (Raza et al. 2020d; 2021b). For instance, tomato plants treated with 40 mg dm^{-3} Cd and 0.1 μM MeJA restored the R/S ratio and lowered the Cd translocation and accumulation in both roots and shoots. MeJA treatment also increased the proline and glutathione (GSH) content and activities of POD and SOD than control plants (Yan et al. 2015b). After seven days, the treatment of *C. frutescens* with 50 mg L^{-1} Cd resulted in reduced root dry weight and Chl b concentrations. However, 0.1 μmol L^{-1} low MeJA concentrations renovated the Chl b and root growth in seedling suppressed by 50 mg L^{-1} Cd. Low MeJA supplementation also enhanced the POD and CAT activities, while high exogenous MeJA levels improved the POD, APX, and SOD activities and inhibited the CAT activities (Yan et al. 2013). Exogenous MeJA alleviated the Cd-induced oxidative stress by increasing antioxidant enzyme activities like POD, CAT, and SOD and non-enzymatic antioxidant contents GSH and AsA (Zhao et al. 2016).

Moreover, HMs toxic effects counteracted through JA mediated osmolytes accumulation and carotenoids plus enhanced antioxidant enzyme activities. JAs provides self-defense against Cu stress by stimulating the osmolyte proline accumulation and antioxidant enzymes like SOD and POX (Poonam et al. 2013). *Phaseolus coccineus* treatment with 50 μM $CuSO_4.5H_2O$ for five days, MeJA inhibited the POX activity in leaves and decreased the roots' CAT and SOD activities. Thus, MeJA effectively alters the antioxidant enzyme activities and metabolites accumulation under non-stress and

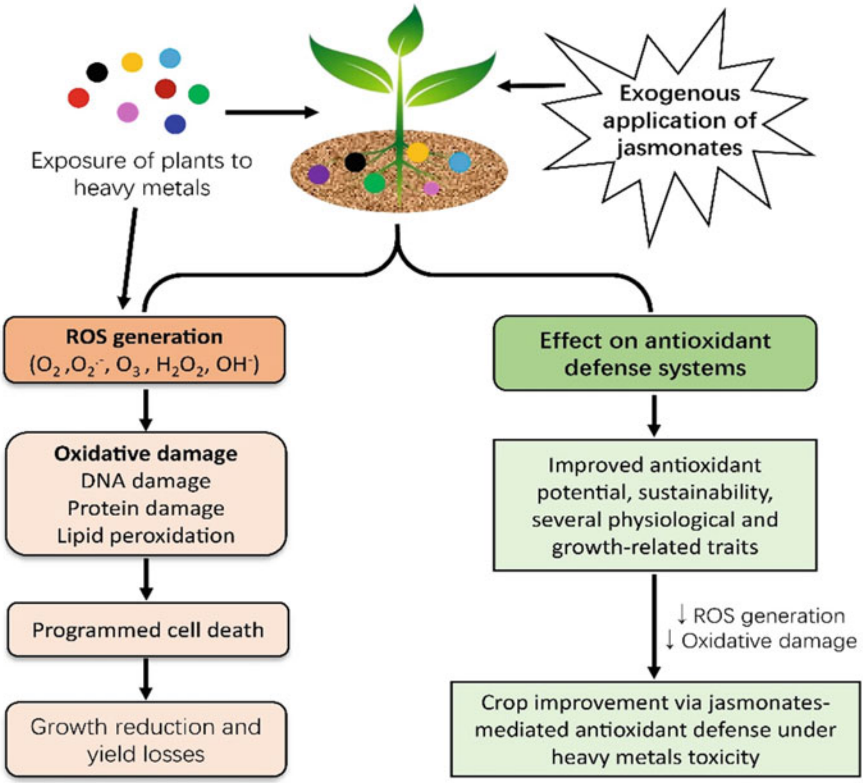

Fig. 3 A systematic illustration indicates the critical role of jasmonates-mediated antioxidant defense systems under heavy metals toxicity in plants

Cu-stress situations (Hanaka et al. 2016). Leaves and roots biomass of alfalfa significantly improved upon JA addition than Cu-stress treatment. Likewise, Chl concentrations, MDA, antioxidant enzyme activities, H_2O_2 also improved accordingly (Dai et al. 2020). MeJA alleviated the B toxicity in *Artemisia annua* by lowering lipid peroxidation and inducing antioxidant enzymes (Ali and Baek 2020).

JA can help plants survive against abiotic stresses by relieving the oxidative damage to plants and alleviation mainly attributed to enhanced enzyme activities that reduce ROS formation. Under B stress, H_2O_2 and O_2^- were observed to increase, and POD and SOD activities increased by JA application, showing that JA facilitated the ROS elimination in *P. tenuiflora* resulted from excess boron and subsequently reduced the oxidative damage (Zhao et al. 2019). JA increased soybean Ni tolerance by regulating Ni uptake and accumulation and lowers Ni-induced membrane damage by reducing ROS levels, MDA, lipoxygenase activity, and electrolyte leakage. Enhanced CAT and SOD activities, also balanced redox status under JA priming, performed a significant role in accomplishing JA mediated ROS removal in Ni stressed plants (Mir et al. 2018). Treatment of soybean seedlings with 2 mM Ni and 1 nM JA

Table 2 Evidence of JA-mediated antioxidant defense systems in enhancing heavy metals stress tolerance in different plant species

Plant specie	Stress conditions	Dose and type of JA	The main effect on antioxidant defense systems	References
Cadmium				
Solanum nigrum	40 mg dm^{-3} Cd; 7 d	0.01, 0,1, 10, and 1000 µM MeJA	↑ POD ↓CAD, SOD	Yan et al. (2015b)
Capsicum frutescens	50 mg L^{-1} Cd; 7 d	0.1, 1, 10, and 1000 mmol L^{-1} MeJA	↑POD, SOD, GPX ↓CAT	Yan et al. (2013)
Oryza sativa	50 µM $Cd(NO_3)_2$; 10 d	5 µM MeJA	↑SOD, POD ↓CAT, GR	Singh and Shah (2014)
Copper				
Cajanus cajan	5 mM Cu; 12 d	1 µM, 1 nM, and 1 pM JA	↑SOD, POD	Poonam et al. (2013)
Phaseolus coccineus	50 µM $CuSO_4.5H_2O$; 5 h	10 µM MeJA	↓SOD, CAT, APX ↑POX	Hanaka et al. (2016)
Medicago sativa	100 µM Cu; 3 weeks	1, 5, and 10 mM JA	↑CAT, POX, APX	Dai et al. (2020)
Arsenic				
Brassica napus	50 and 200 µM $NaAsO_2$; 14 d	0.1, and 1 µM MeJA	↑AsA, GSH, PAL, PPO	Farooq et al. (2018a)
Oryza sativa	25 µM AsIII; 2 weeks	0.25 µM MeJA	↓POD, SOD, APX, CAT	Verma et al. (2020)
Oryza sativa	0, 25, and 50 µM As; 65 d	0, 0.5, and 1 µM MeJA	↑CAT, SOD, APX	Mousavi et al. (2020)
Boron				
Artemisia annua	0, 1, and 2 mM H_3BO_3; 60 d	300 µM MeJA	↑CAT, POX, SOD	Aftab et al. (2011)
Puccinellia tenuiflora	250 mg L^{-1} B; 2 weeks	0.1–1.0 mM JA	↑SOD, POD, CAT	Zhao et al. (2019)
Vitis vinifera	0, 10 and 20 mg B kg^{-1} soil; 48 h	0, and 100 µM MeJA	↑CAT, SOD	Sarabandi et al. (2019)
Nickel				
Glycine max	4 mM $NiCl_2$; 4–8 d	1 pM JA	↑SOD, CAT	Mir et al. (2018)
Glycine max	2 mM Ni; 15 d	1 nM JA	↑SOD, POD, CAT, APX, AsA	Sirhindi et al. (2016)
Alyssum inflatum	0, 100, 200, and 400 µM Ni; 21 d	0, 5, and 10 µM JA	↑SOD, POD, CAT ↓APX	Kakavand et al. (2019)

(continued)

Table 2 (continued)

Plant specie	Stress conditions	Dose and type of JA	The main effect on antioxidant defense systems	References
Lead				
Lycopersicon esculentum	0, 0.25, 0.50, and 0.75 mM $Pb(NO_3)_2$; 30, 45, and 60 d	0, 0.01, 1, and 100 nM JA	↑AsA, GSH, APX, MDHAR, DHAR	Bali et al. (2018)
Lycopersicon esculentum	0.25, 0.50, and 0.75 mM Pb; 15 d	100 nM JA	↑CAT, POD, GST, GR, GPX, PPO	Bali et al. (2019a)
Aluminum				
Vaccinium corymbosum	100 µM $AlCl_3$; 0, 24, and 48 h	5, 100 µM MeJA, and 100 µM Al + 5 µM MeJA	↑CAT, SOD	Ulloa-Inostroza et al. (2019)

Note "↑" means increased or up-regulated, and "↓" means decreased or down-regulated

resulted in low accumulation of H_2O_2, NADPH oxidase, and MDA, which helps in biomolecules stabilization. Also, SOD, POD, CAT, and APX activities improve by 28.22, 40.04, 48.53, and 56.79%, respectively, than control plants. Co-application of JA facilitates the seedlings to combat the detrimental effects of Ni through enhanced osmolytes, the activity of antioxidant enzymes, and gene expression (Sirhindi et al. 2016).

Arsenic stress caused oxidative damage by increasing root growth and increasing lipid peroxidation and ROS. Plant treatment with MeJA resulted in low H_2O_2 and O_2^- contents also improved antioxidant activities. Furthermore, MeJA induced the secondary metabolites related enzymes like PPO and PAL under As stress (Farooq et al. 2018a). MeJA provides tolerance to arsenic and attenuates the damage caused by AsIII. MeJA alters the expression of AsIII transporters and promotes arsenic detoxification by *OsNRAMP1*. MeJA + AsIII supplemented tissues exhibited low CAT, SOD, APX, and POD activities due to reduced oxidative stress than arsenic-treated plants (Verma et al. 2020). Thus, exogenously supplied MeJA effectively alleviates the HM damage by improving the antioxidant enzyme activities, secondary metabolites, Chl contents, and lowering the ROS and MDA contents (Yu et al. 2019). Under Pb toxicity, JA treatment (100 nM) expressively raised the AsA, GSH, APOX, MDHAR, DHAR, and GR contents in Pb-treated tomato plants as compared to control (alone Pb) (Bali et al. 2018). In the next experiment, they also reported the up-regulation of CAT, POD, GST, GR, GPOX, and PPO in JA-treated tomato plants under Pb toxicity (Bali et al. 2019a). Thus, JA treatment improved plant growth and reduced the oxidative injury under Pb toxicity.

5 Cross-Talk and Interaction With Other Phytohormones Under Metal Toxicity

The equilibrium among protective mechanisms and growth and/or development is a complex procedure in controlling plant systems. Scientists have faced problems in getting insights into numerous phytohormones' role and their cross-talk in developmental growth procedures. Consequently, reviewing the phytohormonal interplay is vital to recognize the hormonal responses under stress conditions. Numerous studies have exposed that JA plays an influential role in modulating plant growth and/or development under HM toxicity, and the phytohormonal interaction among JA and other phytohormones related to several developmental procedures. A hormonal cross-talk comprises both positive and negative responses, disturbing hormone production, movement, and signaling. Furthermore, this synergistic or antagonistic connotation among JA and other phytohormones helps plants advance tolerance counter to HMs toxicity (Raza et al. 2019b, 2020d; Wasternack and Strnad 2018; Ku et al. 2018).

Previously, Pauwels et al. (2010) have described a novel understanding of the practice of precise molecular responses to control gene expression via stress- and growth-associated signaling mechanisms. According to Grunewald et al. (2009), there is a collaboration among the JA and auxin signaling pathways, and auxin can modulate the transcript level of the JA-suppressive gene (*TIFY10A/JAZ1*) in *A. thaliana*. Though selenium (Se) is an important plant micronutrient, it can be lethal in higher amounts (Hasanuzzaman et al. 2020a). Recent investigations have exposed that JA and ethylene synergistically normalize Se-induced selenite resistance in *A. thaliana* (Tamaoki et al. 2008). The interaction between JA and salicylic acid had promoted the growth traits of *Alyssum inflatum* under Ni stress by reducing the production of ROS and regulating the antioxidant defense systems (Kakavand et al. 2019). In the recent past, several scientists have reviewed and reported the JA-associated cross-talk and interaction under different abiotic stresses such as salinity, drought, temperature, waterlogging, etc. (Raza et al. 2019b, 2020d; Per et al. 2018; Wasternack and Strnad 2018; Ku et al. 2018; Wang et al. 2020a). Under HM toxicity, there is a dire need to explore the cross-talk of JA signaling pathways in the present and in the near future to get insights into the role of HMs in JA cross-talk and interaction with other phytohormones.

6 Conclusion and Future Directions

JAs and their methyl esters play a noteworthy role in plant growth and development under HMs toxicity. It has been recognized that JAs as growth regulators alleviate the harmful effects of HMs toxicity by regulating several physiological, biochemical, and molecular mechanisms. In-plant classifications, JAs regulate gene expression responsible for general plant growth, antioxidant defense, osmolyte biosynthesis, metabolite production, and physiological traits. However, the examination of plant observation of HMs signals followed by JA biosynthesis and response to numerous HMs has not been completely discovered. Investigations presented that there might be a cross-talk (synergistic or antagonistic) among JA and other phytohormones signaling pathways for regulations of the plant responses to HMs toxicity. Consequently, forthcoming research on manipulating key understandings into JA's role and stimulation under HMs can bring yield auspicious outcomes. Additionally, JA signaling machinery and their roles in signaling cross-talk at the organ, tissue, or cell levels are also required more attention in the future. Likewise, under HMs toxicity, JAs' interaction and cross-talk with other phytohormones still desire more investigation.

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Jasmonates: The Fine-Tuning Bio-regulators and Their Crosstalk with Plant Reproductive Biology

Deepu Pandita

Abstract Jasmonates [free jasmonic acid (JA) and methyl jasmonate (MeJA) conjugates] are ubiquitous lipid-derived phytohormones in the plant kingdom. So far, innumerable regulators of plant growth and development have been recognized, amongst which small Jasmonate molecules are the potential regulators. The fundamental and critical roles of Jasmonate internal signals include plant growth and development and survival aspects of plant biology by defending against various biotic and abiotic stresses. During biotic and abiotic stress conditions, plants prioritize JA-mediated defense over growth and development for survival by significant inhibition of plant growth. Jasmonates also act as central players in the biology of plant reproduction of normal growing healthy plants. Genes of jasmonate biosynthetic pathway show floral organ-specific expression. Jasmonate's most prominent function in plant development includes the regulation of various aspects of reproductive growth and development and formation and differentiation of reproductive organs such as, floral buds, flower, androecium and gynoecium, embryo, tassels and spikelets, expansion of flower petals, maturation of viable pollen grains and/or their germination, dehiscence of anthers, fruit coloration by production of anthocyanin pigments, fruit ripening, volatile aroma of fruits, seed germination and maturation, delay of flowering and sex determination in monoecious plants.

1 Introduction

Lipid-derived Jasmonate (JAs) phytohormones regulate plant growth and development (Siddiqi and Husen 2019). Jasmonates (jasmonic acid and its derivatives) have imperative role to play in plant fertility, stamen and pollen development, flowering (Wasternack and Hause 2013), stamen and pollen nutrition (Dobritzsch et al. 2015), leaf senescence, primary root growth, reproductive development, development of flowers and growth of seedlings (Ueda and Kato 1980; Dathe et al. 1981; Wasternack and Hause 2013), development of carpels in tomato (Li et al. 2004; Schubert

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et al. 2019) and high JA content activates precocious anther dehiscence (Cecchetti et al. 2013). JA insensitive *Arabidopsis thaliana* are male sterile nonvital pollen and delayed anther dehiscence (Browse 2009a). The JA biosynthetic mutants of *Solanum lycopersicum* are female sterile. The biosynthesis of Jasmonates takes place from α-linolenic acid in green chloroplast to major active (-)-JA or MeJA and most bioactive (+)-7-iso-JA-Ile in cell cytoplasm through octadecanoid pathway in 3 cellular compartments of photosynthetic chloroplasts, peroxisomes, and cytoplasm in plants (Wasternack and Strnad 2016; Fonseca et al. 2009; Staswick and Tiryaki 2004). The role of Jasmonic acid in plant reproductive biology is a novel concept and this chapter will highlight this less explored research area.

2 Biosynthesis and Metabolism of JA

The Jasmonic acid and Me-JA biosynthesis pathway was deduced by Vick and Zimmerman in 1983 and Hamberg and Hughes in 1988. JA biosynthesis pathway is also termed the octadecanoid pathway and follows a sequential lipid esterification pathway which takes place in first in subcellular compartment of green pigment containing chloroplasts, then peroxisome, and lastly in cell cytoplasm (Fig. 1). The

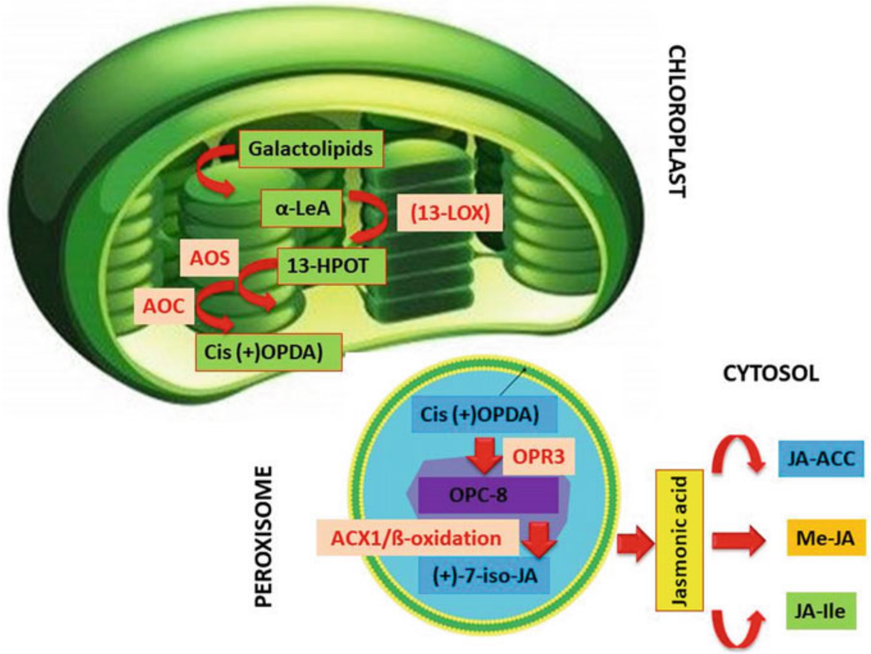

Fig. 1 Graphics of JA Biosynthetic Pathway

starting step consists of generation of original precursor 18 C polyunsaturated fatty acids (PUFA) α-linolenic acid (18:3, α-LeA) substrate from membrane based chloroplastic galacto- and phospholipids by enzymatic action of lipid hydrolysing phospholipases, Phospholipase 1 (PLAs), which consist of DEFECTIVE IN ANTHER DEHISCENCE 1 (DAD1) in *Arabidopsis thaliana* (Ishiguro et al. 2001; Ahmad and Jhon 2005; Cervilla et al. 2007; Wang et al. 2019). Subsequently, biosynthesis of JAs includes phospholipid α-linolenic acid oxidation wherein oxygen is incorporated at C13 of substrate by 13-LIPOXYGENASE (13-LOX), to form fatty acid hydroperoxide known as 13-hydroperoxy-9, 11, 15-octadecatrienoicacid (13-HPOT) (Caldelari et al. 2011; Chauvin et al. 2013, 2016). Only 13-HPOT intermediate from α-linolenic acid may be used by two different enzyme families of the 7 divergent divisions of lipoxygenase (LOX) pathway, termed AOS-ALLENE OXYDE SYNTHASE for dehydration into unstable allene oxide, 12, 13-EOT {(9Z, 13S, 15Z)-12, 13-oxido-9, 11, 15 octadecatrienoic acid} and ALLENE OXYDE CYCLASE (AOC) cyclized 13-HPOT to racemic stable cis(+)-oxophytodienoic acid (cis (+)-OPDA) (Feussner and Wasternack 2002; Staswick and Tiryaki 2004; Bannenberg et al. 2009). The preferential product of AOC-allene oxide cyclase is enantiomer, 9S, 13S/cis (+)-OPDA. Above and beyond enzymatic biochemical reactions, unprompted hydrolysis activates unstable epoxide into α- and ÿ-ketols and the non-enzymatic cyclization into racemic 12-oxo-phytodienoic acid (OPDA) (Brash et al. 1988). The biochemical conversion of α-LeA to OPDA takes place inside chloroplast (Fig. 1).

The succeeding steps of JAs biosynthesis takes place in subcellular compartment of peroxisome (Fig. 1), wherein cis(+)-OPDA is transported by some unknown mechanism. To date, a single gene COMATOSE protein localized in peroxisome and belonging to ABC-ATP binding cassette transporter class has been connected with cis(+)-OPDA transportation from chloroplast into peroxisome (Theodoulou et al. 2005; Dave et al. 2011). Conversely, Arabidopsis COMATOSE loss of function mutants produce JA, suggesting involvement of other transporters as well. In peroxisome organelle, cis-OPDA undergoes reduction via OPDA REDUCTASE (OPR) preceded by 3 β-oxidation steps through ACX (ACYL-CoA OXIDASE), l-3-ketoacyl-CoA-thiolase (KAT) and MFPs (multifunctional proteins) peroxisomal enzymes. Activation occurs by Co-A synthetases and 4-coumaroyl fatty acid co-esters: Co A ligases. In this way, production of jasmonic acid (JA) occurs by its conversion into (+)-7-iso-JA by OPR (12-oxo-phytodienoic acid reductase) (Breithaupt et al. 2006; Cruz et al. 2004; Fonseca et al. 2009).

The (+)-7-iso-JA is then exported via a mysterious mechanism to the cytoplasm (Fig. 1). Where it epimerizes into more stable trans-configuration of (-)-JA or JA derivatives such as Me-JA and (+)-7-iso-JA-Ile (Wasternack and Strnad 2016). After a chain of reactions, (+)-7-iso-JA and derivatives are formed (Kombrink 2012; Wasternack and Hause 2013). (+)-7-iso-JA and its derived molecules have at best 12 metabolic pathways with amino acid (aa) carboxylation, methylation, esterification, decarboxylation, sulfation, hydroxylation, conjugation, O-glycosylation and can be converted into more than 30 distinct inactive, partially active, and active jasmonates found in angiosperms, gymnosperms, pteridophyta and algae as clearance metabolites with substantial functions in hormone homeostasis for tuning developmental and defense responses (Sembdner and Parthier 1993; Jimenez-Aleman et al. 2015). Most characterized are from GRETCHEN HAGEN3s (GH3s) class, which by conjugation of JAs with numerous amino acids however utmost markedly isoleucine (isoleucine conjugate, (+) -7-iso-JA-Ile) through enzyme transcribed by JA resistant 1 (JAR1) gene, leading to most bioactive JA-L-Ile compound (Staswick and Tiryaki 2004; Fonseca et al. 2009). Other major active Jasmonate forms are free JA, cis-jasmone, and MeJA in plants (Fonseca et al. 2009).

3 JA-Mediated Crosstalk with Other PGRs (Phytohormone)

Equilibrium between defense machineries and growth and development in plants is very complex course in regulatory plant networks. Understanding function of diverse hormones and their crosstalk is difficult. Thus, hormonal interaction is indispensable to comprehend biochemical reactions of hormones under stress conditions, plant growth and development. JA regulates growth and development in plants in stress environments. Hormones crosstalk between JA and PGR linked developmental processes, involving positive and negative feedback in biosynthesis of hormones, transportation and signaling of phytohormones (Ku et al. 2018; Vos et al. 2015). The synergistic or antagonistic connotation between JAs and phytohormones benefits plants for abiotic stress tolerance (Wasternack and Strnad 2018; Wang et al. 2020). Understanding JA mechanism of action in abiotic stresses and JAs crosstalk with additional plant growth regulators involves precise mechanisms at molecular levels which regulate gene expression by stress induced and growth-connected signaling pathways (Pauwels et al. 2010). Communication between IAA and JAs signaling pathways, confirms activation of JA repressive TIFY10A/ JAZ1 expression in *A. thaliana* (Grunewald et al. 2009). MeJA sustains acceptable quantity of CKs for plant development. MeJA use modulated activity and CK oxidase expression under salt stress. JA regulated CKs amount in wheat by regulation of CK dehydrogenase/oxidase activity (Avalbaev et al. 2016). JA and ABA pathways adjust responses of each other and extra metabolic pathways in abiotic stresses (de Ollas and Dodd 2016). ABA receptor (PYL4) gene regulates metabolic reprogramming in *Nicotiana tabacum* and *A. thaliana* in signaling of JAs as well (Lackman et al. 2011). Thus, confirming JA and core ABA signaling relationship, to track elicitor-induced reprogramming of growth and metabolism in plants and also in responses of plant during drought (de Ollas et al. 2015). The JAs signaling is modified by core repressor (DELLA proteins) of gibberellic acid signaling, wherein DELLA proteins fight with stable MYC2 which binds with JAZ proteins without GA and MYC2 then stimulates JA responsive gene expression (Hou et al. 2010).

Pathways of two essential signaling molecules i.e., JA and SA get triggered by ecological stresses for plant defense response. Incompatible action of SAs and JAs signaling pathway is also recognized (Van der Does et al. 2013; Spoel et al. 2003).

Interaction of JAs and BR plays critical roles in development and stress response (Yang et al. 2011). Jointly antagonistic connotation is reported between JAs and the BRs signaling pathways in *Oryza sativa* (Nahar et al. 2013). Jasmonates contribute to stress response and associate with supplementary hormones (Per et al. 2018). ERFs are main controlling channels for signaling in stress conditions along with JAs and ethylene (ET) hormones (Müller and Munné-Bosch 2015). ABA dependent pathway and ABA independent pathway regulate prospective effects of JAs. Fighting of water deficiency is allied with signaling of JA in rice. OsbHLH148 protein provides tolerance to low water stress in *Oryza sativa* and networks with OsJAZ1 for activation of OsDREB1 expression (Seo et al. 2011). Exogenous JAs enhances ABA levels in plants (Sánchez-Romera et al. 2014). JA-insensitive mutant, amidosynthetase1-1 under water deficiency, salinity, and high temperature stress showed obstructed ERF1expression indicating essential role of Jasmonic acid and ET to activate ERF1 during diverse abiotic stresses. Jasmonic acid cause closure of stomata, and drought inhibits conversion of 12-OPDA into Jasmonic acid. The OPDA independently or in permutation with abscisic acid enable closure of stomata for water deficiency tolerance (Savchenko et al. 2014). JA affects stomatal closure under drought stress. Auxins which are stomatal opening regulators aid in JA up regulation signalling repressors JAZ1 genes (Thines et al. 2007; Chini et al. 2007). The SAs overturns JA activated RSOsPR10 in rice during water deficiency and salinity (Takeuchi et al. 2011). JAs and ET antagonist signaling pathways control the responses to heat stress and crosstalk by communication of JAZ and EIN3/ EIL1 which are targeted by JAZ (Zhu et al. 2011). Me-JA and SA together improve citrus cold tolerance machineries. Crosstalk of the cold transcription factor mediated induction of expression of CBF and avoidance mechanisms of ROS of JAs and SAs signal transduction pathways fights chilling stress (Sharma and Laxmi 2016). Defense gene (SAR and pathogenesis related protein [PR1]) expression shows that MPK4 (MAP kinase 4) acts as a mediator in JAs and SA crosstalk (Leon-Reyes et al. 2010). JAs alleviate damaging effect of abiotic stress but crosstalk of its signaling factors needs to be discovered at levels of cell, tissue or organ. Flower development is under regulation of plant hormones and their crosstalk (Marsch-Martínez and de Folter 2016). Jasmonic acid and its derivatives have significant roles in development of flowers among phytohormones (Wasternack and Hause 2013). Flower development is under regulation of plant hormones and their crosstalk (Marsch-Martínez and de Folter 2016). JA and derivatives have significant roles in development of flowers (Wasternack and Hause 2013).

Exogenous JA treatment of flower buds reduced mRNA levels of genes which encode enzymes of ethylene biosynthesis (Dobritzsch et al. 2015). The JA facilitated influence on biosynthesis and function of ethylene was studied in JA deficient SlAOC-RNAi plants. ET insensitive Never ripe (Nr) mutant lacks senescence of flower petals and androecia (Lanahan et al. 1994) and has non-synonymic point mutation in Solyc09g075440 gene which encodes ETR3, causing an interchange of proline into leucine (Wilkinson et al. 1995). Nr mutation is partly dominant making plant nonresponsive to endogenous or exogenous ethylene (Lanahan et al. 1994). Cross breeding of Nr and jai1-1 mutants, generated JA and ET insensitive double mutants with complementation of jai1-1 pollen dehiscence (Dobritzsch et al. 2015). Jasmonates allow temporal inhibition of generation of ET to avoid early dehiscence of anthers and to safeguard accurate time of development of the flowers. In Arabidopsis, both JA and ET hormones act in analogous way for regulating timing of the abscission of floral organs (Kim 2014). Jasmonates play vital functions in maturation of tomato carpels, androecia and pollen grain development, pollen nutrition at initial stages of development and regulate biosynthesis and activity of ethylene at later phases of the development (Li et al. 2004; Dobritzsch et al. 2015; Schubert et al. 2019). The Jasmonic acid insensitivity and deficiency cause non-viable pollen and delay in dehiscence of pollen grains from anthers in Arabidopsis (Browse 2009a), and raised concentrations of JA prompt mature dehiscence of anthers (Cecchetti et al. 2013).

4 Function of Jasmonic Acid in Plant Developmental Processes

Jasmonates (JA/JA-Ile) regulate with an assertive role growth, differentiation and development of stamen, spikelet, tassel, embryo and several biological processes such as growth inhibition, seed germination, protein storage in seeds, flowering and flower development, senescence of leaves and flowers, tendril coiling, root growth, trichome formation, mitochondrial death, potato tuberization and tuber formation, fruit ripening, wounding and immune signalling across plant species and other functions (Fig. 2). JA signaling molecule or phytohormone regulates reproductive growth of plants, storage of the nutrients, and assimilates movement, metabolic functioning, signaling, and fungi arbuscular micorrhizal association, genes expression in stamen tissue, interaction with other phytohormones and adapts plants to different kinds of ecological stresses (Browse 2005; Wasternack 2007; Katsir et al. 2008; Balbi and Devoto 2008; Browse 2009b; Yoshida et al. 2009; Reinbothe et al. 2009; Song et al. 2011; Pieterse et al. 2012; Kombrink 2012; Farhangi-Abriz et al. 2019; Alisofi et al. 2020). Jasmonic acid regulator regulates morphogenesis of the leaves and roots and fertility in *Glycine max* plant (Xue and Zhang 2007).

5 Functions of Jasmonic Acid in Plant Reproductive Biology

Jasmonate (JAs) phytohormones control plant defense counter to biotic and abiotic stresses, plant development of root, stamen, flowers and leaf senescence (Howe and Jander 2008; Wasternack and Hause 2013; Goossens et al. 2016). Exogenous JAs inhibit various characteristics of growth in the seedling, such as primary growth of roots, expansion of leaves, and elongation of hypocotyl (Song et al. 2014; Kim et al.

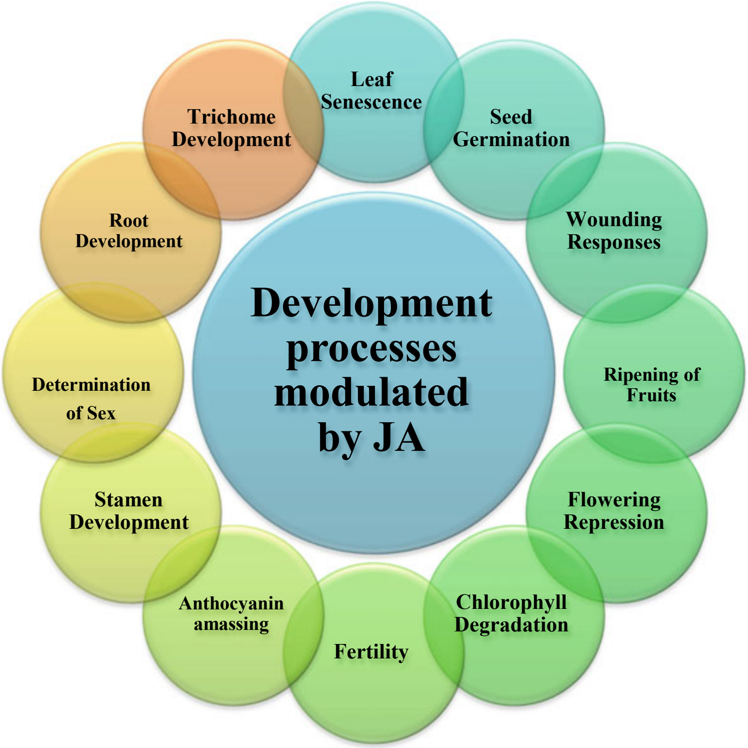

Fig. 2 Jasmonic acid mediated regulation of developmental processes

2015; Wasternack and Hause 2013). Despite variances in the male or female reproductive development in monocot and dicot flowers, categorically jasmonates act as fundamental phytohormones for reproduction in plants. The jasmonic acid mediated plant reproductive biology includes below mentioned developmental processes (Fig. 3).

5.1 Stamen Development

The JA and Me-JA occur in male anthers and pollen grains of 3 *Camellia* species (Yamane et al. 1982). Previously JA only and not Me-JA, was proposed as endogenous regulator of the germination of the pollen grains. Beyond ten years, N-[(-)-jasmonoyl]-(S)-isoleucine and N-[7-iso-cucurbinoyl]-(S)-isoleucine jasmonates were recognized in pollen grains of *Pinus mugo* (Knöfel and Sembdner 1995). The jasmonates play vital functions in maturation and/or germination of pollens. The structure of N-[(-)-jasmonoyl] tyramine in *Petunia hybrid* pollen grains was elucidated by LC–MS-MS, GC–MS and CD assays (Miersch et al. 1998).

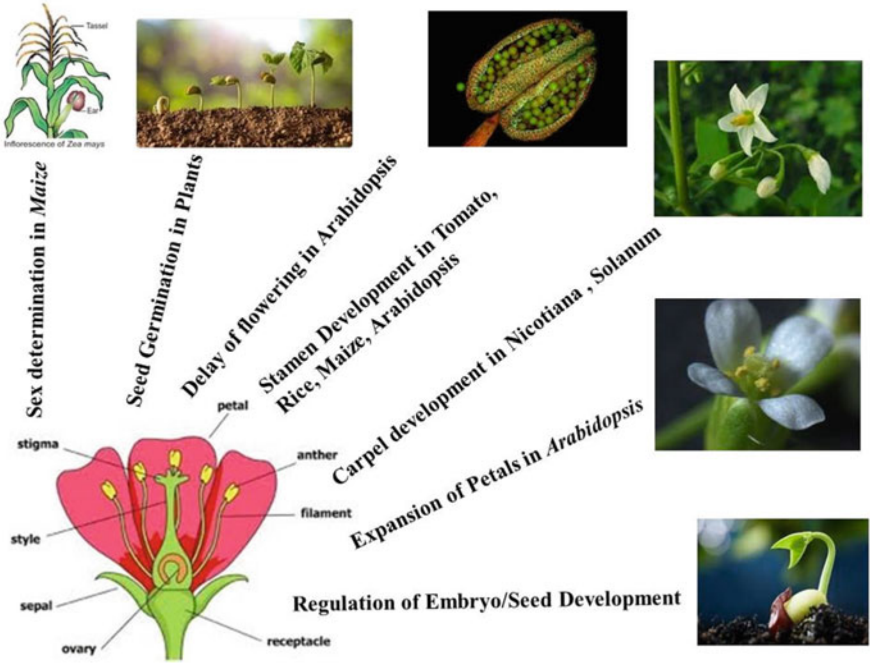

Fig. 3 Jasmonic acid mediated plant reproductive biology developmental processes

5.1.1 Stamen Development in *Arabidopsis thaliana*

Arabidopsis jasmonates play herculean tasks in the development of Stamen (Ishiguro et al. 2001; Sanders et al. 2000; von Malek et al. 2002). Jasmonate pathway is a main pathway for stamen maturation in *A. thaliana* (Song, Huang et al. 2013; Yuan and Zhang 2015). The development of stamen which contains pollen grains in anther is indispensable for the plant fertility. Role of JAs in the reproductive process of plants became more recognizable when JA deficient fad3 fad7 fad8 mutants in Arabidopsis, defective in anther dehiscence1 (dad1), lox3 lox4, aos, and opr3 were characterized to be male sterile due to small stamen filaments, indehiscence in male anthers, and non-viability of pollens at tricellular stage of development. So, JAs are imperative for development of pollen grains, elongation of androecium and correct time of anther dehiscence (Liechti and Farmer 2006). Overexpression transgenic lines of JA CYP94B3 gene; JA signaling mutant coi1; and JAZ1Δ3A and JAZ10.4 transgenics showed male sterility because of blocked development of stamens at time of anthesis. The acx1 acx5 was exception with deficiency only in pollen grain viability (McConn and Browse 1996; Stintzi and Browse 2000; Ishiguro et al. 2001; Sanders et al. 2000; Park et al. 2002; Thines et al. 2007; Schilmiller et al. 2007; Chung and Howe 2009; Caldelari et al. 2011; Koo et al. 2011; Song, Huang et al. 2013).

Jasmonate application restores development of androecium in JA biosynthesis deficiency mutant, however not in JA signaling mutants. Male-sterile Arabidopsis mutants lack enzymes for conversion of α-LeA to Jasmonic acid (Stintzi and Browse 2000; von Malek et al. 2002). The coi1 mutants in A. *thaliana* produced non-viable pollens and showed male-sterility (Feys et al. 1994). Reinstated COI1 expression in filaments and anthers improves elongation of filaments of stamens, dehiscence of anthers, and development of the pollen grains (Jewell and Browse 2016). Overexpression of MYB21 restores development of androecia (Song et al. 2011) whereas MYC5 and MYC3 partly re-establish development of androecia and male fertility in coi1-1 mutants (Qi et al. 2015a). The MYC2E165K restores fertility of JA-deficient aos mutant (Gasperini et al. 2015) and IIId bHLH/JAM TFs overexpression inhibits development of male reproductive organs (Nakata et al. 2013; Nakata and Ohme-Takagi 2013). The Arabidopsis mutant delayed dehiscence 1 (dde1) mutated in 12-OPR gene (Stintzi and Browse 2000), exhibited deferred anther dehiscence and thus unproductive fertilization of pollen grains and ovules. Exogenous Jasmonate use restored wild-type phenotype, and male-sterile mutant plants produced seeds. At advanced stages of development of flowers, DDE1 transcript levels accumulate precisely in carpel, flower petals, and filaments of stamens without stomium. The opr3 mutants had sterile phenotypes.

Exogenous application of signaling jasmonate induced and coordinated elongation of anther filaments, opening of stomium at anthesis, and generation of viable pollen grains in *A. thaliana* (Stintzi and Browse 2000). In opr3 mutants, 13 JA-inducible MYB21 and MYB24 TFs for development of androecia were characterized and their responses to JAs in androecia development was studied in Arabidopsis (Mandaokar et al. 2006). MYB57, MYB24, R2R3-MYB and MYB21 are targeted by JAZs, which play coinciding roles to mediate Jasmonate regulated maturation of androecia (Mandaokar et al. 2006; Song et al. 2011; Cheng et al. 2009). The myb21 myb24 double mutants were male sterile owing to undersized filaments, deferred anther dehiscence, and non-viable pollens. MYB108 regulate development of pollen grains and dehiscence of anthers downstream of MYB21 (Mandaokar and Browse 2009). Genes of jasmonate biosynthetic pathway precisely showed organ-specific expression in carpel ovaries, petals and sepals of flower and JA-dependent signals are transferred to stomium for punctual anther dehiscence (Cheong and Choi 2003; Sanders et al. 2000). MYB21, MYB24, MYC2, MYC3, MYC4, MYC5 IIIe bHLH factors (MYB-MYC complexes) are regulators of maturation of male stamens (Qi et al. 2015a). The quadruple myc2 myc3 myc4 myc5 mutants with repressed MYB21, MYB24, MYB57, MYB108 expression, show defects in androecium anthesis like coi1-1 mutants. These finally become fertile leading to partial sterility of stamens (Qi et al. 2015a). MYC5-EAR domain when overexpressed, constrains development of androecium and expression of MYB (Qi et al. 2015b; Figueroa and Browse 2015). The studies in Arabidopsis mutants having fertility issues in transposon tagged population identified delayed dehiscence2-2 (dde2-2) mutants. The dde2-2 mutant plants had complications in elongation of male filaments, dehiscence of anthers and exhibited male sterility. Exogenous MeJA restored wild-type phenotype suggesting mutants had problems in genes which encodes AOS enzyme of jasmonate biosynthetic pathway (von Malek et al. 2002). Mutant dad1 had mutation in anther dehiscence1 (dad1) gene which encodes phospholipase A1 involved in α-LeA formation in chloroplasts (Ishiguro et al. 2001). These mutants had defective pollen grain maturation, anthesis, and produced male-sterile phenotype in Arabidopsis. Exogenous JAs or α-LeA saved dad1 mutants with normal phenotypes, and low JA content in the floral buds (Ishiguro et al. 2001).

Gibberellic acid suppresses DELLA repressor proteins. This activates DAD1 gene expression, JAs biosynthesis, and MYB to stimulate elongation of stamen filament (Cheng et al. 2009). TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING F-BOX PROTEINs, INDOLE-3-ACETIC ACID 8, and AUXIN RESPONSE FACTOR6 /ARF8, control biosynthesis of JAs and MYB expression involved in elongation of stamen filaments and dehiscence of the anthers (Nagpal et al. 2005; Cecchetti et al. 2008; Wang et al. 2013). AGAMOUS, E3 ligase DAD1-ACTIVATING FACTOR and DAYU induce JA biosynthetic gene expression to impact dehiscence of the anthers and germination of pollen grains, whereas NO APICAL MERISTEM/ ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR/ CUP-SHAPED COTYLEDON, ANTHER INDEHISCENCE FACTOR and JINGUBANG suppress dehiscence of anthers and pollen grain development (Ito et al. 2007; Peng et al. 2013; Li et al. 2014; Shih et al. 2014; Ju et al. 2016).

5.1.2 Stamen Development in *Zea mays*

In maize, the development of male reproductive flowering organ- tassel was abnormal in tassel ts1 and ts2 seed mutants, leading to formation of female flowers on male tassel (Browse 2009c). TS1 protein is 13-lipoxygenase which is important enzyme of JAs biosynthetic pathway. JA content in tassels of ts1 homozygous plants was 1/10th of that of tassels in wild maize. Exogenous application of JAs to ts1 mutant tassels recovered partially the wild-type phenotype suggesting jasmonate as crucial signal for determination of male distinctiveness in the tassels of *Zea mays* (Browse 2009c).

5.1.3 Stamen Development in *Oryza sativa*

The mutants of important enzymes involved in JAs biosynthesis pathway unquestionably enhance comprehension of multifaceted physiological reproductive mechanisms (Yu et al. 2006). The JA deficient rice mutant, coleoptile photomorphogenesis (cpm)1, osjar1, cpm2/hebiba, and extra glume (eg)1; JA signaling mutant eg2-D (with a dominant mutation in OsJAZ1); RNAi transgenics of OsCOI1a and OsCOI1b; transgenic lines of truncated JAZs; and rice transgenics expressing carboxyl methyltransferase gene display complete/incomplete male sterility owing to aberrations in spikelets, anomalous or condensed androecia, glumelike structures, stigma-like organs, and weakened dehiscence of anthers (excluding cpm1 and COI1a/b RNAi transgenics with anther dehiscence deficiencies only) (Biswas et al. 2003; Xiao et al. 2014; Riemann et al. 2013; Li et al. 2009; Cai et al. 2014; Yan et al. 2012; Hori et al. 2014; Kim et al. 2009). Rice P0491E01 RNAi transgenic plants deficient in protein similar to protein of Arabidopsis DAD1 (DEFECTIVE IN ANTHER DEHISCENCE1) in JA biosynthesis showed male-sterility or decreased fertility. The development of anther was normal at initial stages, but development of the microspore into mature pollen grains was compromised. The P0491E01 transcript levels were reduced in transgenic plants, suggestive of role of jasmonates in late phases of anther maturation (Yu et al. 2006).

5.1.4 Stamen Development in *Solanum lycopersicum*

Tomato jai1 mutant defective in JA signaling and male reproductive function, exhibits reduced pollen grains viability, premature anther dehydration and anther dehiscence, pollen germination but no male sterility. But pollen grain fertilizes wild flowers. JAs regulate pollen nutrition and pollen maturation, timing of androecia dehiscence, premature dehiscence and pollen grain release (Li et al. 2004; Dobritzsch et al. 2015). The jai1-1 Never ripe (jai1-1 Nr) double mutant is insensitive to ET as well, and displayed salvage of jai1-1 phenotype about pollen dehiscence. Jasmonates inhibit early increase in ethylene in jai1-1 Never ripe (jai1-1 Nr) to avoid premature stamen desiccation and stamen development (Schubert et al. 2019).

5.2 Female Reproductive Organs

Rice MYC2 undergoes interaction with JAZ1 and regulates development of spikelets via OsMADS6, OsMADS5, and OsG1 genes (Cai et al. 2014; Zhang et al. 2016).

5.2.1 Carpel Development in *Nicotiana tabacum*

The enzyme encoded by *Nicotiana tabacum* cv. Petit Havana SR-1 is capable of synthesizing Me-JA. Thus, its function gets questioned in flowers of the *Nicotiana tabacum* plant. The Arabidopsis amino acid sequences for allene oxide cyclase, AOS, LOX, and 12-OPR on TBlastN in TOBEST database showed lack of AOS gene in TOBEST. The absence of AOS can be by chance or points to stringent JA biosynthesis regulation in carpels of the *Nicotiana tabacum* flower (Laudert and Weiler 1998). The demonstration of LOX, allene oxide cyclase and 12-OPR and JA methyltransferase backs connection of jasmonates in development and physiology of female reproductive organs in *Nicotiana tabacum* (Hause et al. 2000; Li et al. 2001, 2004).

5.2.2 Carpel Development in *Solanum lycopersicum*

Jasmonates contribute to regulation of the female reproductive organs in tomato (Hause et al. 2000; Li et al. 2001, 2004). Tomato mutants show female sterile phenotype with modifications in significant genes of jasmonate biosynthetic pathway. In *Solanum lycopersicum*, orthologous mutant jasmonate-insensitive1-1 (jai1-1) mutated in JA-Ile co-receptor COI1, has defective development of ovules and has as a result female-sterile flowers. The jai1-1 flowers have stigma protruded out of androecium cone and senescing tip of androecial cone. Contrary to Arabidopsis, Jasmonic acid mediates development of flowers and is female-sterile (Li et al. 2001, 2004; Schubert et al. 2019). The Jasmonic acid, 12-OPDA and JA-L-Ile conjugate in tomato, accumulates twofold higher in flower tissues than plant leaves. The histochemistry displayed boundless allene oxide cyclase protein accumulation in ovules of ovary, transmitting tissue of carpel style, and vascular bundles of receptacles, connecting biosynthetic pathways of JAs in regulation of carpel development in *Solanum lycopersicum* (Hause et al. 2000).

5.3 Expansion of Flower Petals in Arabidopsis thaliana

Arabidopsis JA-deficient mutants (aos and opr3) (deficient in jasmonate biosynthesis) and JA perception mutant coi1 show large dimensions of petals than wild Arabidopsis at anthesis. This indicates that phytohormone JAs limits flower petal expansion in *A. thaliana* (Brioudes et al. 2009; Reeves et al. 2012). Arabidopsis TFs ARF6 and ARF8 promote expansion of petals, activate JAs production and JAs stimulate MYB21 and MYB24 which encode R2R3 MYB TFs functional in expansion of petals and stamen growth (Reeves et al. 2012). Mutants (aos and coi1) had reduced MYB21 expression in petals of Arabidopsis from the opening of floral bud to scattering of flower petals after the anthesis, leading to limited growth of petals (Reeves et al. 2012). Instead, MYB21 expression is improved in flower petals of aos and coi1 mutants, causing determined expansion of petals and big flower petals (Reeves et al. 2012). The opr3 mutant flowers have larger petals and larger cell size and cells have increased transcript levels of bHLH transcription factor BIGPETALp after exogenous jasmonate use (restricts dimensions of petals by regulating post-mitotic cell expansion) encoded by BPEp which is under control of jasmonate (Brioudes et al. 2009).

5.4 Sex Determination in Zea mays

In *Zea mays*, tassel and ear development is outcome of developmental cascade involving abortion of carpel and androecium primordial development and development of unisexual florets. In *Zea mays* mutants sex determination tassel seed1 (ts1), ts2 (lipoxygenase genes involved in jasmonic acid biosynthesis), and opr7 opr8, the male tassels are transformed to fertile female ears which can set seeds. The jasmonate application reinstates tassel maturation, representing that JAs regulate male flower development in *Zea mays* (Acosta et al. 2009; Yan et al. 2012). Nevertheless, function of tassel seed2 (TS2) at molecular levels in Jasmonic acid biosynthetic pathway is unidentified.

5.5 Regulation of Embryo/Seed Development

A tomato JA-deficient mutant prosystemin-mediated response with transmutation in FAD7 has late or blocked embryo development because of increase in programmed cell death (Goetz et al. 2012). JA insensitive1 (jai1) mutant tomato cannot produce viable seeds, has ovule-specific accretion of allene oxide cyclase (AOC) and is female sterile due to knock down of CORONATINE-INSENSITIVE1 (COI1) (Li et al. 2004; Goetz et al. 2012). A wound stimulated endogenous increase in 12-oxo-phytodienoic acid (OPDA) marginally reinstates seed maturation in JA-insensitive mutant jai1. OPDA- and JA-deficient t spr2 showed delay in the development of embryos. This indicates OPDA signaling has a role to play in maternal control of seed development (Goetz et al. 2012). Tomato mutant acx1a sets viable seeds, develop normal embryos and produces OPDA which plays vital role in embryo development and residual quantity of JA. Tomato SiOPR3 RNAi have silenced OPR3 gene, but contains analogous quantity of OPDA as in wild plants and produces scarce number of viable seeds. Me-JA application reinstates seed production in SiOPR3 tomato (Scalschi et al. 2015). Thus, JAs play function in the maternal regulation of the seed development and OPDA or OPDA-related compounds in embryo development.

5.6 How JA Affects Seed Germination in Plants

Exogenous application of JA suspends ABA-mediated inhibition of germination of seeds in *A. thaliana.* The jar1 and coi116 mutants have improved sensitivity to inhibition of seed germination by abscisic acid (Staswick et al. 1992; Ellis and Turner 2002). The OPDA effectively impedes germination of seeds in *A. thaliana* in a CORONATINE INSENSITIVE1 independent but abscisic acid synergistic manner (Dave et al. 2011). Arabidopsis thaliana encodes an enzyme for peroxisomal importation of substrates for β-oxidation. Many cts alleles and double mutants with knocked COMATOSE (CTS) gene which encodes an ABC transporter show blocked seed germination in cts. Thus, OPDA in conjunction with ABA controls seed germination in *A. thaliana* (Dave et al. 2011). In course of cold induced germination by release of dormancy in seeds of wheat and other plants, JAs biosynthesis connected gene expression and biosynthesis of Jasmonic acids rise swiftly in dormant embryos after transference to 20 °C. Blocking JA biosynthetic machinery with acetylsalicylic acid stopped cold induced seed germination. JA mediate suppression of TaNCED1 and TaNCED2 genes during biosynthesis of dormancy promoter abscisic acid in dormant embryos of wheat to stimulate cold-induced seed germination (Xu et al. 2016).

5.7 Late Flowering in Arabidopsis thaliana

Jasmonate hormones impede flower development and flowering time in *Arabidopsis thaliana*. JA-insensitive mutant coi1 mutant and JAZ1Δ3A transgenics show premature flowering, indicating that JAs act via CORONATINE INSENSITIVE1 (COI1)-JAZ for inhibition of flower development (Zhai et al. 2015). APETALA2/ERF domain transcription factors, TARGET OF EAT (TOE) 1 and TARGET OF EAT (TOE) 2 on interaction with jasmonate-ZIM domain proteins, inhibit and delay flowering time in Arabidopsis thaliana by inactivating transcription of FLOWERING LOCUS T florigen gene (Zhai et al. 2015). TFs and JAZ underlie JA-mediated flowering regulation. The TOE1 and TOE2 overexpression suppresses premature flowering in coi1 mutants (Zhai et al. 2015). The IIId bHLH factors damagingly control JA-mediated delay in the flowering process (Song, Fan, et al. 2013). The period of flowering is postponed in bhlh17 bhlh13 bhlh3 bhlh14 mutants, however, enhanced in overexpression transgenic of bHLH17 and bHLH13 (Song, Fan, et al. 2013). JA-insensitive mutant coi1 mutant in *Arabidopsis thaliana* show male sterility. Seeds are not produced due to anther dehiscence, insufficient elongation of filaments, and non-germinating pollen postponed anther dehiscence (Feys et al. 1994; Xie et al. 1998).

6 Conclusion

Lipid-derived Jasmonate (JAs) bio-regulators regulate growth, development and reproduction, and defense responses in plants in a jasmonate-dependent signaling pathway. Jasmonates control physiological, morphological and biochemical aspects of the plant reproduction, growth and development, together with development of male reproductive organs in *Arabidopsis thaliana*, flowering and petal expansion in *Arabidopsis thaliana*, carpel and androecia development in *Oryza sativa*, development of tassels in *Zea mays*, sex determination in maize, stamen development in tomato, parental regulation of embryo development in Solanum, carpel development in tobacco and tomato, and seed germination and embryo development in various other plants.

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Role of Jasmonates in Pathogenesis and Crosstalk of Jasmonates with Other Hormones

Shreshtha Yadav, Simran, Nisha Sella, and Shabir A. Rather

Abstract As plants lack the locomotory capabilities, they have to defend themselves from all the stresses standing at the same place. Therefore, plants have developed various defence mechanisms, and the phytohormones play a very significant role in developmental processes as well as the response of plants against the biotic and abiotic stresses. The plants induce localised and systemic responses to defend themselves against the fungi and other microbial pathogens. Phytohormones, mainly ABA, Jasmonic Acid, and Salicylic Acid, have been shown to play a crucial role in mediating or regulating stress responses in plants. A localised hypersensitive response is triggered when a pathogen interacts with the resistant host plant, and a complex molecular mechanism regulates the spread and the intensity of these responses. Plants are protected against a wide range of insect herbivores, which feed on plants like chewers, suckers, and cell content feeders by jasmonate response. Various experiments have been done to prove the role of Jasmonic acid in plant defence against pathogenesis especially against the necrotrophic fungal and bacterial pathogens, insects, nematodes, etc. During the defence response, there is a crosstalk between jasmonic acid pathways with other phytohormones. In this chapter, we will focus on the role of Jasmonate in plant defence against pathogens and the crosstalk of Jasmonate with other hormones.

1 Introduction

Going through this evolution process, every organism has to face a lot of biotic and abiotic stresses. Therefore, to tackle this environmental stress, plants have developed various strategies and defense systems for their protection without compromising the

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resource for their other developmental processes (Vijayan et al. 1998; Thaler et al. 2004; Okada et al. 2015; Checker et al. 2018). The plant/host defense strategy is successful only when the host rapidly able to identify the attacking pathogen and triggers the downward signalling cascade, which will activate the host's defense mechanism, making the host either resistant towards the pathogen attack or minimizing the damage caused by it (Okada et al. 2015). Plant induces localized and systemic responses to defend them from pathogen attacks like fungal and microbial attacks (Vijayan et al. 1998; Oka et al. 1999).

When a pathogen attacks a host plant, a localized hypersensitive response got triggered in the host, and its intensity is under the regulation of complex molecular mechanisms. Along with this hypersensitive response, within plants, long distance signals that got initiated at the site of infection will trigger the expression of pathogenesis-related genes (PR genes) in the uninfected regions of the plant (Ryals et al. 1994; Van Loon 2000; Oka et al. 1999). In the defense system, various phytohormones have been known to play a very crucial role; the phytohormone mainly jasmonic acid (JA) and its derivative, salicylic acid (SA) and its derivative and ethylene (ET) are critical regulators of the defense response against the pathogens (Okada et al. 2015; Berens et al. 2017; Checker et al. 2018; Acevedo et al. 2019).

The JA and its derivatives regulate the process of growth, development, and response to stress by interacting antagonistically or synergistically with the signalling pathways of other phytohormones or vice versa, referred to as signalling crosstalk and thereby regulating the expression of a various downstream resistant gene present in the host against the attacking pathogen (Checker et al. 2018).

2 Role of Jasmonate in Pathogenesis

Jasmonic acid and its derivatives are well known to protect the plant against many herbivore insects that feed on the plant, e.g., phloem sap suckers like aphids, chewers like the leafhoppers, cell content feeders, etc. and pathogens like fungus, nematode, bacteria, and virus (Walling 2000; Thaler et al. 2002, 2004).

2.1 Fungus as Pathogen

Interaction between Fungi and plants occurs in many ways. Each interaction leads to different alterations in plants and fungi (Zeilinger et al. 2016). Both partners secrete a wide range of molecules helping in crucial functions like signalling, development and stress response (Vincent et al. 2019; Delaunois et al. 2014). Fungi interact in both ways - positively and negatively with plant roots and above-ground parts of plants in the rhizosphere called mutualistic fungi and pathogenic fungi, respectively (Zeilinger et al. 2016; Grigoriev 2013). Mutualistic fungi increase the plant defence response against pathogens or its nutrient uptake, whereas pathogenic fungi lead to deleterious effects on the plant's physiology (Zeilinger et al. 2016).

When a plant interacts with pathogenic fungi then, it results in plant destabilisation and when it interacts with beneficial fungi, then both the partners get the stability. Plants destabilisation then further leads to the survival pressure and hence, faster plant evolution (Zeilinger et al. 2016; Jones and Dangl 2006). When both of the interactions are seen from the evolutionary point of view, when the plant interacts with a biotrophic pathogen, then the fungi get evolved in order to become a successful parasite (Zeilinger et al. 2016).

There are receptors present on the plasma membrane of the plants, i.e., Pattern recognition receptors (PRRs), which recognizes MAMPs/PAMPs, which further leads to the activation of Pattern triggered immunity (PTI) through MAPK cascade. Effectors released by a pathogen, here fungi interfere with PTI, hence inactivation of PTI which leads to induction of susceptibility i.e., Effector Triggered Susceptibility (ETS). Meanwhile, effectors are recognized by the R proteins of plants, which activate Effector Triggered Immunity (ETI) of the plant and hence activating the host defense genes (Fig. 1) (Zeilinger et al. 2016).

Jasmonic acid is the mainstay hormone in response to necrotrophic pathogens (Scalschi et al. 2020). There are diverse sets of receptors present on plants which

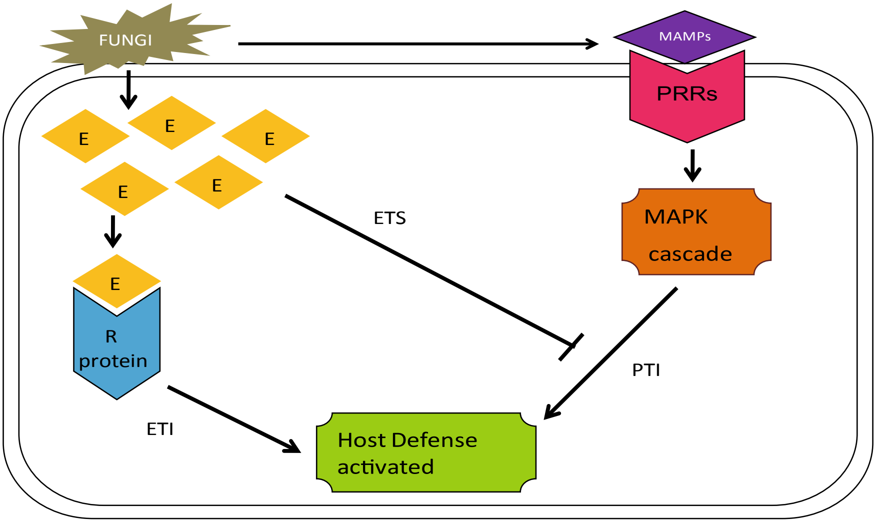


Fig. 1 Schematic representation of signaling in plant-fungal pathogen interaction. The fungal pathogen Microbe Associated Molecular Pattern (MAMPs) are recognized by the Pattern Recognition Receptors (PPRs), leading to the downstream signaling and activates pattern triggered immunity (PTI). Finally, the host defense mechanism is activated. The fungal pathogen will release some effector molecules into the host, causing the effector-triggered susceptibility against the PTI making the host susceptible. The effector (E) molecules recognized by the R-proteins of the host will induce the Effector Triggered Immunity (ETI), and defense system of the host activated, and host become resistant to the fungal pathogen

perceives signal from outside which further activates plants immune system. Receptors sense a wide range of signals from the outside, like signals by pathogen like elicitors to internal signals like phytohormones production, like Jasmonic acid (JA), Salicylic Acid (SA), Ethylene (ET), etc. (Antico et al. 2012).

2.1.1 The Positive Effect of Jasmonates: Defend the Host Plant Against the Fungal Attack

In *Arabidopsis* as the Host Plant and *Pythium mastophorum* as the Pathogenic Fungi

Pythium mastophorum is a fungal pathogen causing root rot disease. It occurs periodically and leads to loss of plant vigour and uneven plant growth.

Mutant Plants (fad3–2 fad7–2 fad8) highly prone to *Pythium* Infection as mutants, of course, does not stockpile the jasmonates as mutant were deficient in lipid precursor of jasmonate, i.e., linolenic acid was studied. In research, it was found that fad3–2 fad7–2 fad8 mutant plants were susceptible to a large extent to *Pythium mastophorum*, which causes root rot disease, i.e., it is a root pathogen and the wild type plants even though growing in the adjacent space of these mutant plants were not affected whatsoever by this root pathogenic fungi (Vijayan et al. 1998).

Jasmonate directly does not affect the fungal growth or infectivity as it was thought initially that jasmonate has a direct role in pathogenesis against fungi. Mutant plants were treated externally by methyl jasmonate, reducing the disease symptoms, close to the wild type plants. However, later found that Jasmonate does not directly affect fungi growth or fungal infection. Instead, it acts by directly inducing plants' defense genes, which act against the fungus. A jasmonate-insensitive mutant coi1 was taken and similar treatment with Methyl Jasmonate was given which was not able to protect the plant from fungal infection, indicating that jasmonate does not have direct antifungal action, rather induce plant defenses against the fungus (Vijayan et al. 1998).

Jasmonate-Responsive Genes activated in Wild-Type plants but Not Mutant Plants by *Pythium*. In contrast, this study that in wild type plants, 3 Genes—Lipoxygenase encoding genes, Chalcone synthase catylase gene (a critical step in a wide range of secondary metabolite production) and Arabidopsis PDF1.2 gene have considerable increase at the transcriptional level. Mutant plants, on the other hand, do not show any increase in the transcriptional level of these three genes (Vijayan et al. 1998).

In the Case of Tomato (*Solanum lycopersicum*) as the Host Plant and *Botrytis cinerea* as the Pathogenic Fungi

The fungus *Botrytis cinerea*, a necrotrophic plant pathogen, causes gray mold in vegetables and fruit softening. It has a broad range of hosts like tomato, potato, grapes, strawberry, etc. JA Signalling provides resistance against *B. cinerea* isolate for which there are two JA-dependent genes- proteinase inhibitors I and II (PI I and PI II). In wild type (cv Moneymaker), expression levels of these 2 genes were checked and it was found that out of two isolates (B191 and B8403) of B. cinerea, B8403 leads to an increased level of JA—dependent genes, PI I and PI II while other isolate B191, able to induce lower level. In wild-type cv, Castlemart, mutants def1 (for Defenseless1) and Spr2 (for suppressor of prosystemin-mediated responses2) shows the same results. Mutants were prone to *B. cinerea* isolate B8403; unlike WT, the lesion's size was 2 times large in mutants (El Oirdi et al. 2011).

A polypeptide provides Resistance to Tomato against *B. cinerea* which is Systemin, present after infestation by both isolates of Botrytis and by quantitative RT-PCR analysis, it was found that there is systemin Systemin (a polypeptide) is an elicitor of JA signalling in tomato. In WT, the antisense (AS) line was prone to isolate B8403. Also, lesion size was fivefold more than WT plant. Level of PI I and II were dependent on systemin (El Oirdi et al. 2011).

B. cinerea secretes an exopolysaccharide that acts as a suppressor of the JA Signaling Pathway, suppressing the plant immune system. High molecular weight carbohydrates (EPS) is known as b-(1,3) (1,6)-D-glucan which is produced by many pathogenic fungi and bacteria. 5-week old tomato plants were taken. The control was treated with water and experimental plants with EPS; it was found that there is a reduction in PI I and PI II expression. So, it is concluded that EPS suppresses the JA signalling pathway and promotes the growth of *B. cinerea* (El Oirdi et al. 2011).

2.2 Nematode as the Pathogen

Nematodes are microscopic parasitic roundworms that are pathogenic to 1000s of the crop plant species (Vovlas et al. 2005; Castillo et al. 2008; Zwart et al. 2019). The damage caused by the pathogenic nematode in the host plant reduces the functionality of roots, due to which the infected host plant is unable to take up nutrients and water properly. Therefore, the plant shows deficiency symptoms as chlorosis, wilting, stunting, reduced number of flowers and pods, reduction in the ability of the plant to cope with abiotic stresses and this will reduce the overall yield drastically (Williamson and Hussey 1996; Castillo et al. 2008; Zwart et al. 2019).

There are various types of pathogenic nematodes infecting the crop plant species all over the world. Depending upon the symptoms, the severity of the infection, and the amount of damage caused by them on the major crop plants all across the world, the following are the primary type we are going to discuss and also the role of jasmonate antagonistic or synergistic with the plant defense system against this pathogenic nematode.

Root Knot Nematodes (RKN) is a group of roundworms with microscopic sedentary endoparasites (Vovlas et al. 2005; Zwart et al. 2019). Female nematode penetrate the roots of various host plant species. After reaching the vascular bundle, they trigger

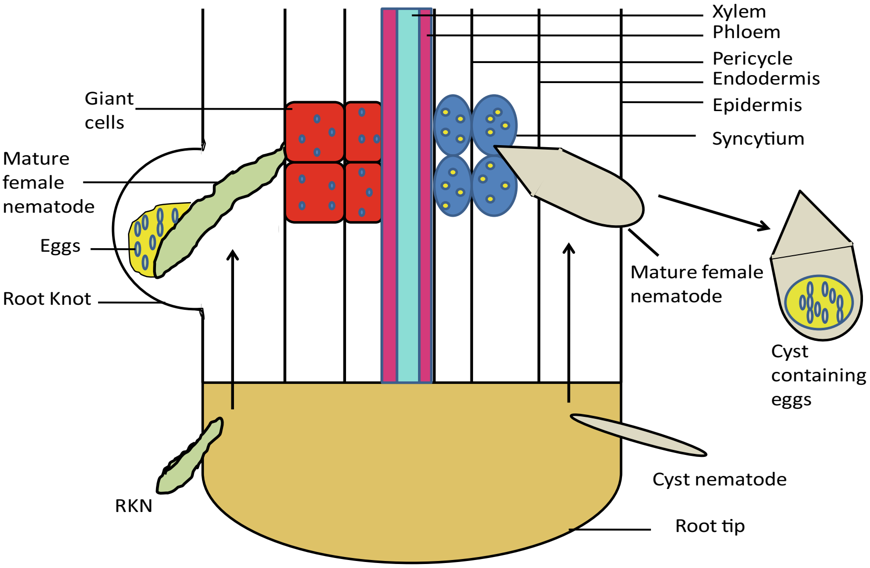


Fig. 2 Schematic representation of the root infected from the Root-Knot Nematode (RKN) and Cyst Nematode

some changes which result into the gall or the root-knot formation and some specialized feeding cells, called "giant cells" in the root of the host plant (Fig. 2) (Williamson and Hussey 1996; Milligan et al. 1998; Zwart et al. 2019). *Meloidogyne* spp. rank as the most economically damaging RKN to the agriculture crop worldwide due to their broad range of host and wide geographical distribution (Jones et al. 2013).

Cyst nematodes are microscopic sedentary semi-endoparasite. After infestation in the root, the nematode reaches the vasculature and form permanent feeding sites characterized by "Syncytia cells" (Greco et al. 1992; Nombela et al. 1992; Sharma et al. 2003). The female nematode increases in size and ruptures the root tissues, which then protrude from the root surface, forming a visual cyst containing eggs in it (Fig. 2) (Kaloshian et al. 1986; Zwart et al. 2019). *Heterodera* spp. are the most economically damaging cyst nematode worldwide causing damage to different crop plants like chickpea, garden beet, table beet, canola, and various ornamental plants (Saxena et al. 1988; Di Vito et al. 2001; Zwart et al. 2019).

2.2.1 The Positive Effect of Jasmonates: Defend the Host Plant Against the Nematode Attack

Various experimental pieces of evidence show the role of jasmonate in plant defense against the nematode. Just after the nematode infestation, the synthesis of JA triggered rapidly, both at the site of infestation (locally) and in the undamaged parts of the plant (systematically). It prevents the nematode from feeding upon the host plant,

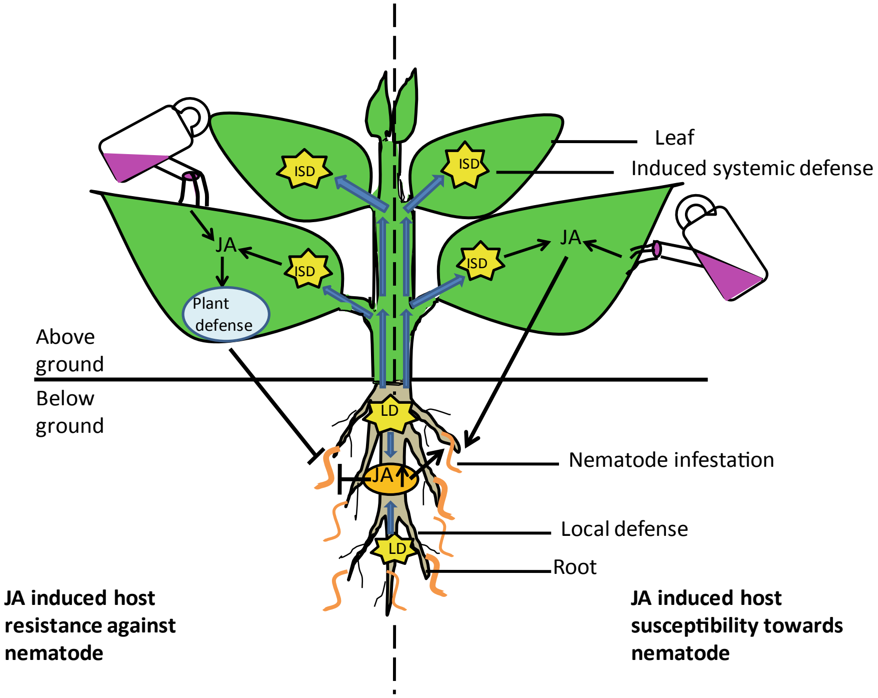


Fig. 3 Schematic representation of local and induced systemic defense stimulated in the host plant due to nematode infestation in the root. The foliar spray of methyl jasmonate (MeJA) onto the different infected host plant species had shown a positive role by increasing the host resistance in some and a negative role by increasing the host susceptibility to the nematode infestation in others

suppresses their growth and reproduction through activating defense-related gene expression, production of toxic secondary metabolites, and generation of volatile compounds (Fig. 3) (Cohen et al. 1993; Cooper et al. 2005; Yan and Xie 2015).

In Case of Tomato (*Solanum lycopersicum*) as a Host Plant and *Meloidogyne* sp. as the Pathogenic Nematode

Plants have various resistance genes against these nematodes, for example:

Mi gene in tomato (*Solanum lycopersicum)* effective against common RKN species like *Meloidogyne arenaria, M. javanica, M. incognita* (Vos et al. 1998; Milligan et al. 1998; Rossi et al. 1998). The effectiveness of the Mi gene is temperature dependent; at moderate temperature, it can effectively resist the nematode feeding and reproduction, but at higher temperature (>28 °C) the gene loses its effectiveness (Abdul-Baki et al. 1996; Cooper et al. 2005). JA foliar application induces systemic defense response in the susceptible tomato plant which significantly reduced avirulent nematode (*Meloidogyne javanica* isolate 557R) reproduction but not the virulent nematode (*M. javanica* isolate VW5 and *M. incognita* isolate 557R). This JA mediated defense proved to be heat stable compared to the Mi mediated defense response which reduces at a higher temperature (Cooper et al. 2005).

Protease inhibitor (*Pis*) and multicystatin (MC) gene expression in tomato increases after the nematode infestation, and a negative correlation was found between the Pis and MC expression and RKN infection (Fujimoto et al. 2011). The exogenous foliar application of methyl jasmonate (MeJA) was given to the infected host plant. It was observed that as the concentration of MeJA increases, there was a significant decrease in the RKN infection rate. Furthermore, the MeJA mediated defense was independent of these two gene expressions in the host plant (Fujimoto et al. 2011).

In the Case of Rice (*Oryza sativa*) as a Host Plant and *Meloidogyne graminicola as* Pathogenic Nematode

OsPR1a and OsPR1b pathogenesis-related genes in rice (*Oryza sativa*) are effective against nematode *M. graminicola* (Nahar et al. 2011; Trang Nguyen et al. 2019). It has been observed that the nematode infestation in the root of rice plant could attenuate the defense genes in root galls and down-regulate the JA-responsive PR genes *JiOsPR10* (Nahar et al. 2011). The *hebiba* mutant of rice contains a mutation in the allene oxide synthase (AOS) was hyper-susceptible to the RKN infection and also the experimental blocking up of JA biosynthesis in rice by lipoxygenase (*LOX*) inhibitor has increased the host susceptibility towards the RKN (Nahar et al. 2011).

The exogenous supply of methyl jasmonate and ethaphone to the infected host plant induces the strong systemic defense into the roots by upregulating these defense-related genes and also by preventing the nematode in counteracting root defense pathways, hence making the plant more resistant to the nematode infection (Nahar et al. 2011).

In Case of *Arabidopsis* sp. as the Host Plant and *Meloidogyne hapla* as Pathogenic Nematode

The mutants of Arabidopsis, i.e., *fad3-2 fad7-2 fad8* and *dde2-2* were more susceptible to *M. hapla* as they are deficient in the biosynthesis of JA and its precursor *cis-(+)-12-oxo*-phytodienoic acid (OPDA), the mutant *delayed dehiscence 2* (*dde2-2*) lack JA biosynthesis as it is defective in allene oxide synthase (AOS), which indicate that JA or OPDA are key defense molecules in the interaction of plant and nematode (Sanders et al. 2000; Stintzi and Browse 2000; Gleason et al. 2016).

The application of methyl jasmonate (MeJA) or the JA -mimic coronatine (COR) on *Arabidopsis* accumulates OPDA along with JA/JA-Isoleucine, indicating a positive feedback loop and has significantly reduced the number of galls caused by the RKN *M. hapla* (Gleason et al. 2016).

In Case of Sugar Beet as Host Plant and *Heterodera schachtii* as Pathogenic Nematode

The reason for significant yield loss of sugar beet (*Beta vulgaris*) and other food crops including garden beet, table beet, canola, etc., is the infestation by a cyst forming nematode *H. schachtii* (Ghaemi et al. 2020). The infested plant shows a pale yellow colour and wilting (Khan et al. 2016; Ghaemi et al. 2020).

The exogenous application of methyl jasmonate on the host plant after the invasion has significantly reduced the number of female plants compares to the untreated control, showing the positive role of JA in systemic defense of sugar beet against the *H. schachtii* (Ghaemi et al. 2020).

2.2.2 The Negative Effect of Jasmonates: Jasmonate Making the Host Susceptible to the Nematode Attack

Some experimental results show that the JA promotes the host susceptibility to RNK (Machado et al. 2018; Bhattarai et al. 2008; van Dam and Heil 2011). Various studies have demonstrated that the main reason behind this is the defense response induced in the host plant by the above-ground herbivory which systemically affects the below-ground defense response and thus indirectly the below-ground pathogen or the root feeder (Fig. 3) (Kafle et al. 2017; Wang et al. 2017; Hoysted et al. 2017, 2018; Machado et al. 2018; Mbaluto et al. 2020).

In Case of *Nicotiana attenuata* as a Host Plant and *Pratylenchus hexincisus*, *Meloidogyne incognita* and *Ditylenchus* sp. as Pathogenic Nematode

In *Nicotiana attenuata*, it has been proposed by many workers that jasmonates work as the regulatory signal in a plant that mediates an interaction between the leaf-feeding caterpillar *Manduca sexta* and parasitic root nematode (van Dam and Heil 2011; Machado et al. 2018).

This interaction was found to be negative for the host plant as it decreases the reproductive capability of the plant (the evidence of which are the reduction in the number of the flower counts) and positive for the nematode (the evidence for which are the increased number of the eggs and easy infestation of the nematode in the roots of the host plants) (Machado et al. 2018).

In the Case of *Arabidopsis* as a Host Plant and *Meloidogyne* spp. and *Heterodera schachtii* as Pathogenic Nematode

The two isoforms mutants of *Arabidopsis* 13-lipoxygenases (13-LOXs), i.e., l*ox3* and l*ox4,* were examined for the response to the infection by the sedentary nematodes RKN (*M. javanica*) and cyst nematode (*H. Schachtii*) (Ozalvo et al. 2014).

The lox4-1 mutant of *Arabidopsis* accumulated high JA content and is more susceptible to RNK and cyst nematode, as shown by an increase in the number of female nematodes. Therefore, this positive correlation between the high JA level and high female nematode count in the host shows that JA has a role in increasing host susceptibility towards the pathogen (Ozalvo et al. 2014).

In the Case of Tomato (*Solanum lycopersicum*) as a Host Plant and *Meloidogyne* spp. as the Pathogenic Nematode

Different mutants of tomato were evaluated in the presence or absence of RKN resistance Mi-gene (Dropkin 1969; Li et al. 2001, 2004b); the jasmonic acid-insensitive1 (*jai1*) and defenseless1 (*def1*) tomato mutant have altered JA signalling. The *jai1* mutant can produce endogenous JA but is impaired in JA perception (Bhattarai et al. 2007b).

To confirm the role of JA in the defense, the mutant *jai1*, and *def1*, along with the control plants, were evaluated for the count of female nematode and number of egg mass per root. The result shows that *jai1* reduced host susceptibility to RKN compared to the *def1* mutant and the control host plant. Therefore, an intact JA signaling pathway is required for tomato susceptibility to RKN but its effect is independent of Mi mediated defense (Bhattarai et al. 2008).

2.3 *Virus as the Pathogen*

Viruses are biotrophic pathogens requiring living tissue for their multiplication (Pallas and García 2011). Their transmission of the virus from one host plant to the other is always through some vector mainly insect vector-like aphid (*Myzus persicae*), whitefly (*Bemisia tabaci*), leafhopper (*Nephotettix cincticeps, Sagotella furcifera*), or planthopper (*Nilaparvata lugens, Laodelphax striatellus*) (Dietzgen et al. 2016). Sometimes human contact with the infected plant then the healthy plant can also transmit the virus. The virus interacts with the host in many ways and finally took over the machinery of the host or/and vector, start using it for its multiplication (Dietzgen et al. 2016).

The infection of the virus will trigger the hypersensitive response (HR) into the host due to some specific molecular interaction when a product of plant resistance (R) gene directly recognizes the product of corresponding viral pathogenic avirulence gene (Heath 2000; Carr et al. 2010; Dietzgen et al. 2016). Due to HR phytohormones, especially JA and SA, start accumulating in the host (Kenton et al. 1999) and necrotic lesions start forming to prevent the systemic spread of the virus (Seo et al. 2001; Oka et al. 2013). The viral effector proteins target the JA-mediated plant defense mechanism and interact at a different level, for example, directly with the MYC gene or with JAZ, with downstream signalling pathway (Table 1) (Fig. 4) (Wu and Ye 2020; Kazan and Lyons 2014). The viral infection will cause various disease symptoms,

Table 1 Virus effector proteins targeting JA mediated defense mechanism in the host increases their transmitting vector's feeding onto the infected host

Virus	Viraleffector protein	Target in plant	Resulted function	Vector	References
Cucumber mosaic virus	2b	SCF-COI1 mediated JAZ Ubiquitination	Intact JAZ will inhibit MYC, therefore, inhibiting downstream gene regulated defense mechanism	Aphid *Myzus persicae*	Wu et al. (2017), Wu and Ye (2020)
Tomato yellow leaf curl virus	C2	SCF-COI1 mediated JAZ Ubiquitination	Disrupted JA mediated secondary metabolite (terpene) biosynthesis and defense-related gene activation	Whitefly *Bemisia tabaci*	Li et al. (2019), Wu and Ye (2020)
Tomato yellow leaf curl China virus	βC1	MYC2	Destabilize defense gene-related activities and compromise terpene synthesis	Whitefly *Bemisia tabaci*	Li et al. (2014), Wu and Ye (2020)
Tomato yellow leaf curl Sardinia virus	C2	CSN5 mediated Ubiquitination	Reduced JA mediated defense against the vector	Whitefly *Bemisia tabaci*	Lozano-Durán et al. (2011), Kazan and Lyons (2014)
Tobacco spotted wilt virus	Ns (nonstructural protein)	SA-JA antagonistic pathway	JA-SA antagonism disturbed, SA level increases, and JA mediated defense reduces	Thrip *Frankliniella occidentalis*	Abe et al. (2012), Kazan and Lyons (2014)
Beet curly top virus	L2	CSN5 mediated Ubiquitination process	JA defense downstream signaling reduces	Beet leafhopper *Circulifer tenellus*	Lozano-Durán et al. (2011), Kazan and Lyons (2014)

(continued)

Table 1 (continued)

Virus	Viraleffector protein	Target in plant	Resulted function	Vector	References
Cauliflower mosaic virus	2b	JA responsive defense gene	Reduced JA mediated defense against the vector	Aphid *Myzus persicae*	Lewsey et al. (2010), Kazan and Lyons (2014), Ziebell et al. (2011)
Tobacco curly shoot virus	βC1	JA responsive defense genes (PDF1,2 and PR4)	JA production on wounding got reduced, and therefore the vector could quickly infect the host with the virus	Whitefly *Bemisia tabaci*	Zhang et al. (2012), Jiu et al. (2007), Kazan and Lyons (2014)
Tomato spotted wilt orthospovirus	Ns (nonstructural protein)	MYC2, MYC3, MYC4	Disabled JA mediated host defense against the vector	Thrip *Frankliniella occidentalis*	Wu et al. (2019), Wu and Ye (2020)

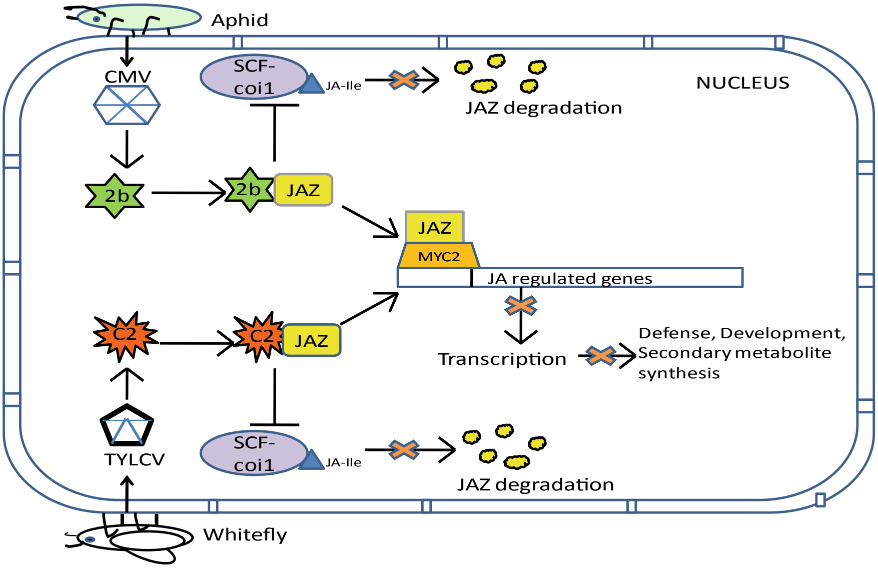


Fig. 4 Schematic representation of the virus hijacking the JA mediated defense mechanism of the host plant. The effector molecule 2b of cucumber mosaic virus (CMV) and C2 of tomato yellow leaf curl virus (TYLCV) interacts with the JAZ molecule (inhibitor molecule of transcription factor MYC2). It prevents it from degradation by SCF^{coi1} mediated Ubiquitination machinery. Therefore, no further downstream defense signaling will occur, and the host will become susceptible

mainly mosaic leaf patterns, crinkled leaves, stunted plant growth, yellowing of leaves (Isleib 2012).

2.3.1 The Positive Effect of Jasmonates: Jasmonate Defends the Host Plant Against the Viral Attack

Jasmonic acid and its derivatives play an important role in plant defense against the viral attack directly or by resisting their vector attack on the host, especially the insect vector (Okada et al. 2015; Zhang et al. 2016).

In the Case of *Oryza sativa* (Rice) as the Host Plant and *Rice Ragged Stunt Virus* (RRSV) as the Pathogenic Virus

miRNAs have a critical role in modulating the host–pathogen interaction, leading to antiviral immunity or viral pathogenesis (Du et al. 2011; Wang and Luan 2015; Yang et al. 2016). The rice plants were inoculated with viruliferous *Nilaparvata lugens* carrying RRSV. The RRSV infected rice plants were analyzed for the amount and function of miRNA319 (Zhang et al. 2016). The result shows that the RRSV induces a higher accumulation of miRNA319a and miRNA319b and the host plant displayed a diseased phenotype. It enhanced susceptibility to RRSV, indicating the role of miRNA319 in disease induction and host susceptibility. The miRNA319 manipulated the JA pathway in the host, making it susceptible to the viral infection (Zhang et al. 2016).

The exogenous supply of methyl jasmonate to the wild-type (WT) plant and then inoculation with RRSV shows an increase in the production of pathogenesis-related genes PR1a, PR1b, PR5 and PR10, decreased RRSV accumulation. The JA biosynthesis pathway was blocked by applying diethyldithiocarbamate acid (DIECA), a lipoxygenase inhibitor, making the host less resistant to the RRSV attack (Zhang et al. 2016). All this evidence shows that an intact JA biosynthetic pathway and a high amount of endogenous production are required for the host resistance against the RRSV infection (Zhang et al. 2016).

In the Case of *Triticum aestivum* (Wheat) as the Host Plant and *Rice Black-Streaked Dwarf Virus* (RBSDV) as the Pathogenic Virus

RBSDV is a member of the genus Fiji virus (family Reoviridae), infects a wheat plant and induces stuntedness with dark green leaves and white tumor, or black-streaked swellings along the veins on the back of leaf blade and sheath (Morales 2008; Zhang et al. 2016).

Using Liquid Chromatography-Mass Spectrometry (LC–MS) technique, it was estimated that in the RBSDV infected wheat plant, the amount of miRNA319 had increased significantly, and there was a twofold decrease in JA accumulation (Zhang et al. 2016). Therefore, considering the results, miRNA serves as a critical regulator to facilitate the infection of viruses in different plant species by suppressing the JA-mediated defense (Zhang et al. 2016).

2.3.2 The Negative Effect of Jasmonates: Jasmonate Making the Host Susceptible to the Viral Attack

Jasmonic acid plays a negative role as it was found that it is more active against necrotrophic pathogens than the biotrophs (Nahar et al. 2011; Zhang et al. 2016). The virus hijacks the host machinery and the external supply of jasmonates was found to promote the systemic movement of the virus and hence making the host more susceptible to the infection (Oka et al. 2013).

In the Case of *Nicotiana tabacum* (Tobacco) as the Host Plant and *Tobacco Mosaic Virus* (TMV) as the Pathogen Virus

When the tobacco mosaic virus-infected the stable transgenic tobacco cultivar having the N-resistance gene and suppressed JA biosynthetic pathway, a hypersensitive (HR) response got induced in the host plant (Oka et al. 2013). It was observed in the experiment that the exogenous application of methyl jasmonate reduces the local resistance to the TMV and the necrotic lesions increased as it permits the systemic viral movement (Oka et al. 2013). Silencing of allene oxide synthase (AOS), a JA biosynthetic enzyme, and CORONATINE-INSENSITIVE 1 (COI1), a JA receptor in the tobacco, enhanced the resistance to TMV in the host tobacco plant possessing the N-resistance gene.

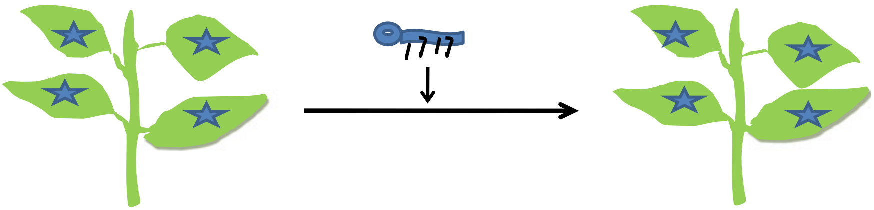
This evidence shows that JA negatively regulates the defense against the tobacco plant's TMV (Felton et al. 1999; Oka et al. 2013). Further analysis found that the endogenous level of SA got increased in the AOS and COI1 silenced plants; therefore, SA was found to play a positive role in the defense mechanism. Also, in the case of tobacco plants lacking both N-resistance gene and the COI1 JA receptor, the susceptibility to the virus does not change; this shows that JA is not directly involved in the susceptibility but is indirectly affecting it through inhibition of the SA mediated resistance (Hind et al. 2011). Therefore, a balance between the SA and JA level is required for the plant resistant ability against virus infection (Oka et al. 2013).

2.4 *Herbivore Insect*

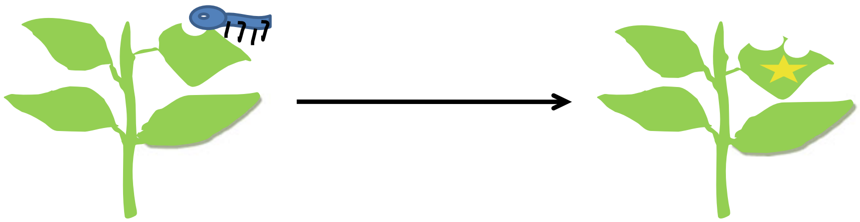
Interaction between plants and insects occurs in many different ways (Calatayud et al. 2018). In an ecosystem, both interact in a very complicated way. Plant–Insect interaction can be classified into three different categories—Mutualistic, Antagonistic and Commensalistic. In Mutualism, both partners are benefitted, neither one is harmed, for examples, when insect act as a pollinator, defender, Seed dispersal, on the other hand, plant act as a food provider, shelter provider, oviposition site provider (Mello and Silva-Filho 2002; Calatayud et al. 2018). In Antagonism, one partner is benefitted and the other one is harmed, for example, Insectivory (plant feeding on the insect, i.e., Insectivorous plants) and phytophagy (insect feeding on plant i.e., Insect as a pest). In Commensalism, one partner gets benefitted but another one neither harmed nor benefitted, for example, the relation between monarch butterfly with certain milkweed species for defense. Insects and plant community gets co-evolved and this was first highlighted by the pioneer scientist Charles Darwin (Calatayud et al. 2018).

Plant defends themselves from pathogen attack in two different ways—either by the constitutive defense or induced defense, which involves basal resistance and highly specific resistance (Fig. 5) (Jones and Dangl 2006).

In constitutive defense, herbivores are repelled either by direct toxicity or by decreasing tissues' digestibility (Mello and Silva-Filho 2002). In induced defense, herbivores are prevented by some substances which are produced in response to herbivore attacks like an antibiotic or antixenotic metabolites (Zhang et al. 2018; Bleeker et al. 2009; Luan et al. 2013) and by the release of certain volatile compounds which gives signal to parasitoids or predators of that herbivore (Fig. 5) (Turlings et al. 1990; Kessler and Baldwin 2001; Dicke et al. 2009; Zhang et al. 2018).



(a) Constitutive Defense- always present irrespective of any insect attack



(b) Induced Defense- Activated in response to insect attack

Fig. 5 Schematic representation of (**a**) Constitutive defense present in the host every time irrespective of the insect attack, providing the basal level of resistance to the host against the attacking insect, (**b**) Induced defense activated only when the pathogen attacks the host plant

Jasmonic acid (JA) signaling is very important in induced defense responses against herbivore attacks (Zhang et al. 2018; Ament et al. 2004; Kessler et al. 2004; Thaler et al. 2012). In some cases, SA and ET signaling is also vital. It gets triggered when certain herbivores attack the plant and it perceives elicitors or herbivore—associate molecular patterns (HAMP) along with certain anti herbivores defense responses (Zhang et al. 2018; Schmelz et al. 2009).

For example, in a tomato plant, after blocking of JA production or its action makes the plant vulnerable to herbivore attack (Zhang et al. 2018; Bosch et al. 2014).

2.4.1 Role of Jasmonic Acid in Plant Defense Against Insects

In *Arabidopsis* as the Host Plant and *Bradysia impatiens* as the Insect Pest

Fungus gnat, *Bradysia impatiens*, is a common root pest of plants on liliaceous crops and edible fungi.

Mutant Plants has very Low Levels of Jasmonate—The fad3–2 fad7–2 fad8 mutant of Arabidopsis was used in the experiment. It was found that there is a very negligible level of Jasmonic acid's precursor Ie, Linolenic acid. The mutant plant also shows a very high mortality rate upto 80% due to the attack by larvae of a common saprophagous fungal gnat, *Bradysia impatiens* (Diptera: Sciaridae). Wild plants growing nearby were not affected whatsoever (McConn et al. 1997).

The Jasmonic acid level in both wild type and mutant type plants was measured before and after wounding in both leaves and roots (Table 2) (McConn et al. 1997).

It can be seen from the Table 1 that unwounded leaves have a very low level of Jasmonic acid, in both WT and mutant type, but after wounding increased to many folds in both, in case of the leaf; however, in roots, this is not so. In both WT and mutant, the level of jasmonate more or less is the same (McConn et al. 1997).

Jasmonate is both important and sufficient for plant defense. Mutant plants were first sprayed with water and subjected to *Bradysia impatiens*; about 80% of plants died and wild type plants remained unaffected. Other sets of mutant plants

Table 2 Jasmonate level in mutant and wild type plants in wounded and unwounded leaves and roots

	Leaf		Root	
	Unwounded (per g [fresh weight])	Wounded (per g [fresh weight])	Unwounded (per g [fresh weight])	Wounded (per g [fresh weight])
Wild type plant	Less than 35 ng of jasmonate	increased more than 20-fold to 725 ng after 1 h of wounding	less than 7 ng	less than 7 ng
Mutant type plant	34 ng of jasmonate	326 ng after 3 h of wounding	only 8 ng	only 8 ng

Table 3 Transcript level of wound induction of gene expression in wild-type (wt) and fad3–2 fad7–2 fad8 Arabidopsis

	Wild type		Mutant type	
	Unwounded	Wounded	Unwounded	Wounded
AtVSP		+ + + + + + + + + + + + + + + + (after 4 h incubation)	0	0
DHS1	+ +	+ + + + + (after 2 h incubation)	–	–
PAL1	+ +	+ + + + (after 2 h incubation)	–	+ + +
GST	–	+ + +	–	+

0 Zero Levels, – Basal Level, + Normal Level/Increased Level

were sprayed with Methyl jasmonate and the mortality rate reduced to 12%; most of the plants show no or very negligible damage (McConn et al. 1997).

When linolenic acid gets breakdown, it yields several other compounds through the hydroperoxide lyase pathway required in plants' defense (Croft et al. 1993; Farmer 1994). Major compounds are—trans-3-hexenol, trans-2-hexenal, cis-3-hexenol, and traumatic acid (Croft et al. 1993). To test the efficiency of these compounds in plants defense along with jasmonic acid, another spray experiment was conducted, in which 0.001% Jasmonate taken as positive control and water spray taken as negative control along with an additional spray of an aqueous solution of 0.01% trans-3-hexenol, 0.01% trans-2-hexenal, 0.01% cis-3-hexenol, and 0.01% traumatic acid, each compound at 10 folds higher. Only 0.001% of Jasmonate was efficient enough to protect plants from a fungal gnat, which indicates that Jasmonate Is Both Important and Sufficient for Plant Defense against larvae attack (McConn et al. 1997).

Expression of Wound-Induced Genes in Wild-Type and Mutant Plants (Table 3).

AtVSP gene—stands for Arabidopsis Vegetative Storage Protein. It is an Anti-Insect Acid Phosphatase (Liu et al. 2005), which encodes a protein homologous to soybean VSP alpha VSP beta (Berger et al. 1995; Liu et al. 2005). This gene gets induced by wounding, methyl jasmonate, and insect feeding (Liu et al. 2005).

DHS1 gene—stands for Deoxyhypusinesynthase, which encodes a key enzyme in lignin ie, 3-deoxy-D-arabinoheptulosonate-7-phosphate Synthase (Keith et al. 1991).

PAL1 gene—encodes for phenylalanine ammonia-lyase, a key enzyme in catalyzing the first reaction in the biosynthesis of L- phenylalanine (Wanner et al. 1995).

GST gene—stands for glutathione S-transferase, which protects plants from oxidative tissue damage caused by wounding or pathogen attack (Kim et al. 1994).

A complimentary experiment was carried out to know the jasmonate's role, in which unwounded wild type and mutant plant were given water and 0.001% methyl jasmonate spray (Table 4) (McConn et al. 1997).

Table 4 Transcript level of Jasmonate induction of gene expression in wild-type (wt) and fad3–2 fad7–2 fad8 Arabidopsis (after 1.5 h incubation)

	Wild type		Mutant type	
	Unwounded (Control)	UnWounded (0.001% Jasmonate)	Unwounded (Control)	UnWounded (0.001% Jasmonate)
AtVSP	+ +	+ + + + +	–	+ +
DHS1	+ +	+ + + +	–	+ +
PAL1	–	–	–	–
GST	–	–	–	–

0 Zero Levels, – Basal Level, + Normal Level/Increased Level

GST Gene, which gets activated in wounding, does not show any response after jasmonate treatment showcasing that there is another wound signaling pathway independent of jasmonate (McConn et al. 1997).

In the Case of Tomato as the Host Plant and *Bemisia tabaci* as the Herbivorous Insect

Bemisia tabaci, also informally referred to as the silverleaf whitefly, is one of several whiteflies species that are currently important agricultural pests. In this study, Wild type tomato plants {Castlemart (CM)} and mutant plants (JA silenced spr-2 and def-1, 35 s::prosys), in which there is constitutive activation (35s::prosys) and impairment of JA signaling pathway (spr-2 and def-1) were taken and comparison was made about the performance of *B. tabaci* adults and nymphs on both wild type and mutants, along with wild type treated with exogenous JA or SA (Zhang et al. 2018). After *B. tabaci* infestation on tomato plants, changes in the endogenous level of JA and transcript level of JA regulated defense-related genes were studied (Zhang et al. 2018).

Results are as follows

Adult performance of *Bradysia impatiens*—Number of eggs laid per day per female and adult survival rate did not differ on the wild type and mutant type, which indicates JA-dependent defenses do not affect the adult performance of *B. tabaci* (Zhang et al. 2018).

Nymph performance of *Bradysia impatiens*—The number of nymphs was more or less the same in CM, spr-2, def-1, and 35s::prosys plants; however the proportion of 4th instars was high on spr-2 and def-1 plants as compared to CM. On the other hand, on 35s::prosys, the number was low than on CM plants, indicating nymph development increased in JA defense impaired plants (spr-2 and def-1) and decreased in constitutively activated JA genes plants (35s::prosys) (Zhang et al. 2018).

When wild type plants sprayed with exogenous JA, there was a significant reduction in fourth instars of the nymph as compared to controls while on the other hand there was no effect of SA spray on a nymph, which indicates that JA signaling pathway is important for defense against *B. tabaci* nymphs (Zhang et al. 2018). These results are parallel with research done prior in *Arabidopsis* that impaired JA defense genes lead to an increase in nymphs performance (Zarate et al. 2007; Zhang et al. 2013) and a decrease in nymph performance when JA defense genes get activated in tomato (Sánchez-Hernández et al. 2006).

Endogenous JA levels in response to *B. tabaci*feeding—There was a significant increase in JA level in leaf infested with *B. tabaci* as compared to non-infested ones in wild type after 6–48 h, but dropped after 48 h and did not differ from the level in non-infested leaves (Zhang et al. 2018).

Endogenous JA levels Induced by *B. tabaci*—After applying saliva of *B. tabaci*, which have elicitors recognized by plant, JA dependent genes (LOX, AOS and Chi9) gets activated in tomato plant (Su et al. 2015). When there is an infestation for an extended period of time of B. tabaci, it can suppress JA defense. There is a decrease in the level of JA and JA dependent gene which is the same in non-infested leaves and the level of LoxD genes which is another JA-dependent gene, is even very low than in non-infested leaves (Zhang et al. 2018).

This also indicated different transcriptional response induces by adults and nymphs (Zhang et al. 2018). Parallel different transcriptional response also was seen in *B.tabaci*- squash interaction (Van de Ven et al. 2000). Hence Jasmonic Acid plays a major role in plant defense against the insect.

3 The Crosstalk Between Jasmonate and Other Plant Hormones Signalling

Plants being sessile are under constant biotic (such as attack by microbial pathogens and herbivores) and abiotic stresses (such as cold, drought, heat and salt stress). To overcome this stress plants have evolved various defence mechanisms (Pieterse et al. 2012). Jasmonate is a crucial hormone that modulates plant responses to these attacks. However, Jasmonate does not work independently. Crosstalk between different plant hormones has been observed, which amend the specificity of the overall defence response (Kazan 2015). These hormones either synergistically or antagonistically interact downstream or upstream of the Jasmonate signalling pathway to regulate plant defence responses and various physiological processes. Cross talk helps the plant to minimize energy costs and create a flexible signalling network that allows the plant to finely tune its defense response to the invaders encountered (Bostock 2005).

3.1 Crosstalk Between Jasmonic Acid (JA) and Salicylic Acid (SA)

Salicylate and Jasmonate have a key role in plant defence mechanisms. Jasmonate mediated responses respond to necrotrophic pathogens and Salicylate mediated responses are in response to biotrophic pathogens (Koornneef and Pieterse 2008). SA and JA signalling crosstalk at multiple points. Mutually antagonistic crosstalk has been dominant between SA and JA signalling pathways (Thaler et al. 2012). The suppression of the JA responsive genes by SA occurs downstream of the JA biosynthesis pathway (Leon-Reyes et al. 2010).

The molecular mechanism of SA/JA crosstalk includes various regulatory proteins including mitogen-activated protein kinases (MAPK), redox regulators glutathione (GRX), WRKY transcription factor, TGAs, MYC2, plant defensin 1.2 (PDF1.2), thioredoxin (TRX), and vegetative storage protein 2 (VSP2).

Non-expression of PR genes1 (NPR1) is a coactivator of SA responsive PR genes (Dong 2004). NPR regulates this suppression of JA through a novel function in the cytosol (Spoel et al. 2003, 2007). It induces the WRKY70 gene transcriptional activity which binds to the promoter region of PR1 and induces defense response (Shim et al. 2013). Therefore, WRKY70 acts as a positive regulator of SA regulated defences and represses the JA response. Further, NPR polymers are monomerized by thioredoxin and the monomers are transported to the nucleus. These monomers bind to TGAs and regulate the expression of PR1 genes (Fu et al. 2012). It is also suggested that the wild type NPR1 negatively regulates SA production during an attack by the herbivore, thereby restraining crosstalk between SA and JA to promote JA-mediated defense against herbivores.

An additional regulator in the JA/SA crosstalk is the glutaredoxin GRX480. Its expression is dependent on the NPR1 of the SA signalling pathway. The GRX480 binds peculiarly to the TGAs, and block the TGAs mediated JA defence response system (Gatz 2013).

Mitogen-activated protein kinase 4 (MPK4) positively regulates JA signalling while negatively regulates SA signalling (Petersen et al. 2000). Inactivation of MPK4 results in elevated SA and expression of PR genes and increased vulnerability to the necrotrophic pathogen. GRX480 is positively regulated by MPK4 in SA signalling pathways, while MYC2 in the Jasmonate pathway is negatively regulated. MPK4 also positively regulates JA responsive genes PDF1.2 and THi2.1 (Wasternack and Hause 2013).

The TGA transcription factors positively regulate the SA-signalling pathway (Zander et al. 2010). The balance between JA and SA pathways occurs during leaf senescence (Hu et al. 2017), during abiotic stresses such as thermotolerance (Clarke et al. 2009), and root interactions with biotrophic and necrotrophic pathogens (Gutjahr and Paszkowski 2009) (Fig. 6).

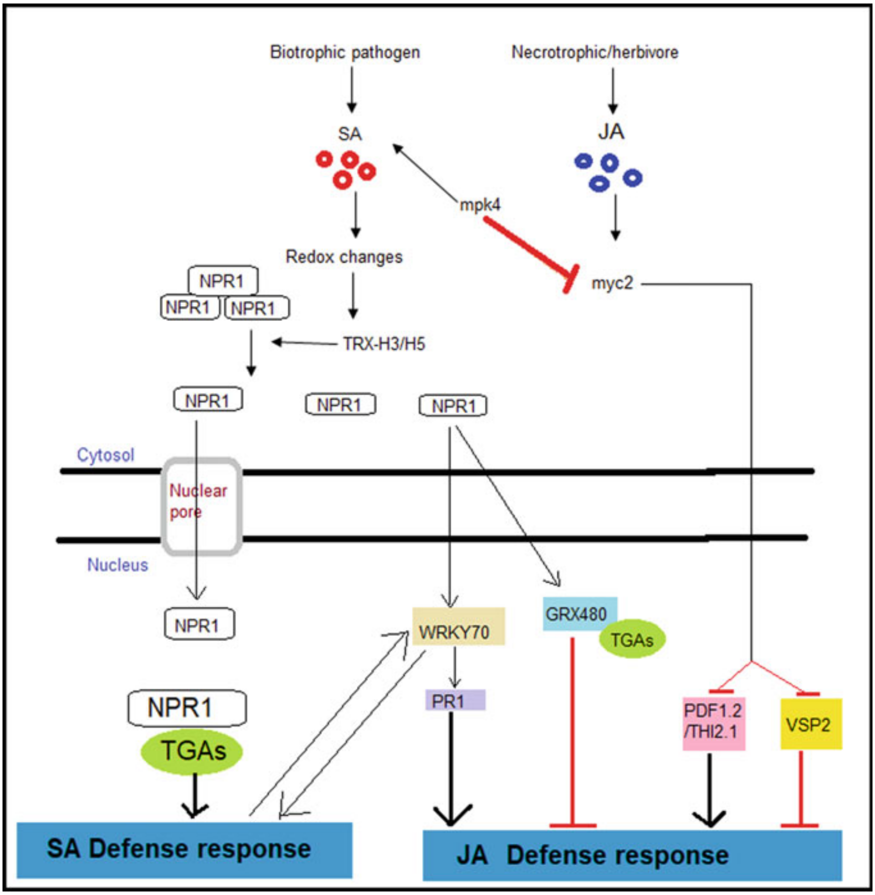


Fig. 6 Schematic representation of SA and JA crosstalk (see text for details)

3.2 *Crosstalk Between Jasmonate and Gibberellic Acid*

The interaction between JA and GA occurs synergistically and antagonistically to regulate the coordination between defence and plant growth (Navarro et al. 2008). However, the defense response is deployed at the expense of restricting growth (Yang et al. 2012). The molecular players that play a role in this crosstalk are DELLAs, myc2, PIP3, and JAZ proteins.

DELLAs affect the JA signalling by direct interaction with JAZs (Hou et al. 2010). The C-terminus of JAZ can interact with Myc2 as well as DELLA thereby acting as a competitive binder. JAZ domain interacts with myc2 and inhibits the activity of myc2 hence suppressing its transcriptional activity. At low levels or in the absence of GA, stable DELLA interacts with the JAZs and releases myc2. This restores the expression of JA responsive genes (Hou et al. 2010). As the GA level increases,

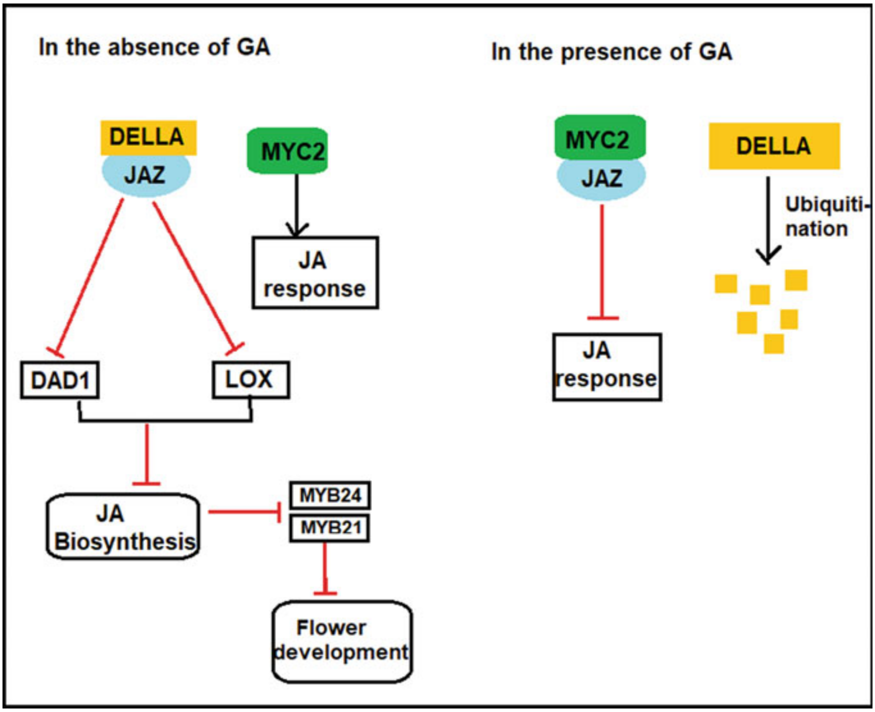


Fig. 7 GA mediates plant response to JA through interaction between DELLA and JAZ in the presence of JA signals

DELLA proteins are ubiquitinated releasing JAZ to bind to myc2 causing suppression of myc2 dependent JA responses (Fig. 7) (Hou et al. 2013). In the absence of GA, DELLA also inhibits the expression of Delayed anther dehiscence 1(DAD1) and Lipoxygenase (LOX), hence regulating JA biosynthesis (Song et al. 2011).

During JA signalling, myc2 initiates the expression of DELLA protein RGL3. This RGL3 interacts with JAZ, further releasing myc2 and restoring JA response genes (Wild et al. 2012). This crosstalk between JA and GA signalling regulates the expenditure of energy into defence in case of attack and growth under suitable conditions (Yang et al. 2012).

The interaction also regulates various developmental processes:

3.2.1 Hypocotyl Elongation

In the absence of GA, DELLAs interact with Phytochrome Interacting Factor 3 (PIF3), thus inhibiting their transcriptional activity and supressing hypocotyl elongation. At the same time, the presence of GA leads to ubiquitination of DELLAs, thereby restoring the activity of PIF3 to advance hypocotyl growth (Feng et al. 2008).

3.2.2 Stamen Development

The suppression of JA biosynthesis genes DAD1 and LOX by DELLA-JAZ complex is restored in the presence of GA when DELLA is degraded, which in turn stimulates the JA biosynthesis. These genes in the downstream unregulate the expression of MYB21 and MYB24 (Cheng et al. 2009) and are directly targeted by JAZ to regulate stamen development (Song et al. 2011).

3.2.3 Sesquiterpene Biosynthesis

JAZ and DELLA proteins interact with myc2 and inhibits its expression. JA and SA, however, destabilize JAZs and DELLAs respectively, thereby releasing myc2 from repression. myc2 binds to the promoter of sesquiterpene synthase genes TPS11 and TPS12 (Hong et al. 2012) and leads to the production of sesquiterpenes which play a role in pollination and defence against herbivores (Baldwin 2010).

3.2.4 Trichome Formation

Trichome is important for protecting plants against herbivores, insects etc. The JA and SA signal destabilize JAZs and DELLAs respectively and WD-repeat complexes are released to initiate trichome formation (Qi et al. 2011) (Fig. 8).

4 Conclusion

Jasmonic acid is a very important phytohormone that plays a major role in various developmental processes in plants and stress responses. Along with being a hormone, it is also a signalling molecule in plants that regulates various responses like root elongation, germination, fruit ripening etc. Jasmonic acid plays a central role in switching on the inducible defence response in plants and averts plants from various natural enemies like fungi, insects, viruses, and nematodes.

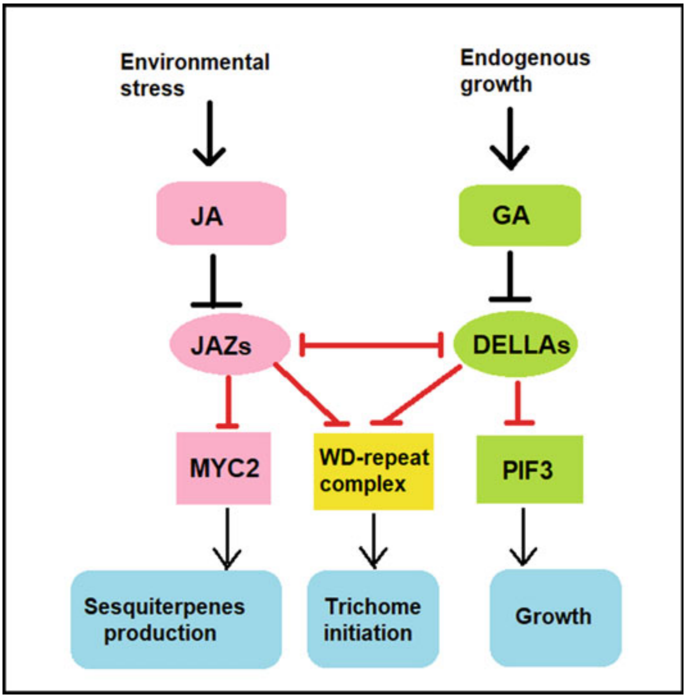


Fig. 8 Schematic diagram of crosstalk between Jasmonate and Gibberellin signaling pathway

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Methyl Jasmonate and Its Application for Improving Postharvest Quality of Fruits

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Abstract The phytohormone, methyl jasmonate (MeJA) is an important signalling molecule that plays a vital role in regulating plant defense responses as well as antioxidant systems. This is widely studied for postharvest benefits, demonstrating induced plant resistance to various storage stresses (biotic and abiotic). This also influences the production of secondary metabolites and enhances of antioxidant potential. The mode of action and postharvest application of MeJA is still a major area for research. This chapter summarises the contribution of MeJA on ameliorating postharvest quality of fruits with special reference to chilling injury and disease resistance.

1 Introduction

Jasmonic acid is present naturally in higher plants and acts as elicitors or signaling molecules in various metabolic processes in plants (Creelman and Mullet 1997). Methyl jasmonate (MeJA) is a well-known derivative of jasmonic acid (JA), along with its free acid grouped as jasmonates (JAs). These compounds are essential regulators and modulate various developmental processes, including germination, ripening and senescence (Wasternack 2014). Jasmonates induce plant defense responses upon pathogen or insect attack, mechanical wounding or abiotic and biotic stresses such

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as drought, salinity, low temperature, etc. (Yu et al. 2011; Moreira et al. 2012; Fahad et al. 2015; Farooq et al. 2016).

Application of MeJA in postharvest treatments mainly focuses on reducing the stress-related injuries that occur during storage period of horticultural commodities. Major types of stresses include chilling injury (CI), mechanical and chemical stress, and postharvest pest and diseases (Sayyari et al. 2011; Dar et al. 2015; Chakraborty and Basak 2019). MeJA treated fruits show improved quality with stimulated antioxidant systems during storage (Zhu and Tian 2012; Flores and del Castillo 2014; Zapata et al. 2014). Enhanced resistance due to MeJA treatment could be the reason for positive impact on the quality and shelf life of harvested fruits during storage (Cai et al. 2011; Wang et al. 2014; Modesti et al. 2018). The chapter focuses on the exogenous application of MeJA and its effect on postharvest quality and shelf life of fruits.

2 Synthesis and Role in Plant System

The octadecanoid pathway is a major pathway for jasmonates biosynthesis. Cellular organelles such as plastids (Wasternack and Song 2017) or peroxisomes (Arendt et al. 2016) are considered as the primary site(s) of its biosynthesis. Oxygenation of α-linolenic acid (chloroplast membrane), which is produced by the action of phospho lipase A1 (PLA1), initiates the biosynthesis of JA.

This event is conducted in chloroplast and results in the formation of cis-(+)-12-oxo-phytodienoic acid (OPDA) by the successive action of enzymes allene oxide synthase (AOS) and allene oxide cyclase (AOC). JA is synthesised from OPDA, which is formed in the AOC catalysed step. JA synthesis involves the reduction and β-oxidation of OPDA. Further steps catabolize JA into its volatile derivative MeJA and numerous other conjugates (Cheong and Do Choi 2003).

3 Pre-harvest Effect of MeJA

The diverse effects of MeJA on fruit crops as preharvest spray, depends on the type of fruit crop, doses and growth stage. It has been reported that fruit size, weight, bioactive compounds and other quality parameters significantly improved in MeJA treated plum cultivars (Martínez-Espla et al. 2014). Application of MeJA (0.5 mM) in two plum cultivars namely Black Splendor and Royal Rosa, at three crucial stages of fruit development, viz., pit hardening, initial colour development and onset of ripening, improved the fruit quality, antioxidant enzyme activity and delayed ripening and thereby improving the shelf life (Zapata et al. 2014). MeJA was sprayed in sweet cherry at a stage of yellow straw color of fruits, 3 weeks before the anticipated harvest and this resulted in the delayed fruit colour development and ripening by inhibiting ethylene synthesis. Treated cherry fruits had better fruit quality and increased bioactive compounds level during harvest (Saracoglu et al. 2017). A single application of MeJA in apples showed a significant increase in red colour, total phenols (cyanidin 3-galactosides, chlorogenic acid, phloridzin, flavanols and flavonols) in peel and lead to production of more export-grade fruits (Shafiq et al. 2013). In strawberries, MeJA applied at flowering stage showed a significant delay in fruit decay and better postharvest quality and shelf life of fruits (Saavedra et al. 2016). Sweet cherry treated with 0.4 mM MeJA at fruit set had lesser percentage of fruit cracking during harvest. It also maintained the fruit firmness and other quality parameters (Balbontín et al. 2018). It maintained antioxidants and other bioactive compounds in lemon without hampering the fruit quality (Serna-Escolano et al. 2019). Three levels of MeJA (1, 5, and 10 mmol/L) were sprayed on pomegranate at 4, 34, 64, and 94 days before harvest. Among all, 10 mmol/L concentration was most effective. MeJA increased the crop yield, fruit quality and aril colour by increasing anthocyanin content. Lower concentrations hastened the on-tree ripening of fruits, while higher dose delayed it. MeJA maintained postharvest quality such as weight loss, firmness, vitamin C, phenols and antioxidant activity during storage at 10 C (Garcia-Pastor et al. 2020).

MeJA, in addition, stimulates defense responses in plants against biotic and abiotic stresses (Chakraborty and Basak 2019; Dar et al. 2015). It has been reported that *Colletotrichum acutatum* and *Botrytis cinerea* were effectively controlled by MeJA by inducing systemic acquired resistance in plants (Cao et al. 2008; Yu et al. 2009). MeJA stimulates the pathogenesis related gene expressions, antioxidant systems and also helps with emission of repellent volatile compounds against insects and herbivores (Yu et al. 2011; Moreira et al. 2012; Fahad et al. 2015; Farooq et al. 2016).

Research investigated on the effect of MeJA on the efficacy of bioagents, was found beneficial to minimize the postharvest decay in fruits. The treatment of *M. guilliermondii* added with MeJA (200 μmol/L) significantly lessen the blue mold rot in apple caused by *P. expansum.* As a result decay percentage was found only 21.6% in fruits treated with *M*. guilliermondii induced by MeJA whereas this percentage was double in apples treated with *M. guilliermondii* alone and 100% in control fruits. It also inhibited the spore growth, length of fungal germ tube and colony spread of *P. expansum* by better proliferation of antagonistic yeast population (He et al. 2020). Disease resistant was closely related to the activity of enzymes which up-regulated the gene expression involved in defense mechanism (Li et al. 2014). In apple, gene expression of defense related enzymes was found highest in MeJA induced yeast treatment.

4 Postharvest Effects of MeJA

Lately, the prerequisite of safe and sustainable food all over the world has restricted many countries in fruit marketing to different target markets. There are trade barriers that resist pesticide and other chemical residues in eatables. Thus, MeJA, being a natural compound, has no limitations for use as postharvest treatments to increase the storage life of products (Reyes-Díaz et al. 2016). The positive effect of MeJA on the bioactive compounds (Table 1) and moreover improving the plant defense system against abiotic and biotic stresses by inducing gene expression has studied widely (Zhu and Tian 2012; Wang et al. 2015b). Exogenous MeJA applications not only results in better postharvest life of fruits (Table 2), but also enhance resistance towards postharvest diseases through preventing pathogenic attack (Table 3). In guava, when mature green and ripe fruits were treated with MeJA, it was observed that MeJA had slightly influenced the ethylene synthesis and ripening process while did not control the anthracnose (Silva et al. 2017).

5 Role of MeJA in Chilling Stress

Chilling injury (Cl) turns to be one of the foremost storage problems in tropical and sub-tropical fruits, when stored below their optimum low temperature. CI damages the cell membrane structure by lipid peroxidation, degradation of phospholipid and galactolipids. The consequence of lipid peroxidation is the accumulation of reactive oxygen species (ROS), which in turn causes oxidative stress, loss of membrane structure integrity, disruption of cellular and sub-cellular structures and leads to electrolytic leakage (Aghdam et al. 2013). MeJA treatment alleviates chilling injury in peach by remodeling of phospholipids and JA signaling (Chen et al. 2019). JAs is known to stimulate the production of proteinase inhibitors, antimicrobial compounds, antioxidant enzyme activity, pathogenesis-related and protective proteins, which detoxify and maintain the redox potential (Soares et al. 2010; Gill et al. 2013; Zhou et al. 2013; Guo et al. 2014). Antioxidant enzymes are those which help in the removal of free radicals and prevent oxidative damages in cells (Aghdam and Bodbodak 2013). Some examples of antioxidant enzymes are superoxide dismutase (SOD), glutathione peroxidase (GPX), catalase (CAT) ascorbate peroxidase (APX).

MeJA maintain the integrity and structure of cell membrane in lemon and pomegranate by preventing electrolytic leakage and lipid peroxidation (Sayyari et al. 2011; Siboza et al. 2014). Zhang et al. (2012) studied the effect of MeJA on CI tolerance at transcription levels of genes LeARG1 (AY656837), LeARG2 (AY656838), ADC (L16582), ODC (AF029349) and OAT (AY897573) in cherry tomato fruits. MeJA treated fruits had higher expression of LeARG1, LeARG2, and arginase activity compared to that of control. Ornithine, the precursor of polyamines proline and putrescine (Put) plays a major role in chilling injury tolerance. This ornithine is the product of arginine hydrolization, which is catalyzed by enzyme arginase. In MeJA treated fruits, the catabolism of arginine to Put and proline has been promoted. This can be considered as the mechanism behind increased chilling tolerance in treated fruits. The arginine decarboxylase (ADC) expression was higher in treated fruits, on which the increase in polyamines, mainly Put depends on.

Table 1 Effect of MeJA on secondary metabolites in different fruits

Fruit	Dose	Effect	Reference
Chinease bayberry	10 μmol/ L	Increased concentration of anthocyanin (quercetin-3-O-rutinoside, myricetin, and cyanidin-3-glucoside), phenolics and flavonoid content	Wang et al. (2010)
Japanese plum	1120 and 2240 mg/ L	Increased concentration of chlorogenic acid, catechin, rutin, ferulic acid, maintained total phenolics and antioxidant activity	Karaman et al. (2013)
Apple	1120 and 2240 mg/ L	Increased total phenolics and antioxidant capacity	Ozturk et al. (2014)
Peach	10 μmol/ L	Positive impact on sugar metabolism, maintained higher sucrose and sorbitol content than control, also reduced glucose and fructose content due to slower destruction of sucrose	Yu et al. (2016)
Olive	30 μL/L	Significant decrease of saturated fatty acids And increase in oleic, linoleic and linolenic acids (beneficial), increased phenolics content (chlorogenic acid, gallic acid, vanillic acid, caffeic acid	Flores et al. (2017)
Red raspberry	100 μM	Promoted anthocyanin biosynthesis and helped in intense red colour development of fruits after harvest	Moro et al. (2017)
Dragon fruit	0.1 mM	Increased betacyanin content and also maintained other biochemical compositions	Mustafa et al. (2018)
Blueberry	100 μmol/L	Increased total phenolics, flavonoids, anthocyanin and ascorbic acid levels	Wang et al. (2019)
Mango	10^{-5} to 10^{-4} M	Treated fruit peel had highest levels of gallic acid (33.0%), caffeic acid (80.0%), total phenols (38.4%) and total antioxidant capacity (20.9%) whereas carotenoid content was found higher (48.7%) in pulp	Vithana et al. (2019)
Blood oranges	100 μmol/ L	total phenolic content and anthocyanin (Cyanidin 3-glucoside and cyanidin-3-(6-malonylglucoside) concentration was maintained due to higher PAL and lower PPO activities	Habibi et al. (2020)

(continued)

Table 1 (continued)

Fruit	Dose	Effect	Reference
Kiwifruit	0.25 and 0.50 mM	Maintained the phytochemical compounds	Ozturk and Yucedag (2021)

Table 2 Effect of MeJA on shelf life and storability of different fruits

Fruit	Dose	Effect	References
Loquat	10 µM	Observed positive effect on inhibition of lignin accumulation and chilling injury, maintained better quality and storage life up to 35 days by inhibiting the activity of enzymes PPO, POD and PAL	Cao et al. (2010)
Lychee	1 µg/L	Pericarp browning was significantly lower (27.5%), inhibited degradation of anthocyanin and oxidation of (–)-epicatechin, extended shelf life and maintained quality till 6 days at RT	Yang et al. (2011)
Peach	1 µmol/L	Enhanced chilling tolerance by increasing enzyme activities Involved in energy metabolism and reduced chilling injury index (43.6%) and maintained quality till five weeks of storage at 0 °C	Jin et al. (2012)
Strawberry	60 µL/L	Fruit quality (TSS, TA,vit-C, anthocyanin etc.) were higher in MeJA treated fruits, also reduced postharvest decay and enhanced shelf life (12 days at 4 °C)	Geransayeh et al. (2015)
Pomegranate	0.1 mM	Reduced weight loss, chilling injury and ionic leakage, enhanced polyphenols, anthocyanins, and total antioxidant activity, maintained better quality up to 84 days by slowing down the ethylene and respiration rate	Sayyari et al. (2017)
Medlar	0.1 mM	Effectively delayed quality loss (weight loss, SSC, TA, phenols and flavonoids) and maintained better shelf life at 0 ± 0.5 °C for 60 days	Ozturk et al. (2019)
Kinnow	0.001 µmol/L	Maintained fruit quality and extended shelf life for 75 days, decreased weight loss, spoilage and activity of enzymes PME and cellulases, maintained higher carotenoids, vit-C and sensory attributes	Baswal et al. (2020)
Kiwifruit	0.25, 0.50, and 1.0 mM	Delayed weight loss, maintained the phytochemical compounds	Ozturk and Yucedag (2021)

Table 3 Effect of MeJA on postharvest disease resistance in different fruits

Fruit	Dose	Effect	Reference
Loquat	10 µmol/L	After 4th day of inoculation, decay and lesion diameter was reduced (from 54.4% to 16.7% and from 7.26 mm to 4.00 mm respectively) in MeJA treated fruits, induced higher activities of CHI and GLU and also maintained higher fruit quality during 6 days storage	Cai et al. (2011)
Mandarin	100 µmol/L with *Cryptococcus laurentii*	Helped in rapid proliferation of *C. laurentii*, MeJA and *C. laurentii* combined treatment had best preventive activity by induction of mRNA expression level of PR5 and enhanced defence related enzymes activity in peel, MeJA treated fruits had lowest green mold infection	Guo et al. (2014)
Chinease bayberry	10 µmol/L	Reduced green mould infection by 66.2%, triggered priming mechanism, increased concentration of phenylalanine ammonia-lyase and chitinase, total phenols, lignin and phytoalexin, induced disease resistance by priming of these defense responses	Wang et al. (2014)
Strawberry	60 µL/L	Reduced spoilage caused by *B. cinerea*	Geransayeh et al. (2015)

(continued)

Table 3 (continued)

Fruit	Dose	Effect	Reference
Grape	100 μmol/L	MeJA enhanced disease resistance, maintained higher soluble sugars and antioxidant activity, lowered disease incidence and lesion diameter, also enhanced the concentration of tran-resveratrol and ε-viniferin	Wang et al. (2015a)
Sweet cherry	10 μmol/L	Inhibited the spores of *P. expansum* by germinating and elongation of germ tube, triggered a priming mechanism which enhanced the activity of CHI, GLU, antioxidant enzymes and PR1 gene (NPR1-like and THAU-like)	Wang et al. (2015b)
Kiwifruit	0.10 mmol/L	Reduced the lesions diameter, higher activity of antioxidant enzymes, defense-related enzymes including (CAT, POD, SOD, PPO, CHI, GLU) and reduced membrane lipid peroxidation	Pan et al. (2019)
Blueberry	50 μM	Showed inhibitory effect on disease index caused by *B. cinerea*. Elevated transcriptional levels of genes involved in Phenylpropanoid Pathway	Wang et al. (2020)

6 Application Methods in Postharvest Fruits

Methyl jasmonates are very effective in improving quality and shelf life of fruits mainly by influencing their various stress reactions. It is applied as a pretreatment before storage of harvested fruits. It can be applied in vapour or liquid form. Both forms are effective and easy to use. Application of MeJA in postharvest handling of fruits is safe and economical. Its application methods are same as that of ethylene treatment.

For MeJA-vapour treatment, fruits are enclosed in airtight container and then known concentration of gaseous MeJA is subjected inside the container and left for

24 h at least (Flores and del Castillo 2014). For liquid form of MeJA, mainly dipping method is used (Yang et al. 2011; Ozturk and Yucedag 2021). It can be used as spraying over the fruits or spotted on paper disc (Geransayeh et al. 2015). In paper disc method, a suitable quantity of MeJA liquid is speckled onto the filter paper and then kept in sealed boxes (Wang et al. 2015a; Pan et al. 2020).

7 Effect of MeJA on Nutritional Quality of Fruits

Many reports suggest that methyl jasmonate affects the biosynthesis of important components such as carotenes, chlorophylls and vitamins in numerous fruits. Similarly, some researchers (Karaman et al. 2013; Martínez-Espla et al. 2014; Saracoglu et al. 2017) have confirmed that the exogenous application of MeJA on fruits increased the antioxidant activity and flavonoid content, anthocyanin accumulation and formation of volatile compounds. Although its postharvest application is still in an experimental stage and therefore not commonly practiced in the industries but have great potential for commercial use.

MeJA affects the transcription factor (MYB10) involved in anthocyanidin metabolism in red raspberries (Moro et al. 2017). It was found that MeJA upregulated MYB10 and anthocyanidin synthase (ANS) transcription, which is strongly linked with anthocyanidin buildup. In grapes, dihydroflavonol 4-reductase (DFR) and the transcription factor *Vv*MYBA1, are key regulators of several gene expressions involved in anthocyanin biosynthesis (He et al. 2010; Sandhu et al. 2011). These genes are categorized into two groups on the basis of their expression level. Those who expressed first, such as chalcone synthase (CHS) naringenin-chalcone synthase (NCS) and chalcone isomerase (CHI), take part in flavonoid biosynthesis. On the other hand, genes which express lately, such as DFR and ANS, play an important role in anthocyanin biosynthesis pathway (Lai et al. 2012). MeJA modulates the expression profiles of these genes in red raspberries. In the regulation of anthocyanin related genes, a ternary complex of MYB-bHLH-WD40 acts as a key regulator (Wang et al. 2010; Petroni and Tonelli 2011).

Chen et al. (2012) have demonstrated that one transcription factor involved in the regulation of crucial anthocyanin related gene expression is coded by *Ri*MYB10. In anthocyanidin biosynthesis, DFR reduces dihydroflavonoids into 3,4-cis-leucoanthocyanidin whereas ANS catalyzes the production of anthocyanidins, which are coloured anthocyanins (Tanaka et al. 2008). Moro et al. (2017) suggested that *Ri*MYB10 and *Ri*ANS genes were positively regulated by MeJA and positively influenced the transcription profile in black berry.

8 Effect of MeJA on Shelf Life and Quality

MeJA is known to have beneficial effects on preserving fruit quality and thereby improving shelf-life. The fruit quality during cold storage and shelf life is affected by several factors, including ethylene, respiration rate, spoilage etc. Ethylene is the major factor that triggers ripening and senescence in fruits. Other than ethylene, phytohormones like jasmonic acid (JA) and abscisic acid (ABA) also strongly affect the ripening and senescence processes in fruits (Kumar et al. 2014). MeJA has some influence on the ethylene production in climacteric fruits. Numerous studies have indicated that when JAs were applied at pre-climacteric stage, it enhanced the ethylene production, whereas inhibiting the ethylene synthesis in pome fruits during climacteric and post-climacteric stages (Kondo et al. 2007, 2009).

Lv et al. (2018) studied how ethylene synthesis and signaling process were affected by MeJA at transcription level during postharvest ripening of apple. They observed that four ACS genes (MdACS1, MdACS3A, MdACS6 and MdACS8), two ACO genes (MdACO1 and MdACO2), four ethylene receptor genes (MdETR1, MdETR2, MdERS1 and MdERS2), five CTR genes (MdCTR1-5), two EIN genes (MdEIN2A and MdEIN2B), four EIL genes (MdEIL1-4) and two ERF genes (MdERF1 and MdERF2) were involved in ripening process. MeJA positively stimulated the expression of MdACS1, MdACS6, MdETR1, MdCTR1-3, MdCTR1-4, MdCTR1-5, MdEIN2A, MdEIN2B, MdEIL4 and MdERF1 at early ripening stage, whereas MdEIL3 at the late ripening stage. MeJA also regulated the expression of MdACS3a, MdACS8, MdACO1, MdACO2, MdETR2, MdERS1, MdERS2 and MdEIL1 till the last day of storage, whereas no effect was observed on expression of MdCTR1-1, MdCTR1-2 and MdEIL2. At the peak level of ethylene, MeJA adversely regulated the expression of MdERF2 and MdACS1. These findings indicated the effect of MeJA on the transcription level of ethylene synthesis and its perception in apple fruit at the time of ripening and storage. The effect of this GRAS compounds on extension of shelf life and maintenance of fruit quality were investigated in many fruits (Table 2).

9 Effect of MeJA on Restraining Postharvest Diseases

MeJA is found useful in enhancing the fungal disease resistance in cherry tomatoes (Chen et al. 2014), kiwifruit (Pan et al. 2020), strawberry (Geransayeh et al. 2015) and Chinese bayberries (Wang et al. 2010). This can be probably achieved by either direct inhibition of pathogen growth or indirect induction of disease resistance. Still, the exact mode of action or defense mechanisms behind MeJA is not very clear. In some studies, application of MeJA as a postharvest treatment in Chinese bayberries, induced resistance against infection of *Penicillium citrinum* through defense priming effect (capacity of enhanced cellular defense responses) (Conrath et al. 2002; Wang et al. 2014). Although, it is unknown that priming is the mechanism behind disease resistance induced by MeJA.

Synthesis and expression of some pathogenesis-related proteins, such as chitinase (CHI), β-1,3-glucanase (GLU), N-acetylglucosamine-6- sulphatase (GNS), calmodulin (CaM), non-expressor of pathogenesis related genes 1 (NPR1-like), and thaumatin-like (THAU) and induction of phenylpropanoid pathway has been stimulated by MeJA (Yao and Tian 2005; Wang et al. 2015b). CHI, GLU and GNS hydrolyze the fungal cell wall constituents, and prevent fungal infection by enhancing the plant defense mechanisms (Ferreira et al. 2007; Vilanova et al. 2014). PAL enhances the levels of phenols, phytoalexins, and lignin in fruits, which improve physical barriers against pathogen (Shadle et al. 2003). Enzymes POD and PPO are also important in a way that, both take part in lignin synthesis and help building resistance against various fungal infections (Mohammadi and Kazemi 2002). MeJA inhances these enzyme activities and controls *Alternaria alternata* in cherry tomato (Chen et al. 2014).

A few pathogens such as *Botrytis cinerea, Penicillium digitatum* and *Monillinia fructicola* are not directly affected by MeJA treatment (Tsao and Zhou 2000; Yao and Tian 2005; Darras et al. 2005). But, there are studies that reported the effect of MeJA on inhibition of spore germination, elongation of germ tube and mycelial growth *Colletotrichum acutatum, Penicillium expansum* and *Alternaria alternata* (Cao et al. 2008; Chen et al. 2014; Wang et al. 2015b). The difference in these results might be because of the varied responses of fungi towards MeJA due to their different sensitivities.

The defensive response of *Vitis vinifera* against any pathogenic infection can be attributed to the presence of gene VvNPR1.1, which regulates the expression of PR1 and PR2 (β-1.3-glucanase) (Le Henanff et al. 2011). Recently, it had confirmed that in Kyoto grapes, MeJA application increased the expression of VvNPR1.1 and induced defense mechanism against *B. cinerea* (Wang et al. 2015a). It was also found that the expression of many genes involved in defense responses, which encode CHI, GNS, PAL, SOD and CAT enzymes were significantly enhanced by MeJA treatment. This is further affirmed the priming phenomenon behind MeJA-induced disease resistance against gray mold decay in grapes. Wang et al. (2015b) investigated the MeJA effect at transcription level in sweet cherry against *P. expansum.* They found that expression of PaCAT, PaPAL, and PaTHAU-like genes was significantly higher in treated fruits. Also the expression of the genes for PaCaM, PaGLU, and PaNPR1-like were increased by *P. expansum* and MeJA a combined treatment, but not in fruits treated with MeJA alone. Fruits treated with combined treatment, all six gene expression were significantly higher compared to other treatments.

Phenyl propanoid pathway includes transcription of VaPAL, chalcone synthase (VaCHS), (VaCHI), flavanone-3-hydroxylase (VaF3H), flavonol synthase (VaFLS), and VaDFR and were found elevated in MeJA treated blueberry (Wang et al. 2020).

10 Conclusion and Future Aspects

Application of jasmonates as pre-harvest and postharvest treatments enhances the production of defense related secondary metabolites (anthocyanins, flavonoids, phenolic acids), antioxidants enzymes and proteins involved in defense responses and protect against fungal infections thereby improving the quality and storage period of fruits. MeJA has been considered to be one of the major natural compounds that hinder many storage diseases, mainly fungal diseases and extends storability of fruits. The potential of jasmonates on the control of pathogens other than fungus as well as other insect attack worth advance study. The synergic effect of MeJA with other compounds and/or other advanced technologies known to enhance the postharvest life and quality of fruits can be further researched.

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Salicylic Acid Signalling Under Stress Conditions in Plants

Tibor Janda, Kinga O. Gondor, Magda Pál, and Gabriella Szalai

Abstract Salicylic acid (SA) is widely distributed in the whole plant kingdom. It is generally present either in the free form or as glycosylated, methylated, glucose-ester, or amino acid conjugates. However, the basal level of SA may differ widely among the plant species. The effects of SA in plant stress responses have been studied extensively for a long time. Several physiological processes in which SA may play a role have been reported, including seed germination, growth regulation, flower induction, thermogenesis, and especially, the regulation of plant responses under biotic or abiotic stress conditions. SA may also be involved in different signalling processes. For example, certain hormones involved in plant protective mechanisms may crosstalk with SA, which may lead to reprogramming of gene expression and protein synthesis. SA action may also affect the antioxidative metabolism, modulating the redox homeostasis in the cells. In spite of the extensive research on the effects of SA, there are still a lot of open questions in this field. In the present chapter, certain stress-related defence mechanisms, which are also affected by SA, will be discussed.

1 Introduction

In the past, salicylic acid (SA) was commonly used for preparing jams; and although this is not recommended today, but benzoic acid and especially its sodium salt, sodium benzoate, have been put into practice. Nevertheless, we have not come too far from SA, as they are chemically very close compounds: SA is 2-hydroxybenzoic acid and although its use in the food industry has been declined, it is increasingly being used by the cosmetics and pharmaceutical industries. For thousands of years, people have known about the anti-inflammatory and analgesic effects of willow bark, the active ingredient of which is a SA derivative, salicin. Moreover, let's not forget

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one of the best known drugs, Aspirin, whose active ingredient, acetylsalicylic acid, is also made from SA.

SA can be detected in free and/or bound form in most of the plant species, of course, in very different amounts, depending on the species, organ and stage of development. Results on animal models and human experiments indicate that long-term use of aspirin may also reduce the risk of certain types of cancer (Rothwell et al. 2011; Hurwitz et al. 2019). Studies suggest that the effect is at least in part related to the inhibition of cyclooxygenase enzymes and reduction of prostaglandin production (Chan et al. 2007). In contrast to these results, our recent study showed no direct relationship between the SA content of the extracts from rice or wheat plants and their anticancer activity (Pál et al. 2020). However, despite all the human applications, plants do not synthesize SA for the sake of human population, but for their own, so to speak, best interests.

Traditionally, the aim of the related plant biology research is to reveal what physiological and biochemical processes have a direct or indirect effect on SA, on the one hand, and what conditions influence its synthesis, on the other hand. In addition to these, another direction of the research is of practical nature: the potential use of exogenous SA and some of its derivatives for agricultural production is also intensively studied in order to improve either yield or crop quality. Historically, one of the first papers in which the growth-regulating role of SA was written dates from 1974 (De Kock et al. 1974). In this work, the effect of SA on a water plant, *Lemna gibba* was described. Subsequently, interest in this compound has greatly increased, and a number of studies have been performed that have shown an association between SA and growth. Regarding the role of stress physiology, it was initially studied primarily in the case of biotic stressors. The initial observations that SA can be involved in disease resistance were also reported in 1974 by Chadha and Brown. Later, it was described that the application of aspirin conferred resistance against tobacco mosaic virus in the sensitive tobacco plants (White 1979).

Although the regulation is still poorly understood, the synthesis of SA has been well described, and was recently reviewed (Lefevere et al. 2020). Briefly, SA can be synthesised by two possible routs: the isochorismate synthase (ICS) and phenylalanine ammonia lyase (PAL) pathways; both starting from chorismate. On the PAL pathway, SA is synthesised in the cytosol from phenylalanine via *trans*-cinnamic acid and benzoic acid. On the ICS pathway, isochorismic acid is synthesised from chorismic acid in the chloroplasts, then it is converted to SA in the cytosol.

SA is an important endogenous immune signal in the disease resistance response (Malamy et al. 1990; Dempsey and Klessig 2017). Increases in endogenous SA concentrations can be detected in a number of plant-pathogen interactions, and this increase is associated with activation of defence mechanisms. The SA signalling system activates not only the local resistance, i.e., the resistance that develops around the infection, but also the systemic acquired resistance observed in the distal tissues. Infection of plants with necrotizing pathogens, which promote the accumulation of SA, or treatment of plants with synthetic compounds that can trigger the signalling pathway associated with SA, cause a physiological condition called "priming". All of this allows for faster and more effective responses under stress conditions.

2 What Are the Current Research Directions and the Latest Results on the Topic?

Given the complexity of the topic, the research directions are also diverse. At the level of basic research, one of the most important areas is finding the components that are directly affected by SA. At the beginning, the antioxidant catalase enzyme was hypothesized to be able to bind SA, thereby reducing its activity (Sánchez-Casas and Klessig 1994). This can increase the amount of hydrogen peroxide in the plant, which in turn can activate other defence processes as a secondary messenger (Janda et al. 1999). It is worth mentioning that in connection with antioxidants and reactive oxygen species, a kind of paradigm shift has been observed in recent years: reactive oxygen species can be useful in not very high concentrations as they can prepare the cell to prevent greater damage.

Exogenous stimuli may generate specific calcium signal in the cytosol, which may also trigger SA biosynthesis. A calmodulin-binding protein, CBP60g, is also involved in activating SA biosynthesis, triggering the activation of isochorismate synthase (Wang et al. 2009). Reactive oxygen species may also induce SA accumulation via the induction of the benzoic acid 2-hydroxylase (BA2H) enzyme (León et al. 1995). Nitric oxide also activates SA biosynthesis pathway, by inducing PAL (Klessig et al. 2000). Certain possible crosstalk mechanisms between NO and SA signalling during heat stress have recently been discussed (Rai et al. 2020).

Another well-known effect of SA is that it stimulates non-expressor of pathogenesis-related 1 protein (*NPR1*), but at the same time inhibits NPR3/4 receptors, and the activation of genes playing role in defence mechanisms against pathogens may be increased in both cases (Ding et al. 2018). The structural basis of SA recognition by NPR4 has recently been revealed, providing insights into the structure–function relationships of NPR proteins (Wang, Withers, et al. 2020).

NPR1 serves as a master regulator of the SA-mediated induction of defence genes, as it is a SA receptor, binding specifically to SA via Cys521/529 (Wu et al. 2012). However, other components, such as Mediator (*MED*) genes are also required for SA-activated expression of the defence marker gene *PATHOEGNESIS-RELATED GENE1* (*PR1*) (Wang et al. 2016). Furthermore, other signalling components have also been identified, including high affinity SA-binding protein 2 (SABP2) (Klessig et al. 2000), which is a methyl esterase, the SABP3 with carbonic anhydrase activity (Slaymaker et al. 2002), the SA-inducible protein kinase (SIPK) or different types of glutathione-S-transferases (Csiszár et al. 2014; Tajti et al. 2019). In addition, the other main areas are the exploration of the factors regulating the synthesis of SA and the cross-reactions of SA with other stress-relieving processes. These include, but are not limited to, the synthesis of individual lipids or, for example, overlaps with polyamines and other plant hormones (Fig. 1).

A mechanistic model has also been proposed for the transcriptional control of the expression of a glutaredoxin (*GRX*) gene by stress, via an SA-dependent route. It has also been speculated that redox changes promoted by SA accumulation can also be responsible for the gene activation processes (Herrera-Vásquez et al. 2015).

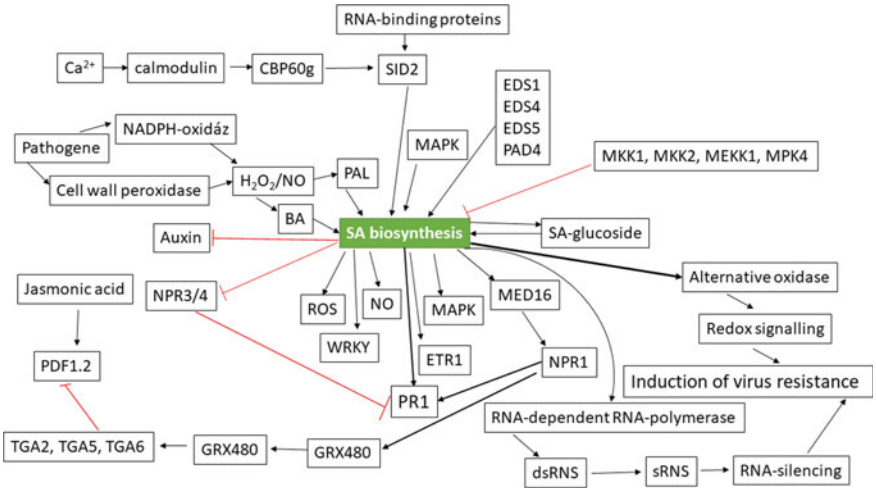

Fig. 1 Possible crosstalk mechanisms between salicylic acid (SA) and other stress-related components. For details see text

Hormonal regulation may also be involved in stress responses, including biotic or abiotic factors, and the interactions between SA and other hormones during abiotic stress effects have also been widely studied (Saleem et al. 2020; Sharma et al. 2020). For example, SA may affect auxin responses. Increased auxin levels were found in the leaves of *NahG* transgenic plants characterised with low SA contents, during the reproductive stages. Furthermore, plants having accumulated SA in leaves show morphological phenotype which are similar to auxin-deficient mutants (Wang et al. 2007). The cross-talk between SA and ethylene signalling has also been studied for a long time (Janda et al. 1999; Szalai et al. 2000). Model of the role of certain TGACG sequence-specific binding proteins (TGAs) as mediators of the SA-ethylene cross-talk has been described recently (Zander et al. 2014).

It has also been shown that priming is epigenetically inherited: descendants of a plant exposed to a disease may also be capable of more effective systemic acquired resistance, where SA also plays an important role. Later, the involvement of SA in abiotic stress tolerance has also been described (Luna et al. 2012; Liu et al. 2015; Chen et al. 2020).

The synthesis of a novel SA-loaded silicon dioxide nanosphere has also been recently shown (Feng et al. 2020). This nanosphere could gradually release SA, and it may have great potential in future environmental-friendly practical application of SA in order to induce stress tolerance in plants.

3 Potential Use of SA in Practical Agriculture

At the publication levels, many results have already reported beneficial effects of SA on the basis of which practical use may be considered (Koo et al. 2020). Examples are stimulation of germination, increase in biomass and/or crop yield, quality improvement e.g. for medicinal or aromatic plants. In principle, several methods of application are possible, including soaking of seeds, irrigation or spraying of adult plants. SA may also enhance seed germination under stress conditions (Rajjou et al. 2006), which is partly related to the role of SA in the regulation of internal glutathione pool (Borsani et al. 2001). Exogenous application of SA has also been shown to provide protection against various types of abiotic stresses. For example, it provided protection, among others, against heat (Dat et al. 1998), cold (Janda et al. 1999), high salinity (Souri and Tohidloo 2019), or heavy metal contamination (Sharma et al. 2020). Senaratna et al. (2000) has shown that both; soaking of seeds and irrigation with solution containing SA was an effective protector against heat, cold, and drought stress treatments. 0.1 mM SA added in hydroponic solution partially recovered the photosynthetic activity in tomato, parallel with an increase in the endogenous ABA content (Horváth et al. 2015). Soaking of barley or maize seed in 0.5 mM SA for 6 h alleviated the effects of Cd by increasing the biomass production both in the shoots and roots (Metwally et al. 2003; Krantev et al. 2008). When the root systems of 20-day-old seedlings were immersed in solutions of SA for 1 day, it reduced the osmotic stress-induced membrane injury, parallel with also an increase in the ABA level (Bandurska and Stroiński 2005). Spraying of wheat leaves with SA significantly inhibited freezing stress-induced reduction in the quantum yield of Photosystem 2. It has been also reported, that hydrogen peroxide and ABA mediate SA-induced freezing tolerance in wheat (Taşgín et al. 2003; Wang et al. 2018).

However, there are only a few results on the application of SA under field conditions. It was shown that when maize seeds were soaked in SA solution before sowing, crop yield increase was achieved, due to the cold tolerance enhancing effect of SA (Szalai et al. 2016). Recent results also demonstrated that exogenous application of SA may provide protection against late spring low-temperature stress under field conditions in wheat (Wang, Wang, et al. 2020). SA application combined with inoculation with plant growth promoting bacteria could also provide an advantageous management practice for improving the production of secondary metabolites from *Mentha x piperita* plants. The exogenous application of SA increased PAL activity leading to an increase in the phenolic content in peppermint plants. In parallel with this, application of SA produced a significant increase in the monoterpene concentrations present in peppermint essential oil (Cappellari et al. 2019). Foliar application of SA to sweet basil (*Ocimum basilicum* L.) or marjoram (*Majorana hortensis*) plants did not only improve certain agronomically important growth parameters, including plant height, number of branches per plant, leaf area, fresh and dry weight of herbs, etc., but it also increased certain physiological and biochemical parameters, such as total carbohydrates, crude protein, total amino acids, free proline, putrescine, spermidine, chlorophyll as well as microelement contents. Besides these, application of

SA also increased the oil percentage and yield per plant. Furthermore, using SA at appropriate concentrations, improved oil quality by increasing the level of sabinene parallel with a decrease in the proportion of *cis*-sabinene hydrate in marjoram plants (Gharib 2007).

4 If the Mechanism Is More or Less Well-Known, and the Practical Use Has Also Been Started, What Is Next? What Trends Can Be Expected for SA in Future Research?

Research on SA is still very intensive. In terms of practical application, studies will certainly be continued. It is also possible that not only SA itself, but one of its related compounds will be better utilized in practice (Janda et al. 2000; Palmer et al. 2019). But it is very important to note that individual results should never be generalized, because it can easily go wrong. SA can affect many points of signalling and can easily turn things around. It affects, for example, the oxidative system, where it can directly or indirectly potentiate the effects of some antioxidant enzymes and inhibit others. The presence of extra SA in the plant may also be perceived as stress, thus inducing processes that may be beneficial in some circumstances and more negative in others.

On a theoretical level, the complex and increasingly widespread "omics" techniques (genomics, proteomics, metabolomics, etc.) have also been brought to the forefront (Szalai et al. 2018). However, despite intensive research, many questions remain unanswered. Some of these? SA can be synthesized in the cell in several ways. The question is, in what way are the individual synthetic routes preferred by various effects? When is one activated, when is the other, or maybe more than one route are active at the same time? How does the effect of externally applied SA relate to the action mechanism of endogenous SA? That is, how much does the uptake of SA matter (and through what mechanisms exactly), or to what extent does the externally applied compound "only" represent a stress signal that will induce a stress response, that is generally considered independent of the compound? The role of the different bound forms of SA has also been recently reviewed (Ding and Ding 2020). In one of our previous studies using radioactive SA, we have shown that SA is taken up by the plant during seed treatment, but stored there in bound form, and newly synthesized SA appears in other organs of the plant (Szalai et al. 2011).

Earlier results indicate that at least partly, methyl-salicylate can be a potential mobile signal in plants (Park et al. 2007). When it was exogenously applied, it was also able to induce different direct and indirect defence mechanisms in poplar plants (Tang et al. 2015). In one of our experiments, the effects of methyl-salicylate were investigated, when it was applied for young wheat plants in 3-leaf stage. This compound was lubricated on the 1st or on the 2nd–3rd leaves of wheat plants, and the levels of the free and bound SA forms, and the activity of the antioxidant enzyme,

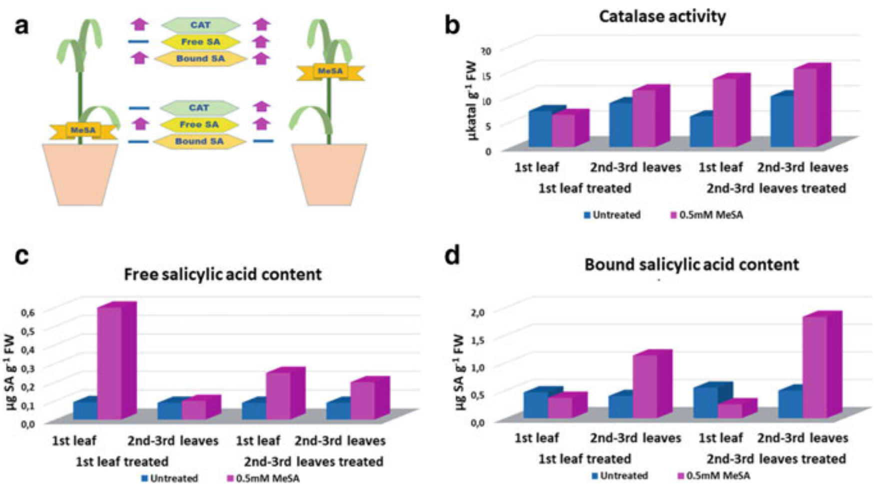

Fig. 2 Effect of methyl-salicylate (MeSA) treatment on catalase (CAT) activity and on the free and bound salicylic acid (SA) contents. **a** schematic visualisation of the experimental design. MeSA label indicates the position of the treatments (1st or 2nd-3rd leaves). **b** catalase activity in the leaves of untreated and MeSA-treated plants, **c** free SA content in the leaves of untreated and MeSA-treated plants, **d** bound SA content in the leaves of untreated and MeSA-treated plants

catalase was measured. When methyl-salicylate was applied on the 1st leaves of the plants, a substantial increase in the free, but not the bound form of SA content was detected in the 1st leaf, without any significant effect on the catalase activity. In contrast to this, SA was mainly increased in the bound form in the 2nd and 3rd leaves, and a slight, but statistically significant increase in the catalase activity was also detected (Fig. 2). Applying methyl-salicylate on the 2nd–3rd leaves induced a slight increase; both in the free SA level content and the catalase activity, with a decrease in the bound form of SA in the 1st leaf. In the 2nd–3rd leaves, a slight and a substantial increase was detected in the free and in the bound form, respectively, parallel with an increase in the catalase activity.

5 Conclusions

SA and its certain related compounds can be potentially used in agriculture for: (1) improving biomass production; (2) inducing stress tolerance; (3) increasing crop quality. However, SA can also be a stressor, so the application must be optimised in each case. The specific plant species and growing environmental conditions must also be taken into account. In spite of the intensive research in the field, the mode of action, especially in the case of the exogenously used SA, is still not well understood. It may be involved in various stress-related processes; however, the question of specificity/aspecificity has not been clarified, yet. SA can be induced by several stressors or by itself. How can the specificity of processes be created, which allows plants to waste neither their energy nor their existing stock of materials on responses, defensive processes that they do not need? It can also be assumed that its receptor, or one of the interacting factors in its downstream signalling route determines the specific reactions. So unfortunately, or fortunately, there are still many open questions to answer. And as it is usually, answering a question raises a number of new questions.

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Function of Mediator in Regulating Salicylic Acid Mediated Signaling and Responses in Plants

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Abstract Mediator is a transcriptional co-regulator required for the transcription of all protein coding genes by RNA polymerase II (RNA pol II) in eukaryotes including plants. Mediator is a complex of around 30 subunits and transmits the signals from promoter bound transcription factors to the RNA pol II. The Mediator is composed of head, middle and tail modules which constitute the core mediator complex to which a forth kinase module is reversibly associated. In plants, phytohormones play an essential role in all stages of growth and development from embryogenesis to flowering as well as response to diverse biotic and abiotic environmental factors by activation of several signaling cascades. Every signaling cascade regulates a large array of genes through a network of transcription factors (TFs). All TFs have to interact with one or more mediator subunits to regulate the corresponding gene expression. Hence, Mediator plays an essential part in orchestrating the transcriptional output of all signaling cascades. Salicylic acid (SA) is a phenolic hormone with important role in plant growth and development as well as critical function in resistance against pathogens. SA has been found to be an essential part of plant innate immune system required for the pattern -triggered immunity (PTI), Effector-triggered immunity (ETI) as well as for the establishment of systemic acquired resistance (SAR). Functional studies of several mediator subunit mutants revealed that different aspects of SA signaling from its biosynthesis to activation of downstream PR gene expression and SAR are regulated by mediator subunits from the middle, tail and kinase modules of Mediator. In this chapter, we will discuss in detail how the Mediator plays a key role in regulating SA mediated signaling and defense responses in plants.

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1 Mediator

Mediator (Mediator complex) is a multisubunit transcriptional co-regulator necessary for the transcription of protein-coding and non-coding genes by RNA polymerase II in all eukaryotes. Mediator was first identified and biochemically purified from *S. cerevisiae* (Kelleher et al. 1990; Kim et al. 1994). Mediator in yeast is comprised of 25 subunits with a molecular mass of around one million Dalton (Kornberg 2005). Subsequently, Mediator has been identified in metazoans such as *D. melanogaster*, *C. elegans*, mouse and humans (Myers and Kornberg 2000). The fundamental role of the Mediator is to transmit regulatory signals from promoter bound transcription factors to RNA pol II. The Mediator interacts with the C-terminal domain of RNA poly II holoenzyme, thereby, acting as a bridge between RNA poly II and transcription factors (Kim et al. 1994, Kornberg 2005). During the process of transcription, there is considerable protein-protein interaction between Mediator, RNA pol II and other general and gene-specific transcriptional regulatory factors. The Mediator differs from other transcriptional factors by its high degree of flexibility (Poss et al. 2013). Mediator is generally required for the assembly of pre-initiation complex (PIC) but also plays a crucial role in nearly all stages of mRNA synthesis (Allen and Taatjes 2015). Mediator can act as both co-activator and co-repressor in transcription. Mediator has also been shown to be involved in the epigenetic and architectural modification of chromatin resulting in alteration in gene expression (Kagey et al. 2010; Lai et al. 2013).

1.1 Role of Mediator in Transcription

In eukaryotes, mRNA synthesis undergoes three discrete stages known as initiation, elongation and termination which is catalyzed by RNA pol II and regulated by gene-specific transcription factors and the Mediator complex. Mediator has a crucial role in all three discrete stages of transcription. It activates pol II transcription by interacting with both DNA binding transcription factor, pol II and pre-initiation complex (Myers and Kornberg 2000; Malik et al. 2005; Balamotis et al. 2009). Mediator makes large contact with pol II which serves as a central scaffold around which rest of the PIC components like TFIIA, TFIIB, TFIIF, TFIIE etc. assemble (Asturias et al. 1999; Bernecky et al. 2011). Mediator has been involved in the post-initiation stage of pol II transcription by recruiting pol II transcription elongation factors, pre-mRNA processing factors and by controlling the phosphorylation of heptapeptide repeats in the C-terminal domain (CTD) of RNA pol II (Boeing et al. 2010; Donner et al. 2010; Conaway and Conaway 2013). Mediator also help in regulating pol II pausing and pause release (Meyer et al. 2010). Thus, Mediator may engage indirectly in all processes of transcription by modulating CTD phosphorylation.

1.2 Modular Organization of Mediator

Mediator is a multi protein complex of around 30 subunits, with the composition and number of subunits varying in different taxonomical groups. The modular structure is the salient feature of the Mediator. The complete assembly of Mediator is organized into three modular structures of head, middle, and tail; together they are known as mediator core (Dotson et al. 2000; Bourbon 2008). In addition to these, there is a fourth module called (CDK) kinase module reversibly associated with mediator core (Fig. 1) (Wang et al. 2001; Elmlund et al. 2006). Each module components is structurally and functionally interlinked. Mediator core linked with RNA pol II enables transcription whereas the binding of (CDK) kinase module to Mediator makes it dissociated from RNA pol II to repress transcription, but positive regulation of kinase module was also reported (Elmlund et al. 2006; Donner et al. 2010). Each module has a unique role in transcription and comprises of different subunits. A combination of electron microscopic studies, subunit localization and biochemical studies of yeast and human mediator complex revealed that head module is composed of MED6, MED8, MED11, MED17, MED18, MED20, MED22, MED27, MED28, MED29, and MED30 (Verger et al. 2019). MED27 and MED29 are considered distant orthologs of yeast MED3 and MED2 and hence, sometimes, referred to as MED2/29, MED3/27 (Bourbon 2008).

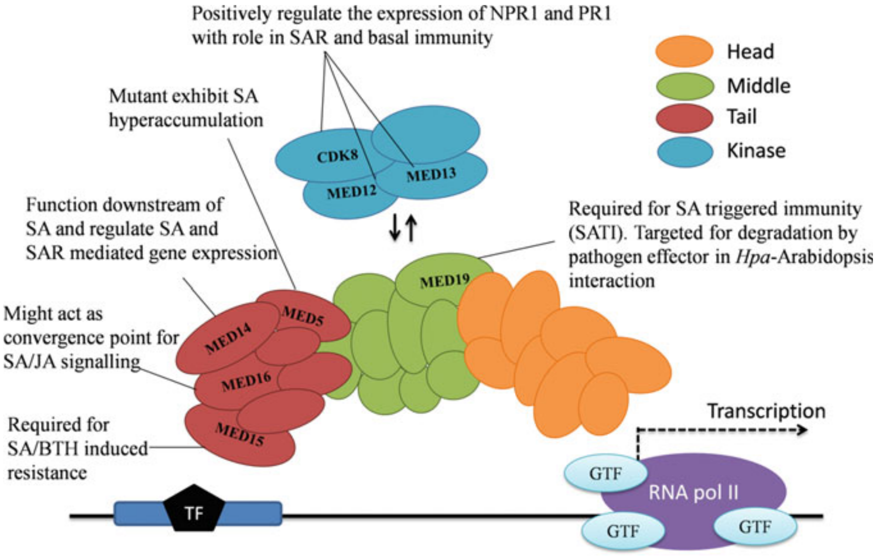

Fig. 1 Schematic representation of the structure and function of plant mediator complex: Mediator subunits with known roles in SA signaling and responses are highlighted. (Individual subunit location shown within each module is arbitrary). GTF: General Transcription Factor, TF: Gene Specific Transcription Factor

The middle module in human and yeast comprises of MED1, MED4, MED7, MED9, MED10, MED19, MED21 and MED31 (& MED26 in human) (Tsai et al. 2014; Verger et al. 2019). Putative orthologs for MED26 and MED30 were identified in plants but were not obtained in the biochemical purification of Mediator, moreover, MED1 homolog has not been identified in plants (Bäckström et al. 2007; Mathur et al. 2011). Head module together with the middle module performs a crucial function during PIC assembly by contacting the RNA pol II and balancing its interaction with general transcription factors (Soutourina 2018). The tail module is composed of MED14, MED15, MED16 which are conserved in yeast, humans and plants with MED2, MED3 and MED5 homologs found in yeast and plants and MED23 and MED25 found in human and plants. The tail module interacts with gene-specific transcription factors. (CDK) kinase module generally contains CDK8, CycC, MED12 and MED13 (Elmlund et al. 2006). Though MED14 is traditionally considered as a subunit of tail module, cryo-EM studies of *S. pombe* shows that Head, Middle and Tail module are connected by subunit MED14 which work as a central backbone (Tsai et al. 2014). Cryo-EM study has revealed high resolution structural information for head and middle modules, yet for tail and CDK kinase module high resolution structural information is not available (Verger et al. 2019).

1.3 Mediator in Plants

In plants, Mediator was first biochemically purified from *Arabidopsis thaliana* which revealed that it is composed of more than 30 subunits and exhibit less homology with other metazoan counterparts (Bäckström et al. 2007). Interestingly, some subunits such as MED34, MED35, MED36 and MED37 that are plant-specific were also identified (Bäckström et al. 2007). MED34 (RecQ2) was recognized as a DNA helicase which shows homology to human RecQ DNA helicase. It can disrupt the D-loop and mediate branch migration of holiday junctions (Kobbe et al. 2008). MED35 is involved in splicing of mRNA by binding to C-terminal domain of RNA pol II (Pearson et al. 2008). MED35 has been identified as homologous to human gene CA150 (co-activator of 150 KDA) and PRP40 gene of *S. cerevisiae* (Bäckström et al. 2007; Kang et al. 2009). MED36 encodes a fibrillarin which has a role in rRNA processing and proper ribosome assembly (Barneche et al. 2000).

In plants, Mediator has been found to be a key regulator in plant development. For example, MED8 function in floral transition (Kidd et al. 2009), cell expansion, organ size (Xu and Li 2012), root development (Sundaravelpandian et al. 2013), and cell wall composition (Seguela-Arnaud et al. 2015). MED25 plays a role in the floral transition, redox homeostasis (Sundaravelpandian et al. 2013), sugar signaling, ABA signaling (Chen et al. 2012), lateral root development (Raya-González et al. 2014) etc. In terms of both sequence similarity and complex composition, human and Arabidopsis Mediator are more alike to one another than that of yeast. Human mediator complex shares 25 of its 30 subunits with yeast and up to 28 subunits with Arabidopsis Mediator (Dolan and Chapple 2017). Through protein sequence study between human, yeast and Arabidopsis, it has been found that the human MED29, MED27, MED24 and Arabidopsis MED32, MED27 and MED33 are orthologs of yeast MED2, MED3 and MED5 respectively (Dolan and Chapple 2017).

2 Role of Mediator in General Plant Growth and Development

The mediator plays a crucial role in the regulation of gene expression which is essential for the normal growth, development and to respond to environmental stresses in plants. The life cycle of plant is sorted into four general stages which comprises of the embryonic stage, the juvenile vegetative stage, the adult vegetative stage and the reproductive stage. There are generally two-phase changes: former is vegetative phase change and later is reproductive phase change or floral transition which ensures plant fitness, survival and reproductive success (Poethig et al. 2003). Early embryogenesis and regulation of seed to seedling transition are regulated by MED12 and MED13 of kinase module. MED12 and MED13 are also involved in vegetative phase change, floral transition and auxin response (Gillmor et al. 2014; Buendía-Monreal and Gillmor 2016). In Arabidopsis, CDK8 subunit of kinase module was shown to be involved in cellular differentiation and cell fate specification in floral meristems (Wang and Chen 2004). Middle module subunit MED7 was found to be involved in regulating the skotomorphogenic growth of Arabidopsis etiolated seedlings (Kumar et al. 2018). Cell proliferation and cell expansion are necessary parts of organ and plant development. Mediator subunits MED25, MED8, MED16, MED33a/MED5a and MED33b/MED5b were found to regulate cell wall composition, cellular growth and expansion etc. (Buendía-Monreal and Gillmor 2016). Floral transition is also positively regulated by the subunits of the head module i.e. MED8, MED17, MED18, and MED20a and MED30 (Zheng et al. 2013; Zhang and Guo 2020). Among the tail module subunits, floral transition is positively regulated by MED15, MED16, MED23 and whereas MED2 and MED5 negatively regulate flowering time (Zhang and Guo 2020).

3 Role of Mediator in Plant Stress Signaling and Responses

In natural environment, plants are persistently confronted by a myriad of biotic and abiotic stresses. Being sessile, plants cannot escape these adverse environmental factors. Biotic stress include pests, pathogens and herbivory whereas heat, cold, salinity and drought etc. constitute abiotic stress. Plant vulnerability to biotic and abiotic stress prompts a disruption in plant metabolism which leads to depletion in fitness and productivity. Plants have evolved sophisticated mechanisms of stress perception, signaling and deployment of an appropriate response against every stress to defend itself. Transcription forms the early step in orchestrating a well-defined response to any stress with the activation and expression of a large number of early stress response genes. Since Mediator has a pivotal role in transcriptional regulation, Mediator and its constituent subunits become central to choreographing any gene expression changes necessary to respond to any stress by interacting with transcription factors. For example, MED25 regulates response to salinity and drought stress by interacting with DREB2A, ZFHD1 and MYB (Elfving et al. 2011). MED25 and MED8 of Arabidopsis are independently involved in defense response and provide resistance against necrotrophic fungi, *Alternaria brassicicola* and *Botrytis cinerea* (Chen et al. 2012; Kidd et al. 2009). MED18 was also found to be regulating plant immunity by contributing to the defense against necrotroph *Botrytis cinerea* through interaction with zinc finger transcription factor YY1 (Lai et al. 2014). In addition to that, MED25 and MED18 were found to be involved in ABA signaling by interacting with ABI5 and ABI4 respectively (Lai et al. 2014). Another mediator subunit of kinase module CDK8 was also shown to have a critical role in ABA signaling and drought responses (Zhu et al. 2020). MED21 was also implicated in resistance to necrotrophic pathogens by interacting with E3 ligase, HUB1 (Dhawan et al. 2009). All these findings point to the fact that Mediator acts as a central integrator of diverse signaling cascades including stress signaling and responses through interaction of different subunits of Mediator with diverse transcription factors.

4 Functional Analysis of Mediator Subunits Involved in SA Signaling

Salicylic acid (SA) is a phenolic compound produced in a plant as a phytohormone. Salicylic acid is involved in PAMP/Pattern-triggered immunity (PTI), effector-triggered immunity (ETI) and establishment of systematic acquired resistance (SAR) in response to pathogen attack (Durrant and Dong 2004; Tsuda et al. 2009). Salicylic acid gets accumulated in infected leaves and induces SAR by enhancing the expression of PR genes (Malamy et al. 1990; Metraux et al. 1990). Transcriptional regulation of SA biosynthesis and SA mediated defense gene expression has been extensively studied (Chen et al. 2020; Ding and Ding 2020). SA mediated immune response involves large scale transcriptional reprogramming. Hence, understanding the role of Mediator in SA induced transcriptional reprogramming is crucial in deciphering the SA signaling and response pathways. Mediator subunits MED5, MED14, MED15, MED16, MED19, CDK8, MED12 & MED13 are found to be involved in SA signaling and responses (Table 1). The role of each subunit is discussed below.

Table 1 Reported function of various subunits of Mediator in SA signaling and responses

Sub Module	Mediator subunit	Function	Reference
MIDDLE	MED19a	Targeted for degradation by biotrophic oomycete pathogen effector. Positive regulator of SA-triggered immunity in Arabidopsis; Involved in SA/JA cross talk	Caillaud et al. (2013)
TAIL	MED5 (*ref4-3)*	Hyper accumulation of free SA and SA conjugates were observed in *ref4-3*. Genes involved in SA biosynthesis and SA dependent markers were found to be upregulated. Kinase activity of CDK8 was found to be essential for the hyperaccumulation of SA in *ref4-3* mutant	Mao et al. (2019)
	MED14 (SWP)	Positively regulates resistance against avirulent pathogens. Functions downstream of SA and regulate the expression of genes involved in SA signaling and SAR. Required for extracellular NAD + mediated signaling	Zhang et al. (2013)
	MED15 (NRB4)	Required for SA or BTH induced pathogen resistance in Arabidopsis. Might function downstream of NPR1 in regulating SA response	Canet et al. (2012)
	MED16 (SFR6, IEN1)	Positively regulates defense responses against virulent and avirulent strain of *Pst*DC3000 in Arabidopsis as well as against necrotrophic fungal pathogens Might act as a convergence point for SA and JA mediated signaling for inducing defence gene expression	Wathugala et al. (2012) and Zhang et al. (2012)
KINASE	CDK8, MED12 and MED13	CDK8 interacts with NPR1, WRKY6, WRKY18 and TGA factors. Positively modulate SA level, SAR and basal immunity Expression of NPR1 and PR1 are also positively regulated by CDK8 and other kinase module subunits MED12 and MED13	Huang et al. (2019) and Chen et al. (2019)

4.1 *MED19*

MED19 is a subunit of Mediator middle module. It is involved in the plant defense mechanism by balancing the gene expression of SA, JA/ET signaling pathways. While studying the effector proteins of oomycetes pathogen (of Arabidopsis) *Hyaloperonospora arabidopsidis* (Hpa), Caillaud et al. (2013) identified an effector called HaRxL44 which interacts with host mediator subunit MED19a and destabilizes it in a proteasome dependent manner. When HaRxL44 was expressed in plants, low levels of salicylic acid (SA)–triggered immunity (SATI) was observed. SA marker genes (PR1, PR2, PR5, LURP1 and WRKY70) are downregulated in HaRxL44 transgenic line. Further low SATI was observed in *med19a* knockout mutants, whereas strong SATI was observed upon MED19a overexpression. Presence of HaRxL44 effector or the absence of MED19a in plants was associated with reduced expression of PR1 expression. It was also observed that SA induced PR1 expression is reduced in *med19a* mutant and was enhanced in MED19a overexpressing lines. Whereas JA/ET marker genes such as PDF1.2, JAZ1 and JAR1 were induced in HaRxL44-lines and in *med19a* mutants. Thus, HaRxL44 mediated degradation of MED19a alters SA dependent transcription, disturbs the balance between JA/ET an SA pathways. These findings suggest that MED19a is involved in SA/JA cross talk and is a positive regulator of SA triggered immunity (SATI) against biotrophic pathogens (Caillaud et al. 2013).

4.2 *MED14*

MED14 is a tail module subunit originally purified as STRUWWELPETER (SWP) which is involved in plant defense by modulating SA signaling. MED14 plays a crucial role in cell proliferation (Autran et al. 2002), and positively regulates extracellular NAD + induced PR1 gene expression (Zhang et al. 2013). By studying the T-DNA insertion mutant of MED14 gene, Zhang et al. (2013) has shown that *med14* plants exhibit susceptibility to aviruelnt pathogen *Pseudomonas syringae* pv. *tomato* (*Pst*) DC3000/*avrRpt2*. Loss-of-function *med14-1* mutant also exhibits inhibition of NAD + induced PR1 gene expression. Whereas NAD + induced PR1 gene expression was restored in complementation lines confirming the role of MED14 in extracellular NAD + mediated signaling. It was also found that resistance to *Pst* DC3000/*avrRpt2* was compromised in *med14-1* suggesting a positive role in resistance against pathogens, with a large number of genes differentially regulated between wild type and *med14* mutant plants after pathogen infection. Many genes involved in SA signaling and SAR, including the master regulator NPR1, was downregulated in *med14* mutant plants post pathogen infection. Though MED14 was found to be required for the induction of SA biosynthesis genes ICS1, EDS5 and AVRPPH3 SUSCEPTIBLE3 (PBS3), SA levels were not affected post pathogen infection in *med14* mutants, suggesting a lack of major role in SA accumulation (Zhang et al. 2013). Whereas treatment with biologically active analogue of SA, benzo (1,2,3) thiadiazole-7-carbothioic acid and S-methyl ester (BTH) showed that the expression of PR1, PR2, PR5 was drastically decreased in *med14-1* mutant plants suggesting the MED14 function downstream of SA. Further, SAR mediated defense gene expression and resistance to pathogen infection in systemic leaves was severely compromised in *med14* mutant plants, indicating a key role for MED14 in establishment of SAR. When compared with *med16-1* mutant plants, transcriptional changes in response to *Pst* DC3000/*avrRpt2* in *med14-1* showed that many genes related to SAR and NPR1 target genes are differentially expressed, indicating that MED14 and MED16 employ different mechanisms in regulating the SA signaling and SAR pathways (Zhang et al. 2013).

4.3 MED15

MED15 is a tail module subunit which was initially identified in a mutant screen as NRB4 (non-recognition-of-BTH4) in Arabidopsis (Bäckström et al. 2007; Canet et al. 2012). Benzothiadiazole (BTH) is an analog of SA and *NRB4* mutants were found to be insensitive to BTH, similar to *npr1-1* mutants. Treatment with SA or BTH resulted in strong resistance in wild type plants against *Pst* DC3000 but not in *nrb4* or *npr1* mutant plants. In addition to that, *Pst* DC3000 or BTH treatment was not able to induce expression of PR1 protein in *nbr4* and *npr1* plants but accumulation of SA is unaffected in *nrb4* mutant. No interaction between NPR1 and NRB4 was observed in yeast two hybrid assay even in the presence of SA and weaker alleles of *nrb4* exhibited varied levels of SAR and defense against pathogens. Further, enhanced response to SA was observed when NRB4 was overexpressed in Arabidopsis. NRB4 (MED15) was found to be non-essential for NPR1 stability and for the concentration of NPR1 in nucleus (Canet et al. 2012). Thus, MED15 appears to be functioning downstream to NPR1 in regulating SA mediated responses.

4.4 MED16

MED16 is a tail module subunit initially identified in a mutant screen as SENSITIVE TO FREEZING6 (SFR6) which was compromised in cold acclimatization and subsequently found to have a role in CBF pathway (Knight et al. 2009). Role of MED16 in plant defense came from studies of Wathugala et al. (2012) and Zhang et al. (2012). Wathugala et al. (2012) reported the role of MED16 in plant defense by studying the mutants of *sfr6* alleles. Zhang et al. (2012) identified MED16 as INSENSITIVE TO EXOGENOUS NAD$^+$ (*ien1*) in a genetic screen to identify mutants which are compromised in PR1 expression in response to exogenous NAD$^+$ and the mutant was subsequently renamed as *med16-1*. In separate studies, MED16 mutants were found to be susceptible to virulent and avirulent strains of *Pseudomonas syringae* with reduced expression of PR1, PR2 and PR5 genes, suggesting an important role for this mediator subunit in plant immune responses against pathogenic infection (Wathugala et al. 2012 and Zhang et al. 2012).

Similar to MED14 mutant plants, free SA levels were not significantly affected upon pathogen infection in *sfr6/med16* mutants, indicating a lack of major role for MED16 also in SA biosynthesis. But SA (Wathugala et al. 2012) or BTH (Zhang et al. 2012) induced expression of PR genes (PR1 & PR2) was severely reduced in *med16/sfr6* mutants indicating that MED16 functions downstream to SA. Further NPR1 protein accumulation and SAR induced expression of defense genes in systemic leaves is also affected in *med16* plants indicating a direct role in SA mediated defense gene expression in plants (Zhang et al. 2012). JA induced as well as ERF5 activated expression of *PDF1.2A* and *PDF1.1* was also compromised in *sfr6/med16* mutants and *med16* mutants are susceptible to necrotrophic fungal pathogens suggesting that MED16 plays a role in both JA and SA mediated defense response pathways (Wathugala et al. 2012 and Zhang et al. 2012). Therefore, MED16 has a key role in plant immunity as it positively regulates SAR and serves as a convergence point in SA and JA/ET mediated defense pathways (Zhang et al. 2012).

4.5 MED5

MED5/MED33 is a tail module subunit. MED5 plays an important role in phenylpropanoid homeostasis as *med5a/med5b* mutant hyperaccumulates phenylpropanoids (Bonawitz et al. 2012). On the contrary, a single amino acid substitution in MED5b (*ref4-3*) results in decreased accumulation of phenylpropanoids (Bonawitz et al. 2012). Genes involved in SA biosynthesis such as ICS1 and SA dependent marker genes PR1, PR2 and PR5 were found to be upregulated in *ref4*-3 mutants. Further, enhanced accumulation of free SA and SA conjugates were also observed in *ref4-3* (Mao et al. 2019). Interestingly, upregulation of SA signaling genes and SA accumulation were eliminated in *ref4-3* mutant with the loss of CDK8 subunit (*ref4-3/cdk8-1*). Moreover, kinase activity of CDK8 was found to be essential for the hyperaccumulation of SA in *ref4-3* mutant. Based on the structure of yeast mediator complex, CDK8 does not physically interact with MED5. Hence, future investigation will provide a better understanding of the functional interaction between MED5 and CDK8 subunits in mediating SA signaling.

4.6 CDK8, MED12 and MED13

CDK8 (Cyclin-dependent kinase 8) is a kinase module subunit of Mediator. Salicylic acid levels and systematic acquired resistance are positively modulated by CDK8. Expression of CDK8 transcripts are upregulated upon pathogen infection, suggesting a positive role for CDK8 in plant immunity (Chen et al. 2019). Studies by Huang et al. (2019) has shown that *cdk8* mutants exhibit enhanced susceptibility to virulent pathogens and defective SAR as well as reduced study state level of SA in uninfected plants. Reduced SA levels are associated with reduced expression of positive regulators of SA accumulation, ICS1 and EDS5 in *cdk8* mutants (Haung et al. 2019). Pathogen induced expression of NPR1 and PR1 transcripts were reduced in *cdk8* mutants. NPR1, which is a master transcriptional regulator of SA mediated gene expression, and was found to physically interact with CDK8 and control its own expression by recruiting CDK8 to its own promoter. CDK8 interacts with WRKY6 and WRKY18 in regulating NPR1 gene expression and CDK8 was found to also interact with TGA factors in facilitating PR1 gene expression (Chen et al. 2019). Further, presence of SA enhanced the interaction between NPR1 and CDK8. It was observed that the complete expression of NPR1 and its target genes required functional CDK8. Mutants of other subunits of kinase module, *med12* and *med13* also exhibited reduced expression of NPR1 and PR1 gene expression as well as compromised SAR (Chen et al. 2019). In addition to that, *med12* mutants exhibited reduced SA levels and reduced levels of ICS1 and EDS5 transcripts (Huang et al. 2019). Taken together, subunits of kinase module are essential for the expression of key genes in SA signaling, thereby, regulating SA accumulation, systemic acquired resistance and basal immunity.

5 Conclusion and Future Perspective

The mechanism of transcription itself is very highly sophisticated and duly orchestrated, involving a large number of proteins with multisubunit complex Mediator being part of it. Mediator is considered as an endpoint for the converging of information from all transcription factors for a suitable transcriptional output.

The function of independent plant mediator subunits and functional relevance of their interaction with individual transcriptional factors is starting to emerge. But it is yet to be understood, the complete array of complex interactions between Mediator and its interacting factors, and the conformational changes within Mediator necessary for the transfer of regulatory signal to RNA pol II in plants. Since Mediator is the converging point of all signaling cascades, the elucidation of the function of all the subunits of Mediator and its interaction with other proteins from transcription factors to epigenetic factors will shed more light on not only the SA signaling pathway but also the other signaling cascades in plants.

Due to the critical role of Mediator in all pol II mediated gene expression; it will be regulating gene expression both upstream as well as downstream to any hormone signaling. Significant progress has been made in understanding the role of individual transcription factors, transcriptional co-regulators and epigenetic regulators involved in SA mediated plant immune responses, yet the complete network of interactions involved is not clear. Studies in other eukaryotic systems have shown that apart from transcription, Mediator functions in post-transcriptional regulation, DNA repair and chromatin remodelling. Hence, the current understanding of the involvement of different subunits of Mediator only gives a partial picture of the actual mechanistic events responsible for the regulation of SA mediated transcriptional reprogramming. Further studies will provide a better insight on the role played by Mediator in regulating the signaling and responses of this key defense hormone in plants.

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The Hidden Pathways Affecting Salicylic Acid Signaling in Plants

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Abstract The role of salicylic acid (SA), a small phenolic compound, in plant defense against a wide range of pathogens is highly significant. The SA function in plants has been widely investigated for years. The presence of SA is critical in responding to various abiotic and biotic stress conditions. Because of its crucial role in developing and regulating plant immunity, it has been extensively studied in plants. The results have shown the role of numerous plant genes in signaling salicylic acid. Much of the efforts have focused on enhancing yield under various unfavorable circumstances and agricultural productivity; therefore, more knowledge about SA signaling can help scientists and other end users to understand the physiological processes of SA and the importance of SA immunity.

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1 Introduction

Over the past decades, researchers have attempted to clarify the function of salicylic acid (SA) signaling as a regulator of the plants' physiological processes under different abiotic and biotic stresses by an abnormality named systemic-acquired resistance (SAR). This endogenous plant growth regulator synthesized from chorismic acid is a final product of the shikimic acid pathway (Ramos et al. 2017). Two receptor-like cytoplasmic kinases named PCRK1 and PCRK2 play a pivotal role in activating SA biosynthesis through pattern-triggered immunity (PTI) (Kong et al. 2016).

Recent studies have indicated that salicylic acid acts as an important regulator in photosynthesis, photosynthetic pigments, photosystem II (PSII), and the action of enzymes such as Rubisco and carbonic anhydrase, under metal stress (Zhang et al. 2015). SA is modified into various forms, the active and the inactive molecules in plants are believed to be in the form of free SA and glucose-conjugated, respectively. Restraining the modification of SA to SA-O-b-D-glucoside results in increased pathogen resistance (Noutoshi et al. 2012). The role of SA in improving tolerance to salinity condition has been extensively confirmed in numerous crops such as *Vicia faba* (Azooz 2009). Phenylalanine pathway is the best prevalent pathway for SA synthesis in crops although the biosynthesis of SA may also be achieved during the isochorismate pathway (Mustafa et al. 2009). Through the function of enzyme phenylalanine ammonia-lyase (PAL), phenylalanine produces Cinnamate 4-hydroxylase (C4H). By oxidizing the side chain and further hydroxylated, cinnamic acid is hydroxylated to produce SA and coumaric acid.

SA in crops has been biosynthesized from shikimic acid via chorismic acid and coumaric acid (An and Mou 2011). Although the role of plant isochorismate synthases in synthesis has been confirmed, plant enzymes transporting isochorismate into SA is largely unknown. Therefore, SA synthesis in crops has not been totally identified. The most remarkable action of SA is being a signal molecule in plant defense responses (Chen et al. 2009). Salicylic acid induction pathway has major impacts on the plant, and results in metabolomics, and genetic and physiological modifications during the plant's adaptation to stimuli (Filgueiras et al. 2019). A large body of literature have demonstrated that SA originated from the genital structures of cycads and the flowers of specific angiosperms that controls thermogenesis (heat production) (Vlot et al. 2009).

2 SA Binding Proteins (SABP)

To understand how SA performs its different functions, especially in triggering disease resistance, two high-performing strategies were involved. In *Arabidopsis*, methods were used both biochemically and biophysically. In these high-throughput probes, more than 100 candidate SABPs were recognized (Manohar et al. 2015). SABPs have been introduced in many plant species (Kohli et al. 2017).

SA-binding protein 2 (SABP2) was originally found due to its proficiency to bind to salicylic acid. However, researchers at the Northeast Structural Genomics Consortium (NESG) solved the current structure of the protein that divulges its function in cleavage of methyl salicylate and restrain of the reaction by salicylic acid. The structure which is available in the Protein Data Bank (PDB) entry 1y7i demonstrated that SABP2 is one of the alpha/beta hydrolase enzymes cleaving other molecules and small esters. The molecule recognizing the acidic group and the special aromatic rings is surrounded by the active site. The cleavage reaction is performed by a catalytic triad reminiscent of the digestive serine proteases (Park et al. 2009).

As part of the signal transduction pathways, SABP2_Tobacco is needed to transform methyl salicylate (MeSA) to salicylic acid (SA) that activates acquired resistance in systemic tissues in *Nicotiana tabacum.* MeSA is thought to be an inactive form that requires to be demethylated to use it as a biological effect. To induce systemic acquired resistance, MeSA is able to catalyze the transformation of acibenzolar-S-methyl into acibenzolar (UniProtKB). Researchers introduced the characterization and purification of SA-binding protein 2 (SABP2), a tobacco protein that existents in low concentration and connects SA strongly. According to the sequence analysis, SABP2 is a lipase that belongs to the α/β fold hydrolase superfamily. To prove this postulation, recombinant SABP2 showed a lipase action against numerous synthetic layers. Furthermore, SA binding stimulates this lipase activity and may cause a lipid-derived signal. Mosaic virus resistance in tobacco inducing pathogenesis-related 1 (PR-1) gene expression by SA, and improvement of systemic acquired resistance were suppressed by the silencing of SABP2 expression (Kumar and Klessig 2003).

SABP2 that possesses methyl salicylate (MeSA) esterase function, catalyzes the transformation of MeSA to SA. Therein, a *SABP2*-like gene, *LcSABP*, was cloned from *Lycium chinense*, which illustrated wide sequence resemblances with SABP2 orthologs from other crops (Li et al. 2019). Results also showed that tolerance to drought was enhanced with the overexpression of *LcSABP* in transgenic tobacco plants. Furthermore, it is indicated that increased rates of *LcSABP* transcripts and endogenous SA amount is associated to enhanced tolerance to dryness (Li et al. 2019). However, NtSABP2 was co-crystallized with SA, Ser81, Ala13, and His238 and remains bound to a carboxylic group of SA with hydrogen bonds (Slaymaker et al. 2002). SABP3 is a carbonic anhydrase (CA, EC 4.2.1.1). Interconverting water and CO_2 into HCO_3^- is a significant action carried out with CA enzymes for all creatures (Frost and McKenna 2014). Carbonic anhydrase 2 (At5g14740) creates an 80-fold decline and another, CA1, SABP3 protein (At3g01500) showed a decline of 75-fold.

The central elements of the SA signaling pathway interact with both proteins, Natural Rubber Biosynthesis 4 (NRB4) and Neuropilin 1 (NRP1), the latter one in SA related method (Medina-Puche et al. 2017). Conversion in CA transcription or protein rates in crops infected with pathogen signifies the critical function of CAs in defense system. Certainly, a beneficial action in plant defense was proven for a chloroplast-localized CA of tobacco named SABP3, the hypersensitive response, which was intervened by the Pto:avrPto resistance (Slaymaker et al. 2002). Under changing atmospheric CO_2 circumstance, CA-interceded alteration in SA responses affects disease resistance rate. Previous studies indicated that in Arabidopsis SA-dependent defenses are regulated under changeable atmospheric CO_2 circumstances (Williams et al. 2018).

In *A. thaliana*, inducing SA collection and generation of the SA pathway is associated with the activation of CA in chloroplastic carbonic anhydrase1 (AtCA1 or AtSABP 3) as well as its binding to SA, which are crucial for curbing the expansion and accumulation of viruses (Poque et al. 2018). Evidence showed that in the defense response to *P. syringae* infection in plants, the elimination of *CA1* and *CA4* gene expression is necessary. Because of the fact that offending SA-mediated signaling the function of *CA1* and *CA4* plays as a negative immunity regulator in plants.

Studies also illustrated that different expressions of *CA1* under various atmospheric CO_2 circumstances is related to a changed rate of disease resistance to *P. syringae*. *CA1* and *CA4* are essential for the impacts of CO_2 on resistance to disease caused by *P. syringae* (Zhou et al. 2020). These reports mostly concentrate on the arrangement of responses to biotic stress by SABP and its structural characteristics of SABP in plants. Nevertheless, study on the connection between abiotic stress and SABP has been missed and the function of the *SABP* gene in the abiotic stress responses has been unrevealed (Li et al. 2019).

3 NPRs, ICSs and PALs

Understanding the regulation of SA production and what molecular machinery acts in the regulation of SA is important. Various genetic screens for SA insensible mutations separately recognized the same gene, NPR1 (Non-expresser of pathogenesis-related 1), genes 1, named NIM1, and SAI1, as the main modifier in the SA signaling pathway (Yan and Dong 2014). The NPR1 pathway is one of the genes that has been introduced as the principal role (Pokotylo et al. 2019). The NPR1 genes are protected through multicellular crops such as bryophytes, showing its function in SA immunity and perception. So far, only one transcript of NPR1/NPR3/NPR4-like gene in *Physcomitrella patens* has been reported (Peng et al. 2017).

In the signaling pathway, NPR1 is considered as a SA receptor. The signaling pathways of NPR1-independent and NPR1-dependent have been recorded; however, it is hardly understood how the signaling pathway intermediates NPR1-independent and NPR1-dependent (Verma and Agrawal 2017). In infected crops, the expression of defense gene by the redox-related activity of the required replication regulator protein NPR1 is induced by SA. The stabilization of the passive oligomer form of NPR1 is done by intermolecular disulfide connections in the cytosol. By SA collection, Glutathione (GSH) contents increase, and the cellular redox potential becomes more negative, resulting in the decline of NPR1 oligomers to a monomeric form. The active form of NPR1, which is monomeric increases in the nucleus and induces the defense (Mou et al. 2003).

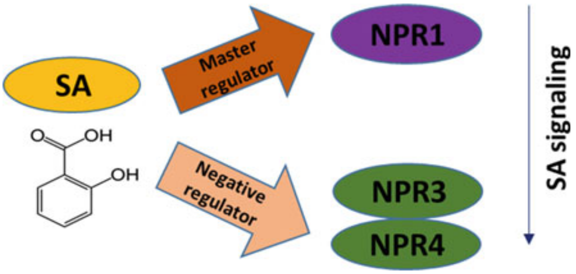

Fig. 1 Salicylic acid NPR binding proteins and controlling its signaling. NPR1 is a positive regulator and receptor of SA, increasing the level of this hormone in defense conditions; on the other hand, NPR3 and NPR4 are the repressors of SA signaling and have role in NPR1 degradation and decrease the level of SA

Using generating blends of transgenics and mutants, Castello and coworkers (Castelló et al. 2018) examined the function of these paralogs in SA perception. The only paralog, which can complete partly an NPR1 mutant was NPR2 (Fig. 1). The SA impression in combination with NPR1 or other paralogs is reduced by null NPR2. During all the conditions tested, NPR2, and NPR1 interacted with each other and other SA-related proteins. According to the genetic background, the rest of the paralogs activated diversely in SA perception (Castelló et al. 2018). It is suggested that NPR3/NPR4 act as E3 ligases that promote NPR1 degradation while NPR1 acts as a transcriptional co-activator (Ding et al. 2018). Research also illustrated that NPR3/NPR4 act as transcriptional co-restrainer and SA prohibits their function to enhance the expression of downstream immune regulators. Due to NPR4-4D which is a gain-of-function NPR4 allele, NPR4 becomes incapable to connect to SA, and mainly inhibits SA-induced immune responses. On the contrary, the equal mutation in NPR1 devitalizes its potency to connect to SA and promotes gene expression to induce SA–defense (Ding et al. 2018).

Isochorismate synthase (ICS) is another fundamental enzyme for SA biosynthesis that transforms chorismate into isochorismate by the help of two genes in *Arabidopsis thaliana* (Macaulay et al. 2017). One ICS (*AtICS1*) is essential for biosynthesis of increased SA in reaction to pathogens and exogenous SA and viral infections in leaf can also stimulate its expression. Another ICS (*AtICS2*) seems to be expressed intensively in the plant vasculature (Macaulay et al. 2017). Studies showed indisputable evidence of the important role of *ICS1* in *Arabidopsis*. Compared to any other plant ICS tested, during expressing *AtICS1* in *N. benthamiana*, a much higher enzymatic action was shown, which affirms the significance of *ICS1* in Arabidopsis SA supply (Yokoo et al. 2018). Under salt stress, the level of applied SA concentration impacts the expression of C4H and ICS and enzymes. Specifically, the induction of C4H and ICS with 1.0 mM SA was much higher than that of with 0.1 mM SA in *Carthamus tinctorius*. In *C. tinctorius*, the isolated genes of ICS and C4H were observed to be important for pathogen resistance and tolerance to salt stress

Table 1 Use of genes in transgenic disease resistance

Source gene	Recipient plant	Pathogen resistance	Note	References
NPR1	*Physcomitrella patens*	*Botrytis cinerea*	Increased SA levels and resistance to *Botrytis cinerea*	Ponce De Leon et al. (2012)
NPR1	*Arabidopsis thaliana*	*Pseudomonas syringae*	Proportional pathogen resistance to *Pseudomonas syringae*	Friedrich et al. (2001)
ICS	*Arabidopsis thaliana*	*Pseudomonas syringae*	Increased SA in reaction to *Pseudomonas syringae* and viral infections in leaf	Macaulay et al. (2017) Maurice Tronchet et al. (2010)
ICS	*Nicotiana benthamiana*	*Pseudomonas syringae*	A much great enzymatic action is shown which affirms the significance of ICS1 in Arabidopsis SA supply	Yokoo et al. (2018)
ICS	*Carthamus tinctorius*	*Pseudomonas syringae*	The isolated genes of ICS and C4H were noticed important for pathogen resistance and tolerance to salt stress	Dehghan et al. (2014)
PAL	*Glycine max* (Soybean)	*Phytophthora sojae*	ICS pathways is crucial for biosynthesis of pathogen-induced SA	Chuanzhong Zhang et al. (2019) Shine et al. (2016)
PAL	*Oryza sativa* (Rice)	*small brown planthopper* (SBPH)	Resistance to (SBPH) with enhanced SA levels	Canxing Duan et al. (2014) Fang et al. (2019)

(Dehghan et al. 2014). Studies demonstrated that PAL (phenylalanine ammonia-lyase) and ICS pathways are both crucial for biosynthesis of pathogen-induced SA in soybean, which is opposite to that in Arabidopsis. The malfunction of each pathway leads to abolish pathogen resistance and SA biosynthesis. Furthermore, unlike in Arabidopsis, pathogen infection collaborates with the inhibition of *ICS* gene expression. The PAL pathway by Pathogen-induced SA biosynthesis associates equally with phenylalanine concentrations (Shine et al. 2016).

The role of PAL is critical in plant defense because of its function in salicylic acid biosynthesis (Chaman et al. 2003). PAL genes of rice have been widely examined for their function in responses to stress (Fang et al. 2019). Of these genes, PAL9 was recently observed to control the activity of tyrosine aminomutase, which led it to be renamed TAM1 (Yan et al. 2015). The water loss and UV-B radiation was observed to increase the activity of PAL and benzoic acid hydroxylase (BA2H) that resulted in SA accumulation (Bandurska and Cieślak 2013). In *Arabidopsis thaliana*, a small gene family via four segments including PAL1 —PAL4 encodes PAL. PAL1/PAL2/PAL3/PAL4 tetraploid mutant had an undersized phenotype that significantly diminishes rates of SA accumulation and enhances vulnerability to the toxic bacterial pathogen *Pseudomonas syringae* (Huang et al. 2010).

In soybean, ICS and PAL are equally crucial for pathogen-induced SA synthesis. Using *P. syringae* pv. *glycinea* (*Psg*) or *Phytophthora sojae* in soybeans a triple enhancement in SA was observed. Through pathogen infection, the silencing of ICS or PAL pathway reduce the accumulation of SA. Moreover, these silenced crops were highly susceptive to infection by either of these two pathogens (Shine et al. 2016). Although, the ICS pathway is highly crucial in *Arabidopsis*, the PAL pathway is very essential for SA supply in rice. Moreover, the regulation of SA biosynthesis can be divergent in the plant. For example, in rice, shoots have more basic SA compared to roots (Duan et al. 2014). Two ICS genes are in *Arabidopsis*, of which ICS1 is responsible for 90% of the SA products, which is induced by UV light or pathogens (Garcion et al. 2008). SA can be modified to several derivatives. The function of these molecules can be in both inactive/storage forms of SA or transportable forms (like methyl-salicylate, MeSA). The later one includes glucosylated SA derivatives; salicylic acid glucoside (SAG) and salicylic acid glucose ester (SGE) (Thompson et al. 2017) (Table 1).

4 PAD4, EDS1 and SAG101 Proteins

Three protein regulators including Enhanced Disease Susceptibility 1 (EDS1), Phytoalexin Deficient 4 (PAD4), and Senescence Associated Gene101 (SAG101) adjust biotic stress-induced SA accumulation (Makandar et al. 2015). In crops, another route is evolved for protecting defenses regulated by SA against genetic perturbations or pathogen. The collaboration of EDS1, PAD4 and promoting SA biosynthesis preserves main SA-related resistance programs leading to an increase in the function of the innate immune system (Cui et al. 2017). EDS1 was introduced first as a protein that plays role in ethylene-, salicylic acid (SA)- and reactive oxygen species (ROS)-dependent defense as well as adaptation responses. EDS1 is a molecular regulator of biotic and abiotic stress-induced cell death (Bernacki et al. 2018).

The interaction of EDS1 with PAD4 and SAG 101 is required to restrict the development of poisonous bacterial strains and for HR foundation (Feys et al. 2005). In Arabidopsis, SAG101 and PAD4 also restrain the post-offensive development of non-pathogenic fungi (Lipka et al. 2005). Many *R* genes mediate a Signaling that requires NDR1 and/or EDS1. Previous studies have illustrated that SSI2 EDS1 plants that need EDS1 for their signaling retain the expression of R genes at high levels (Chandra-Shekara et al. 2007). In basic and TIR- NB-LRR genes (TNL) immunity, EDS1 is associated with Phytoalexin Deficient4 (PAD4), which is the direct partner to promote expression the ICS1, and SA accumulation (Wagner et al. 2013). Transcriptomic data and Genomics also showed an EDS1/PAD4-regulated branch in basic and TNL immunity that function independent of ICS1-generated SA (Gloggnitzer et al. 2014).

Previous results illustrated that conditional or fundamental overexpression of Arabidopsis PAD4 with EDS1 leads crops into an immune response. In a transcriptomic and genetic study, researchers recognized an inherent, primary EDS1/PAD4 signaling function, which is self-determination of ICS1-generated SA that provides a mechanism for conserving the expression of SA-related defense gene and resistance to pathogen (Cui et al. 2017). Although in *Nicotiana benthamiana*, PAD4 illustrated no discernible immune activities, TNL-interceded resistance responses demanded EDS1 complexes that incorporate a Senescence Associated Gene101 (SAG101) isoform. Since SAG101 is limited to those genomes and encoding TNL receptors, Gantner et al. (2019) suggested that it would be essential for immune signaling mediated by TNL in almost all plants other than *Brassicaceae*. Studies showed that SAG101a is necessary for *Xanthomonas campestris pv. vesicatoria* effector protein XopQ-induced resistance responses in *Nicotiana benthamiana* (Gantner et al. 2019). In that study, AtSAG101 transformed into *Brachypodium distachyon* indicated that resistance to *Puccinia brachypodii* and *Magnaporthe oryzae* is induced by overexpression of AtSAG101 in *B. distachyon*. Based on these outcomes, it was concluded that in *B. distachyon*, AtSAG101 causes resistance to pathogens in *B. distachyon* (Gantner et al. 2019).

5 Thioredoxins (TRX)

Specific TRX enzymes, which have the potential for functionally regulating several immune signaling proteins are recruited with the plant immune system. In crops, the TRXs are a major multigenic family with different activities localized in divergent subcellular organelles such as the chloroplast and cytosol (Dos Santos and Rey 2006). Some proteins including superoxide dismutase, thioredoxins, and glutaredoxin have an essential role in redox in crops. These proteins can be involved in the transformation of NRP1 to a monomer while the plant is extracted by a SA treatment and pathogen (Tada et al. 2008). Although Salicylic acid is crucial for NPR1 redox adjustment, the underlying function is still unknown. Thioredoxin TRXh5 catalyzes NPR1 (Kneeshaw et al. 2014). In a high-throughput screen, the chloroplastic thioredoxin-m1 (TRXm1) was demonstrated to connect to SA and acknowledged by surface plasmon resonance (SPR) analysis (Bartoli et al. 2013; Manohar et al. 2015). Since many hormones produce ROS, the interaction throughout hormonal pathways, which is stimulated by exogenous SA occurs with cellular redox signaling. Thioredoxins have been connected to the SA signaling cascade. The oligomeric cytosolic protein NPR1 forms monomers during the SAR (Després et al. 2003).

6 Glutathione S-Transferase

Diverse stimulators induce plant glutathione *S*-transferases (GSTs), which is a big connection of multifunctional proteins. Some interesting features were uncovered in a study that investigated GST expression in response to treatment with 0.01–1 mM salicylic acid (SA). According to the results, GSTs demonstrate specific responses to treatment with SA, suggesting that various mechanisms operate to induce GSTs in SA treatments and hint at class-specific activities for the great and significant gene family (Sappl et al. 2004). SA- interceded signaling also relies on the intracellular redox situation. Astoundingly, cellular SA rates are metabolically bound to those of hydrogen peroxide and GSH (Hossain et al. 2017). Because of an improved replicate rate of antioxidant genes; GPX1, GPX2, DHAR, GR, GST1, GST2, MDHAR, and GS, and an enhanced function of ascorbate (ASA)-GSH pathway enzymes, exogenously sourced SA (0.5 mM) improved salt tolerance in *Triticum aestivum* (Li et al. 2013).

By using transgenic plants, excessive expression of the GSH biosynthetic gene (GSH1), which encodes γ-glutamyl-cysteine synthase, resulted in improving SA rates and up-regulation of expressing the gene PR-1 resistance marker and increased fungal pathogen resistance. However, treatments with SA enhanced cellular GSH rates and raised actions of glutathione S-transferase enzymes and glutathione reductase, as well as enhanced virus resistance (Mateo et al. 2006). To increase glutathione amount in tobacco plants, various approaches were used. One of them was increasing glutathione rates in SA-deficient NahG and wild type that controls Xanthi tobaccos by penetrating half of the plants leafs with watery solutions of 2 mM to decrease glutathione (GSH) or R-2-oxothiazolidine-4-carboxylic acid (OTC) (Sigma-Aldrich, USA) with a *hypodermic syringe* (Hafez et al. 2012).

7 Gapdh

Tian et al. (2015) recognized different members of the protein family of *Arabidopsis* glyceraldehyde 3-phosphate dehydrogenase (GAPDH) that includes two cytosolic isoforms and two chloroplast-localized, as SABPs. Cytosolic GAPDH is a renowned glycolytic enzyme, playing a pivotal role in host and it is required for the *Tomato bushy stunt virus* (TBSV) replication, as a single-stranded RNA virus. Previous research showed that binding GAPDH to the (−) RNA strand of TBSV had high productivity than the (+) strand, which is essential for asymmetric TBSV replication, in which the viral replicase synthesizes higher levels of (+) RNA progeny (Huang and Nagy 2011). GAPDH, which is identified as an SABP has a significant role in TBSV replication. The impacts of SA and GAPDH on TBSV replication was tested in a study and results demonstrated that the binding between GAPDH and SA restrains TBSV replication in yeast cells and the protoplasts of *Nicotiana benthamiana* in both vitro and vivo by suppressing the binding of GAPDH to the viral (−) RNA strand, consequently, exhibiting a new molecular interactions through which SA intervenes in viral replication (Wang and Nagy 2008). GAPDH was formerly illustrated to bind SA both in plants and human studies that explains details of A1 isomer of chloroplastic glyceraldehyde 3-phosphate dehydrogenase (GAPA1) from *Arabidopsis thaliana* binding SA with a K_D of 16.7 nM. Pokotylo et al. (2020) reported that SA limits its GAPDH action in vitro. Binding different isoforms of GAPDH to SA disrupts the ability of SA to bind the (−) RNA of TBSV. Since this function was incorporated to promote TBSV replication, the final outcomes indicate a novel mechanism where antiviral activity of SA can be interceded (Tian et al. 2015).

8 HMGB3—DAMP Protein

Although "damage-associated molecular patterns (DAMPs)" was mentioned to the hydrophobic segment of biological molecules from pathogen cells, dead and dying host that activate immunity (Seong and Matzinger 2004), it is currently utilized to introduce risk signals from damaged host cells (Yatim et al. 2017). As a common process, the cells of multicellular organisms such as plants and animals emit danger signals when they are under the threat of microbe attacking or physical damage. DAMPs is a name adopted to this action, and generally contains extracellular protein fragments or cell walls, nucleotides, peptides, and amino acids.

Exposing on the surface of cells, the receptors of plasma membrane detect DAMPs to promote damage repair and control immune responses against the invader organisms. Additionally, systemic wounding responses are mediated by DAMPs that act as mobile signals in long-distance (Hou et al. 2019). A study showed that the binding affinity was strong between the immobilized 3-aminoethyl SA and this protein (Kd = 1.5 nM). This fact revealed that the protein is a DAMP acting via BKK1 and BAK1 receptor kinases. The exogenous application of purified recombinant High Mobility Group Box 3 (HMGB3) was sufficient to increase Arabidopsis resistance against *B. cinerea* and induced immune reactions (Pokotylo et al. 2019). The study revealed that HMGB3 is a new plant DAMP and infecting by necrotrophic *B. cinerea* HMGB3 was released into the extracellular space (apoplast). While HMGB3 was injected into apoplast restored resistance, the susceptibility to *B. cinerea* was increased via silencing HMGBs. Like its counterpart in humans, binding between HMGB3 and salicylic acid (SA) leads to prohibition of its DAMP function.

An SA-binding site mutant of HMGB3 preserves its DAMP function, which is no longer limited by SA. These outcomes showed cross-kingdom demonstration that HMGB proteins act as DAMPs and SA is their preserved suppressor (Choi and Klessig 2016). In an another study, it was observed that HMGB1 binds salicylic acid (SA) that decreased both HMGB1's chemo-attractant function and disulfide bond-containing HMGB1's competence to promote the expression of Cyclooxygenase-2 (COX-2) and pro-inflammatory cytokine genes (Choi et al. 2015). Through NMR studies and mutational analysis in the HMG-box domains, the SA-binding sites on

HMGB1 were recognized. Chemo-attractant activity was retained by an HMGB1 protein, which was mutated in one of the SA-binding sites, but HMGB1 protein lost binding of and prohibition by SA, hence firmly establishing that SA binds to HMGB1 directly restrains its pro-inflammatory functions. Normal and synthetic SA derivatives with effective capability for prohibition of HMGB1 were also recognized, demonstrating an evidence that new SA-based molecules with significant efficiency is accessible (Choi and Klessig 2016).

9 GH3—Acyl Acid Amido Synthetase

Formerly introduced as a 4-hydroxybenzoic acid-glutamate synthetase, AtGH3.12/PBS3 affects responses to pathogen defense by salicylic acid. A recent study has demonstrated that AtGH3.12/PBS3 exerts isochorismate as a substrate that forms an isochorismate-glutamate conjugated, altering into salicylic acid. The results exhibit that AtGH3.7 and AtGH3.12/PBS3 can also link chorismate to cysteine and glutamate whose functions are as precursors to aromatic amino acids and salicylic acid, respectively (Holland et al. 2019). In Arabidopsis thaliana, both salicylic acid (SA) and indole-3-acetic acid (IAA) are conjugated to modulate auxin and pathogen response pathways by the acyl acid amido synthetase Gretchen Hagen 3.5 (AtGH3.5). Its molecular base was uncovered by its 3D structure of AtGH3.5 for SA function and its dual IAA and its proficiency to affect both SA homeostasis and auxin. The kinetic analysis depicts that the substrate preference of AtGH3.5 is more extensive than what was described originally (Westfall et al. 2016). This information expands the functions of GH3 acyl acid amido synthetases in plant metabolism and recommends that AtGH3.5 intervenes metabolic crosstalk between the SA and auxin and response pathways. The analysis of AtGH3.5 illustrates that using BA as a substrate can facilitate connection of SA efficiently (Westfall et al. 2016). Currently, the biological role of converted BA content is undefined, but BA-Asp possibly supplies a precursor pool for SA throughout pathogen challenges. For SA synthesis, two paths have been suggested, one through metabolism of benzoic acids and another through isochorismate (Widhalm and Dudareva 2015).

10 Alpha-Ketoglutarate Dehydrogenase—Krebs Cycle Enzyme

Through the Krebs cycle, a highly regulated enzyme named Alpha-ketoglutarate dehydrogenase (α-KGDH) could regulate the metabolic flux and catalyzes the transformation of α-ketoglutarate to succinyl-CoA and produces Dihydronicotinamide Adenine Dinucleotide (NADH), which distinctly provides electrons for the respiratory chain. Inhibition of α-KGDH enzyme, which is sentient to reactive oxygen species (ROS) could be essential in the metabolic death and oxidative stress. In the Krebs cycle, aconitase is more susceptible to ROS than α-KGDH, but if α-KGDH is functional, NADH generation remains in the Krebs cycle. Only when α-KGDH is limited by ROS, NADH supply to the respiratory chain is restricted (Tretter and Adam-Vizi 2005). The activity of SA-binding in the recombinant tomato (*Solanum lycopersicum*) alpha-ketoglutarate dehydrogenase (Slα-kGDH) E2 subunit of the tricarboxylic acid (TCA) cycle was identified. In plant defenses against tobacco mosaic virus (TMV), the biological role of this binding TMV was studied via overexpression and silencing Slα-kGDH E2 in plants. In two independent assays, Slα-kGDH E2 was established to bind SA. Slα-kGDH E2 silencing and SA treatment raised resistance to TMV. A study by Liao et al. (2015) illustrated that binding by Slα-kGDH E2 of SA affects the mitochondrial electron transport chain and functions upstream that plays a crucial role in basal defense against TMV. Both SA treatment and Sl α-kGDH E2 silencing decreased resistance to TMV. Improvement in TMV defense by SA in Sl α-kGDH E2-silenced was not observed in tomato plants but a decrease in TMV susceptibility in *Nicotiana benthamiana* plants transiently overexpressing Sl α-kGDH E2 was observed (Liao et al. 2015).

11 MORC Proteins—Epigenetic Regulation

Microrchidia (MORC) proteins contain a family of proteins detected in eukaryotes and prokaryotes. Genetic screen in Arabidopsis mutants helped the discovery of MORC proteins in plants for the first time to resist a viral pathogen (Koch et al. 2017). The following studies developed their function in immunity and uncovered their association in gene silencing and the suppression of transposable elements. Studies suggest that MORC proteins are also involved in the adjustment of epigenetic gene and pathogen-induced chromatin remodeling.

Furthermore, biochemical studies recently showed that plant MORCs include topoisomerase II (topo II)-such as DNA, which modifies essential actions for their function (Koch et al. 2017). Sequence research previously showed that CRT1 (compromised for recognition of Turnip Crinkle Virus) includes the S5 domains and ATPase characteristic of Microchidia (MORC) proteins, which are involved in repairing and DNA modification (Kang et al. 2008). The information about a plant MORC was first released in 2008 by Kang and colleagues, using a forward genetic screen to identify elements that are included in immune signaling of *Arabidopsis thaliana* (famously known as thale cress or mouse-ear cress) (Kang et al. 2008). *Sl*MORC1 (Solanum) binds SA to restrain its ATPase and separation activities excluding its DNA relaxation activity. These results together with *At*MORC1's (*Arabidopsis Thaliana*) showed their function in the commencement of the expression in the defense gene via activating proximal TE-associated enhancers, which in itself recommends that MORC1 proteins may act as translocating to the nucleus reacting to Pst infection as well as they induce the defense genes expression by changing the superstructure of TE-associated chromatin (Koch et al. 2017).

12 Thimet Oligopeptidases + Tripeptidyl-Peptidase (TPP) II Exopeptidase—Proteolysis

Thimet oligopeptidase (TOP) enzymes were recently distinguished as part of the 20S proteasome and SA-binding proteins in *A. thaliana* (Moreau et al. 2013). Three types of TOPs were discovered in *Arabidopsis thaliana.* TOP1 is situated in the chloroplasts and mitochondria which has the AT5G65620 gene. TOP2 is situated in the cytosol, which has the AT5G10540 gene. Eventually, DNA topoisomerase 1 (TOPL) is situated in the cytosol including the AT1G67690 gene (Polge et al. 2009). In *A. thaliana*, between the three recognized thimet oligopeptidase, only TOP2 and TOP1 are the TOP enzymes required in immune system response of SA. They are capable to perform their function in an extended range of pH from 6.5 to 8.5 (Westlake et al. 2015).

In an extensive number of significant biological processes, the function of huge exopeptidase, tripeptidyl-peptidase II (TPP II) is crucial. TPP II exists in the cytosol of numerous eukaryotic cells. The critical role of TPP II seems to degrade the general protein associated with the proteasome (Tomkinson 2019). To reveal cellular function targeted by SA via a functional analog of SA, Arabidopsis protein microarrays were explored. It is illustrated that a class of SA-binding enzymes is established with thimet oligopeptidase (TOPs). Biochemical studies indicated that SA reacts with TOPs and restrains its peptidase activities in both plant extracts and in vitro. The identification of the function of altered TOP expression and mutants illustrated that TOP1 and TOP2 are essential for the immune response to avirulent pathogens and intervene SA-dependent signaling. Previous studies support the postulation that TOP1 and TOP2 work in detached pathways to regulate SA-mediated cellular processes (Moreau et al. 2013).

13 Molecular Mechanisms of SA-Protein Interactions

Mutant-based genetic analysis and a classic biochemical radiolabeling method revealed that in higher plants, the phenylalanine or isochorismate pathway may synthesize SA. It has been introduced that there are differences in two paths of synthesis at the hydroxylation of the aromatic ring (Horváth et al. 2007). In plants, the phenylalanine pathway is one of the common pathways of SA biosynthesis in which phenylalanine changes to trans-cinnamic acid. As a result, after oxidation of the side chain, trans-cinnamic acid’s side chain is oxidized to produce benzoic acid, which is then hydroxylated in the ortho position and trans-cinnamic acid that is hydroxylated to form o-coumaric acid.

A third pathway from shikimic acid via isochorismate acid and chorismic acid has been considered as SA biosynthesis (An and Mou 2011). As the SA rates increase, NPR1 transforms from the cytoplasm into nucleus NPR1 without any interactions with SA receptors for the immune pathway. NPR3 and NPR4 are transcriptional repressors, and both work harmoniously and independently to manage the expression of downstream genes, whereas NPR1 acts as a transcriptional activator (Ding et al. 2018). Compared to NPR4, NPR1 shows minimal SA-binding activity. An N-terminal domain is shared by NPR proteins, which is known as the broad-complex, tram track, and bric-a-brac (BTB) or poxvirus, zinc finger (POZ) domain. This domain is usually found in the substrate receptor subunits of the CULLIN3–RBX1 ubiquitin ligase complexes (CRL3s) (Genschik et al. 2013). NPR3 and NPR4 modulate SA-mediated gene expression by regulating the constancy of NPR since it has been known to be sensitive to SA as they interact with NPR1 (Castelló et al. 2018). In addition to the N-terminal BTB domain, a C-terminal and central ankyrin repeat (ANK) domains are shared by all NPR proteins (Rochon et al. 2006). The loss of any ligand-entry pathway in the configuration of the NPR4 SBC—SA complex illustrates that the apo form of the receptor must approve a divergent configuration, in which its ligand-binding site is available to free SA (Wang et al. 2020). In NPR1 and NPR4, the experiments of domain-swapping were carried out to identify the sequence determinants location of differential SA binding. Results revealed that the structurally defined SBC domain or the NPR4 C-terminal domain are not the only area, collaborating to strong SA-binding activity. Regions such as the ANK and BTB domains that are N-terminal to SBC can efficiently change the ligand-binding function of SBC in the condition of the full-length NPR proteins, probably via surface remains of the SBC (Wang et al. 2020). SPR analysis is a technique in which an immobilized 3-aminoethyl SA is used as a ligand to identify SABPs. This indicates that reactions should happen on the proteins surface, at least in the SABPs, which is recognized with this approach (Pokotylo et al. 2019).

14 Conclusions and Future Prospects

The role of Salicylic acid (SA) as a regulator of important physiological functions in the plants is considerable. For instance, it is involved in photosynthesis, production of glycine betaine (GB), nitrogen, proline (Pro) metabolism, antioxidant defense system, and controlling the hydration of plant cells under stress conditions. As a result, it provides plant protection against abiotic stresses (Lawlor and Paul 2014).

The salicylic acid-binding proteins (SABPs) show an intense propensity to bind SA and provide multiple interactions with more flexibility. SA and its natural and synthetic derivatives also have special targets in animals and/or humans (Klessig et al. 2016). SABPs are frequently related to plant immunity. For example, the silencing of _KGDE2, an SABP, increases plant resistance to viruses (Liao et al. 2015). SA and its components that are involved in protein signaling have been determined to be resistance factors derived from different R proteins. These proteins include increased disease sensitivity susceptibility 1 (EDS1), non–race-specific disease resistance 1 (NDR1), phytoalexin deficient 4 (PAD4), senescence-associated gene 101 (SAG101), and EDS5 (Venugopal et al. 2009).

PAL genes are other important proteins that have a significant role in SA induction. PAL is the basic enzyme in the metabolic pathway of phenylpropanoid to control primary and secondary metabolisms. Besides producing well-investigated flavonoids, focused tannins and lignin, this pathway generates less-investigated benzene compounds and phenolic glycosides (Li et al. 2019). Results demonstrate that the silencing of PAL genes in tobacco or chemical obstruction of PAL function in Arabidopsis, cucumber, and potato reduces the accumulation of SA to respond pathogen (Chen et al. 2009).

Research identified that peptidases TOP1 and TOP2 are vital components in plants responding pathogens and programmed cell death (PCD). TOPs were investigated in different aspects and their related roles in the arrangement of enzymatic function in response to oxidative stress were studied. It was determined that TOP1 and TOP2 interact with each other. It is remarkable to mention that TOP1 and TOP2 have the capability to be involved in dimers influencing SA and the thiol-based reducer Dithiothreitol (DTT) (Westlake et al. 2015). Destabilization of the TOP2 dimer occurred because of protoplast incubation with exogenous SA. This outcome could be the consequence of the direct connection of TOP2 to SA. Although TOP2-SA dependency has a low affinity, this hypothesis is unlikely, and it is functionally unrelated (Moreau et al. 2013). In a study, SA structural basis was recognized by NPR4, and it was the initiation to know the relationships of NPR proteins in some aspects such as structure and function (Wang et al. 2020). Most likely, degrading Jasmonate (JAZ) proteins is done by NPR1 and NPR4 (F426L/T459G), which has been recognized as a necessity for effector-triggered immunity (ETI) (Liu et al. 2016).

It was reported that members of AtGH3 subfamily numbers I and II are responsible for conjugating phytohormone acyl substrates to amino acids in vitro. Beside GH3 enzymes, special amino acid conjugates to its appropriate acyl substrates catalyzes by PBS3. It is important to point out that inhibition of PBS3 activity is done in special ways by SA with an IC (50) of 15 Micron. This suggests that some common mechanisms for the instant and reversible regulation of GH3 action and small molecule crosstalk (Okrent et al. 2009).

GAPDH is another gene in SA signaling, binding SA both in humans and plants. Studies showed that in *Arabidopsis thaliana*, the A1 isomer of chloroplastic glyceraldehyde 3-phosphate dehydrogenase (GAPA1) binds SA with a KD of 16.7 nM, like in other studies on the surface of resonance plasmon. Besides, the inhibition of GAPDH activity by SA was proven in vitro (Pokotylo et al. 2020).

In this review chapter, salicylic acid biosynthesis pathways were discussed. However, the principles of how SA is controlled, and which proteins and genes are induced in the production of this hormone are still unknown. By providing more knowledge about the role of SA in plant defense, new windows of opportunity would be opened to optimize plant mechanisms against pathogens and disease.

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Salicylic Acid (SA): Its Interaction with Different Molecules in the Stress Tolerance Signaling Pathways

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Abstract In present time, the ever-increasing development has contributed a lot towards the polluted environment. This has led to contamination of soil and water bodies used in agricultural fields which adversely affects the crop plants. Thus, it has become a major concern, and there is a need to improve the tolerance of plants towards several kinds of abiotic stresses such as heavy metal, pesticides, salinity etc. as well as various biotic stresses. It is well known that, on stress exposure plants initiate a signaling mechanism against it; therefore the role of different plant hormones is being studied under stressed conditions. Salicylic acid (SA) is one of them; it is an anti-oxidant phytohormone as well as a signal molecule which plays an important role in plant defense against a variety of abiotic and biotic stresses. Against the stress, SA has shown to interact with nitric oxide, hydrogen peroxide and other different molecules which are still being explored. Application of SA has shown to regulate various physiological processes in the plants exposed to stress but whether SA performs this via production of different metabolites or using which mechanistic pathway is still not completely understood. In plants, several signal transduction pathways run in response to disease resistance such as jasmonic acid, ethylene and obviously salicylic acid too. In the future, research on salicylic acid and its application in crop plants may make them more tolerant to pathogen associated diseases and other stresses. This chapter focuses on the major stresses in environment, ROS signaling mechanisms which are linked to SA signal transduction pathway and the ways by which they ultimately execute stress tolerance response in the plants, which is an area of interest still being understood by researchers.

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1 Introduction

Salicylic acid (SA) is a small phenolic compound and is considered as a multitasking molecule that works as a true plant hormone, a signaling component and a secondary metabolite (Vicente and Plasencia 2011). Research report suggests that SA has the potential to provide resistivity against severe plant diseases by involving lignin biosynthesis or by direct defense signaling strategies (Humphreys and Chapple 2002; Hussein et al. 2007). About 0.250–1 $\mu g\ g^{-1}$ FW SA content was found in model plant *Arabidopsis thaliana* and its biosynthesis mainly occurs in chloroplast region of the plant (Vicente and Plasencia 2011). Study of Volt et al. (2009) demonstrated that SA participates in various physiological processes and at every developmental stage of plants. Yusuf et al. (2013) have also described the role of SA in seed germination, cellular growth, stomatal closure and gene expression. Other hormones like jasmonic acid (JA), ethylene (ET) and auxin (IAA) have also been stimulated by SA (Yusuf et al. 2013). Interaction of SA is not only limited to other plant hormones but its potential interaction has also been noticed with some signaling molecules like nitric oxide (NO) (Verma et al. 2020) and H_2O_2 (Mohanta et al. 2018). Previously, it was noticed that exogenous supplementation of NO in ozone stressed *Arabidopsis* plant promoted the SA biosynthesis along with some other defensive gene expression (Ahlfors et al. 2009). It has also been analysed that the foliar application of SA significantly increased the K^+ ion accumulation and reduced the Na^+ accumulation in salt stressed mung bean plants which makes these plants more tolerant against salt stress (Ghassemi-Golezani and Lotfi 2015). A synergistic relation was also found between Ca^{2+}, a secondary metabolite and SA during salt stress condition in tomato plant (Manaa et al. 2014). Recent studies of Shaki et al. (2019) report that exogenous SA improves K^+ and Ca^{2+} uptake under salinity stress.

SA is a wide player phytohormone having multitasking abilities also referred to as “antioxidant phytohormone” which is naturally produced by plants (Batista et al. 2019). Under abiotic stress conditions, SA hindered the overproduction of ROS (reactive oxygen species) which ultimately reduces the chance of misbalancing of antioxidants (Ma et al. 2017; Singh et al. 2020). Various physiological processes of the plant systems governed by SA are (1) it boosts nitrogen metabolism, (2) enzymes related to defense complexes, and (3) induces osmolytes (proline and glycine betaine) in different plant varieties (Batista et al. 2019). Report of Lee et al. (2014) demonstrated the involvement of SA in improving the activity of RuBisCO (ribulose-1,5 bisphosphate carboxylase/oxygenase) enzyme which ultimately increases the rate of photosynthesis in tobacco plant. Overall, SA considerably controls several abiotic stresses like water stress, salinity stress, drought, metal and cold stress in plants by regulating their physiological and biochemical processes throughout their life span (Vicente and Plasencia 2011; Miura et al. 2014). Studies also described that exogenous application of SA results in increased crop yield and it is believed that SA impressively delayed the senescence in plant organs that ultimately increased the grain yield (Imran et al. 2007; Yusuf et al. 2013).

Thus, this chapter focuses to gather all the information about the working mechanism of SA during adverse environmental conditions and its interactive role with other active signaling molecules.

2 SA Biosynthesis/ Metabolism

Biosynthesis of SA is essentially required to execute the defense responses against different biotic and abiotic stresses in plants, which have been discussed above (War et al. 2011). SA is synthesized in plants through two pathways i.e. PAL and ICS pathway.

2.1 *PAL Pathway*

Salicylic acid plays an important role in the signaling in plants, it is synthesized from cinnamate through the action of phenylalanine ammonia lyase (PAL) enzyme (Fig. 1) (Chen et al. 2009). PAL enzyme converts phenylalanine into cinnamate, then cinnamate chain undergoes shortening via beta-oxidation similar to beta-oxidation of fatty acid. Cinnamate converts into benzoate or o-coumarate (after infected with

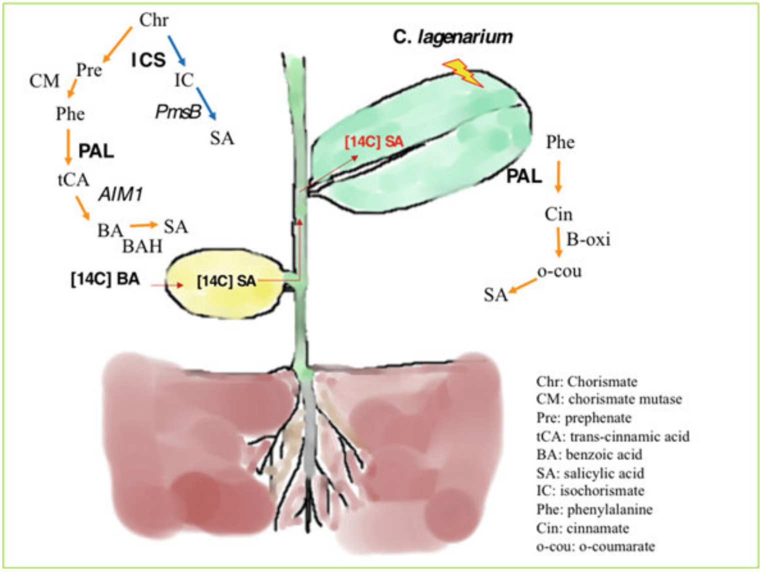

Fig. 1 Illustrates two pathways i.e. PAL and ICS pathways of SA biosynthesis in plants at onset of pathogenesis as its translocation from the cotyledons to the site of pathogenesis

Agrobacterium tumefaciens). However, studies related to TMV-infected leaves and rice seedlings reveal that benzoate is the immediate precursor of SA than o-coumarate (Fig. 1). Enzymes which convert cinnamate into SA are still not reported in plants (Chen et al. 2009). Genetic studies in tobacco, *Arabidopsis*, cucumber and potato prove that PAL route is the major pathway used for SA biosynthesis under biotic stress. Another pathway through PAL is via chorismate mutase (CM) which does catalytic conversion of chorismate to prephenate (Zhong et al. 2020). Prephenate is converted into phenylalanine. PAL enzyme converts phenylalanine (Phe) into trans-cinnamic acid (tCA), ABNORMAL INFLORESCENCE MERISTEM 1 (*AIM1*) gene *AIM1* catalyzes conversion of tCA into benzoic acid (BA), benzoic acid hydroxylase converts BA into SA (Levefere et al. 2020) (Fig. 1).

2.2 ICS Pathway

Major concentration of SA is produced through isochorismate (IC). The avrPphB SUSCEPTIBLE3 (PBS3) enzyme catalyzes conjugation of IC to glutamate and produces isochorismate-9-glutamate. ENHANCED PSEUDOMONAS SUSCEPTIBILITY 1 (EPS1) further decomposes it into salicylic acid and 2-hydroxy-acryloyl-N- glutamate through acyltransferase action (Rekhter et al. 2019). The isochorismate pyruvate- lyase (*IPL*) enzyme is encoded by *PmsB* gene that converts IC into SA (Lefevere et al. 2020) (Fig. 1). IC is conjugated with amino acid after subsequent decomposition and enzymatic conversion, it is converted into SA. In bacteria, SA is produced by the action of two enzymes; namely isochorismate synthase (ICS) and isochorismate pyruvate lyase (IPL). In *Pseudomonas* species, *PmsC* converts chorismate to isochorismate, *PmsB* converts isochorismate to salicylic acid (SA) (Lefevere et al. 2020). *ics1* and *ics2* double mutant *Arabidopsis* plants have shown only 10% SA accumulation under UV stress, proving that ICS pathway is the major route of SA production under biotic as well as abiotic stress as also reported in studies of Catinot et al. (2008) in *Nicotiana benthamiana*. Plant enzymes which convert isochorismate into SA are not identified (Chen et al. 2009). The pathways involved in regulation of SA biosynthesis are yet to be more explored in the plants.

3 Physiological Role of SA in Plants

SA is a potential phytohormone, it is known for its diverse roles in various physiological and biochemical modifications during plant growth, development and in regulation of several abiotic stresses. Involvement of salicylic acid was noticed in seed germination, cell division and tissue formation as well as in other developmental processes like in plant growth, photosynthesis, in their respiratory activity, stomatal opening and closing, flowering and senescence (Vicente and Plasencia 2011).

3.1 Role of SA in Seed Germination

During seed germination, dose dependent responses of exogenous SA application have been reported. The study of Rajjou et al. (2006) showed that high dose of SA (i.e. > 1 mM) inhibited the seed germination in *A. thaliana*. Interestingly, same research group reported that during abiotic stress situation when a low dose of SA was applied exogenously, a significant increase in *Arabidopsis* seed germination was noticed (Alonso-Ramirez et al. 2009a). Interaction of SA with other plant hormones like ABA and GAs have also been noticed during seed germination (Xie et al. 2007).

3.2 Role of SA on Photosynthetic Activity

Recent evidences indicate that SA works as a potential regulator of photosynthesis because it affects the structure of leaves, pigments and regulates the activities of RuBisCO and carbonic anhydrase enzyme (Uzunova and Popova 2000). Exogenous SA alters leaf anatomy by reducing the width of adaxial and abaxial epidermis layer and also the mesophyll tissue (Rivas-San and Piasencia 2011). Hayat et al. (2005) have noticed a dose dependent response of SA on pigment contents. Pigment content was found inhibited under the supplementation of lower dose of SA while on higher dose the effect was not found beneficiary in wheat seedlings.

3.3 Role of SA on Nitrogen Metabolism

Nitrogen containing molecules are very essential for all life processes and studies indicated towards the involvement of SA in nitrogen metabolism processes. Exogenous application of SA enhanced the nitrate reductase (NR) activity in wheat leaves. Hayat et al. (2005) noticed an increase in activity of NR enzyme in both roots and leaves of wheat plants grown with seeds soaked at lower concentration of SA. However, inhibitory role of SA was found at implication of its higher concentrations. Supplementation of exogenous SA inhibited the formation of *Rhizobia* along with the production of nod factors with delayed nodule formation, thereby diminishing the number of nodules per plant (Mabood and Smith 2007).

3.4 Role of SA on Flowering

SA activates alternative respiration, thus, producing heat and causing volatilization of putrid smelling compounds to attract pollinating insects (Chen et al. 2009). Previous studies reported that SA treated *Carica papaya* plants successfully produced higher fruit sets (Martin-Mex et al. 2005). The spray of low concentrations of SA significantly enhanced fruit yield in cucumber and tomato plants (Larque-Saavedra and Martin-Mex 2007). Moreover, report of Alaey et al. (2011) showed that SA delayed the senescence and increased the vase-life of cut rose flowers by regulating plant water content and improving the scavenging capability of cells.

3.5 Role of SA on Senescence

Plant senescence is a physiological process that is characterized by yellowing of leaves because of degradation of photosynthetic pigments (chlorophyll) and increased level of ROS which closely connect with cell death. Participation of SA in regulation of senescence is not unanticipated. It is believed that senescence takes place due to accumulation of SA (Yusuf et al. 2013). In previous studies, it was noticed that in *Arabidopsis* plant expressions of some senescence-related genes i.e. α*VPE*, χ*VPE, WRKY6, WRKY53*, and *SEN1* were activated by SA (Schenk et al. 2005; Miao et al. 2004). The participation of the SA signaling pathway in senescence was confirmed firmly through a detailed analysis of microarray in senescent leaves of *Arabidopsis*. (Buchanan-Wollaston et al. 2005).

4 Regulatory Role of SA in Different Kind of Stress Conditions

Plants undergo continuous exposure to various abiotic and biotic stresses in their natural environment. To survive under these conditions, plants have developed intricate mechanisms for perceiving of external signals that allowed optimal response. PGRs like salicylic acid (SA), is an important phytohormone and signaling molecule that plays a vast role in response to various stresses. Some responses of SA in tolerance of biotic and abiotic stress is summarized in Table 1.

4.1 Biotic Stress Conditions

Biotic stress is generated by the living organisms like bacteria, viruses, fungi, parasites, beneficial and harmful insects, weeds, and cultivated as native plants that cause damage to the plants. It is a major focus of agricultural research, due to the vast economic losses caused by biotic stress to cash crops. Yang et al. (2004) observed that rice plant deficient in SA exhibits increased susceptibility to oxidative bursts when infected with the *Magnaporthe grisea* (blast fungus). Recently, Sorahinobar et al. (2016) reported SA induced induction of antioxidants that protects wheat plants

Table 1 Regulatory role of SA on plants under various (biotic and abiotic) stress conditions

S.No.	Plant name	Kind of stress	Concentration of Sa	Effect of Sa	Reference
1.	*Dianthus superbus* L. (Caryophyllaceae)	Salt stress	0.5 mM	Improved growth, Increased thickness of mesophyll layer and induced expression of salt-induced genes to resist higher salinity	Zheng et al. (2018)
2.	*Rosmarinus officinallis* L.	NaCl stress	100–300 ppm (spray)	Stimulated gene expression of antioxidant pathway and increased non-enzymatic antioxidants	El-Esawi et al. (2017)
3.	*Oryza sativa* L.	Pb^{2+} and Hg^{2+} stress	0.1 or 0.2 mM	Reduced inhibitory effect on seed germination and seedling growth	Pal et al. (2013)
4.	*Oryza sativa*	Cd stress	10 μM (pretreatment)	Induced H_2O_2 signalling, stimulated activity of enzymatic and non-enzymatic antioxidants	Guo et al. (2009)
5.	*Citrus limon*	Chilling stress	2.0 mM	Improved tolerance, increased total phenolics synthesis and PAL activity	Siboza et al. (2014)
6.	*T. aestivum*	Heat stress	0.5 mM	Alleviated stress, increased proline production and restricted ethylene formation	Khan et al. (2015)

(continued)

Table 1 (continued)

S.No.	Plant name	Kind of stress	Concentration of Sa	Effect of Sa	Reference
7.	*Ctenanthe setosa*	osmotic stress	1 µM	Retarded leaf rolling, modulated osmoprotectants and induced antioxidant enzyme activities	Demiralay et al. (2013)
8.	*Capsicum annuum* L	UV-B and UV-C stress	1.5 mM	Moderated Chl and Car reduction and increased the quantity of anthocyanins, flavonoids, rutin, and UV-absorbing compounds	Mahdavian (2008)
9.	*Zea mays* L	Clethodim (herbicide) stress	1 mM	Regulated contents of H_2O_2 and MDA; and activities of SOD and APX similar to controls.	Radwan (2012)
10.	*Petroselinum crispum*	lead toxicity	50 µM	Reduced chlorosis and increased photosynthetic pigments	Alamer and Fayaz 2020
11.	*Fragaria ananassa*	*Botrytis cinerea*	1–2 mM	better fruit quality and decrease in fungal disease	Babalar et al. (2007)
12.	*Lycopersicon esculentum*	*Botrytis cinerea*	5 mM	ethylene, lycopene, fungal disease, better fruit quality	Wang et al. (2011)
13.	*Oryza sativa*	Blast fungus (*Magnaporthe grisea*)	Endogenous	Maintain redox balance and defend rice plants from oxidative stress	Yang et al. (2004)
14.	*Mangifera indica*	*Collectotrichum gloeosporioides*	2 mM	Improved fruit quality	Joyce et al. (2001)

(continued)

Table 1 (continued)

S.No.	Plant name	Kind of stress	Concentration of Sa	Effect of Sa	Reference
15.	*Prunus avium*	*Penicillium expansum*	2 mM	Increase antioxidative enzymes and chitinase, glucanase, and fungal resistance	Yu et al. (2006)
16.	*Pyrus bretschneideri*	*Penicillium expansum*	2.5 mM	Stimulate antioxidative enzymes, PAL, chitinase, glucanase	Cao et al. (2006)
17.	Wheat	*Fusarium graminearum*	200 µM	SA activates antioxidant defense responses and may subsequently induce systemic acquired resistance	Sorahinobar et al. (2016)
18.	Poplar	*Melampsora larici-populina*	–	SA regulate growth and defense responses of poplar	Luo et al. (2019)

from *F. graminearum.* In another study, Luo et al. (2019) found that JA and SA coordinate the growth and defense in poplar plant by integrating signaling pathways of multiple hormones.

4.2 Abiotic Stress Conditions

Apart from its role with respect to biotic stresses and pathogenesis, recent studies have demonstrated that SA also participates in gesturing of several abiotic stress responses, for instance metal stress, water and temperature stress, salinity and radiation stress etc. proper use of salicylic acid could provide protection against these environmental stresses. Here we discuss the regulatory role of SA on diverse abiotic stresses.

4.2.1 Role of Salicylic Acid During Metal Stress

Report on the protective role of SA against abiotic stress factors dealt with heavy metal/metalloid is one of the earliest works (Singh et al. 2019). Foliar application of 15 μM SA could alleviate adverse effects of Al toxicity on photosynthesis by increasing light capture efficiency, promoting electron transport in the ETC and thylakoid lumen deacidification, and accelerating ATP and NADPH synthesis, as well as regulating carboxylation process (Cheng et al. 2020). Alleviated Al toxicity by SA application was also reported by Yang et al. (2003) in *Cassia tora* L. plants, where the increased citrate efflux induced by 5 μM SA treatment. This outcome could also be associated with a decrease in the inhibition of root growth and in the Al content of the root tips. Salicylic acid at concentrations of 10^{-6}, 10^{-5} and 10^{-4} also had a protective effect in soybean against Cd stress (Dražić and Mihailović 2005), against lead stress in *Brassica napus* (Jazi et al. 2011) and against nickel stress in *Brassica napus* L. (Kazemi et al. 2010) when added to the nutrient solution. Cd treatment induces the accumulation of free and conjugated SA in pea (Popova et al. 2009) and maize plants (Pal et al. 2005; Krantev et al. 2008). Exogenous salicylic acid was found to alleviate the toxic effects generated by Cd in maize plants (Pal et al. 2002) and in barley (Metwally et al. 2003). The results obtained when soaking the seeds of *Linum usitatissimum* L. in SA suggested that it could be used as a growth regulator and a stabilizer of membrane integrity to improve plant resistance to Cd stress (Belkhadi et al. 2010). Application of SA produced considerable improvement on growth, photosynthetic pigments and chlorophyll fluorescence characteristics in Cd stressed seedlings (Singh and Prasad 2013). Upon SA treatment SOR, H_2O_2 and MDA contents decreased significantly while the activity of antioxidant enzymes exhibited further rise which suggest that SA regulated the antioxidant defense system in brinjal seedlings efficiently (Singh and Prasad 2013). The inhibitory effect of lead on activity of nitrate reductase enzyme in *Zea mays* was moderated by SA (Sinha et al. 1994). SA at a concentration of 200 μM was found to reduce the inhibitory effect of mercury in *Medicago sativa* seedling by inducing the antioxidant defense system (Zhou et al. 2009). In case of *Oriza sativa* seeds placed on Petri plates containing moistened filter paper with SA and heavy metal solution, 0.1 or 0.2 mM SA was found to alleviate the toxic effect of Pb^{2+} and Hg^{2+} on germination, seedling growth, and its membrane-damaging effect (Mishra and Choudhuri 1999). Exogenously applied SA (10^{-5}M) ameliorated the ill-effects of nickel stress by restoring growth, photosynthesis and physio-biochemical attributes. The activities of enzymes associated with antioxidant defense system, especially the ascorbate–glutathione (AsA–GSH) cycle and glyoxalase system was also reported to be improved (Zaid et al. 2019). Moreover, Mostofa et al. (2020) investigated the mechanistic consequences of selenium (Se)-toxicity, and possible mitigation using SA in rice. This study clearly unraveled that application of SA to rice plants exposed to excessive levels of Se effectively enabled the plants to fight against Se phytotoxicity. SA upregulated several genes associated with reactive oxygen species (e.g. OsCuZnSOD1, OsCATB, OsGPX1 and OsAPX2) and methylglyoxal (e.g. OsGLYI-1) detoxifications.

4.2.2 Role of Salicylic Acid During Salt Stress

In plants exposed to abiotic stress (e.g. salinity and drought), the accumulation of ROS such as superoxide radical, hydroxyl radical, and H_2O_2 is induced, which, in turn, alters the redox homeostasis (Smirnoff 1993). Salinity is one of the most important abiotic stresses, affects the physiology of the whole plant and cellular levels and from seed germination to maturity. The exogenous application of 250 μM SA can trigger the rapid activation of non-enzymatic defense system accompanied by increased production of osmolytes and such non-enzymatic scavengers as proline (Chavoushi et al. 2019). Kim et al. (2017) investigated the effects of exogenous SA (0.1 mM) on stress tolerance in cucumber plants grown under low nitrogen (LN, 40 ppm) and moderate nitrogen (MN, 120 ppm) conditions and reported that exogenous SA enhanced the salt-stress tolerance of cucumbers grown in MN but not LN. Although increased endogenous SA levels are necessary for promoting stress tolerance, the control of the endogenous SA pool also likely plays a key role in alleviating stress damage. In short exogenous salicylic acid alleviates salt-stress damage in cucumber under moderate nitrogen conditions by controlling endogenous salicylic acid levels (Kim et al. 2017). Likewise, low concentration of salicylic acid enabled plants to tolerate salt stress (100 mM NaCl) in long term incubated tomato plants (Tari et al. 2002). Pretreatment of SA also provided protection against salinity via increasing the activity of aldose reductase, GST and APX enzymes (Tari et al. 2010). Further, SA pre-treatment was found to regulate the photosynthetic electron transfer and stomatal conductance of mung bean (*Vigna radiata* L.) under salinity stress (Lotfi et al. 2020). Under saline condition (3, 6 and 9 dS/m^2), low stomatal conductance seems to cause losses in PS II efficiency. Though, application of SA with 1 and 1.5 mM concentrations improves the PS II activity of plants via enhancing the accumulation of K^+ and decreasing Na^+ in leaves (Lotfi et al. 2020). In another study, SA alleviates salt-induced decreases in photosynthesis by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars (Nazar et al. 2011). Exogenous foliar application of SA improves salt tolerance in *Cichorium intybus* genotype, increasing relative water content (RWC), membrane stability index (MSI), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*) and carotenoid (Car) contents and shoot dry weight (SDW) while significant increase in leaf proline content (LPC) and malondialdehyde (MDA) compared to control condition (Poursakhi et al. 2019). Similarly, increased photosynthetic rates under salt stress condition also observed when SA was applied to tomato seedlings via root drenching (Stevens et al. 2006; Poór et al. 2011).

4.2.3 Role of Salicylic Acid During Drought Stress

Drought is one of the most acute abiotic stress factor which limits growth, photosynthesis and yield of agricultural crops worldwide. Accumulation of stress hormone ABA is one of the most specific symptoms of drought stress. Exogenously applied acetyl SA at a range of 0.1–1 mM provides protection against drought stress in muskmelon seedlings (Korkmaz et al. 2007). Similarly, when wheat seeds were soaked in acetyl SA (100 ppm), the seedlings had better resistance to drought stress (Hamada and Al-Hakimi 2001). Addition to this, exogenous application of SA was found to ameliorates the short-term drought stress in *Brassica juncea* seedlings by upregulating the activity of various enzymatic (including MDHAR, DHAR, GR, GSH and GPX) as well as non-enzymatic antioxidant like GSH, and components of AsA-GSH cycle, and also glyoxalase system (Alam et al. 2013). Strengthened antioxidant defense system was also reported in drought exposed *Zea mays* cultivar upon foliar application of 1.0 μM SA (Saruhan et al. 2012). Pretreatment with SA improves drought stress tolerance by maintaining redox homeostasis and proline synthesis (La et al. 2019). In their study, they confirmed that SA significantly improved proline contents by up-regulating the expression of genes encoding enzyme pyrroline-5-carboxylate synthase (P5CSA and P5CSB) and down-regulating the expression of the gene encoding proline dehydrogenase (PDH) compared to non-SA pretreated plants (La et al. 2019). Recently, Wang et al. (2019) reported a salicylic acid carboxyl methyltransferase-like gene LcSAMT (possibly catalyzed the conversion of SA to MeSA) from *Lycium chinense* plants that elevated the drought stress sensitivity in transgenic tobacco plants via significantly reducing chlorophyll content, photosynthesis rate, RWC, and activities of antioxidant enzymes. Further, different concentrations of SA (0, 100, and 150 ppm) was also found to reducing the adverse effects of drought condition on two thymus species (*Thymus vulgaris* and *T. kotschyanus*) through improved morpho-physiological parameters.

4.2.4 Role of Salicylic Acid During Temperature Stress

Temperature is one of the vital factors that determine plants establishment, growth, development, and productivity. Each plant has a unique temperature requirement for proper growth and development, and is called optimum temperature. In current changing environmental scenario, both the low (cold stress) and high (heat) temperature have now become a potential abiotic stress threat for crops. Salicylic acid and other phenol derivatives are known to improve the cold tolerance of plants.

Evidences show that temperature stress affects many physio-biochemical processes in plants and induces molecular mechanisms, and gene expression to modulate plants responses (Wang et al. 2010; Khan et al. 2013; Siboza et al. 2014; Wassie et al. 2020). Salicylic acid (2.0 mM)-mediated increased synthesis of total phenolics and the activity of PAL was reported to improve chilling tolerance in cold-stored *Citrus limon* (Siboza et al. 2014). Mutlu et al. (2013) reported that foliar application of SA results in cold tolerance by enhancing antioxidant enzymes, enucleation activity, and the patterns of apoplastic proteins in *Hordeum vulgare* genotypes. Pretreatment with 2 mM concentration of SA was found to reduce chilling stress very significantly in pomegranate fruit (Sayyari et al. 2009). Added to this, seed treatment with 0.5, 1.0 and 2.0 mM SA for 24 h before chilling at 5 °C for 1 d decreased the chilling tolerance of rice (Wang et al. 2009).

Heat stress is often defined as the rise in temperature beyond threshold level for a period of time, sufficient to cause irreversible damage to plant growth and development. Salicylic acid mediated improved plant tolerance to heat stress has also been reported by many workers (Larkindale and Knight 2002; Larkindale and Huang 2004; Wang et al. 2010; Khan et al. 2013; Khanna et al. 2016). In *Arabidopsis* plants (Larkindale and Knight 2002) and in *Agrostis stolonifera* (Larkindale and Huang 2004), foliar spray of SA was found to reduce the oxidative damage caused by heat stress. Khan et al. (2013) have shown that treatment of 0.5 mM SA can alleviates adverse effect of heat stress on photosynthesis in *Triticum aestivum* through changes in proline production and ethylene formation. Furthermore, the decreased photosynthetic rate under heat stress was significantly alleviated by SA pretreatment in grape leaves through maintaining a high Rubisco activation state and rapid recovery of PS II function (Wang et al. 2010). Recently, Wassie et al. (2020) have shown that exogenously applied SA (0.25 mM or 0.5 mM) ameliorates heat stress-induced damages in seedlings of *Medicago sativa* with improved growth and photosynthetic efficiency.

5 Signaling Role of SA with Other Molecules

5.1 Abscisic Acid (ABA)

SA is an important signal molecule in plant biotic stress responses (Chen et al. 2009). ABA is opposed by SA; studies have reported ABA is able to induce genes such as *AGO1* and *RDRs* only in the absence of SA (Alazem et al. 2019). ABA downregulates SA biosynthesis and opposes SA mediated defense responses such as seed germination in osmotic stressed plants (Alonso-Ramirez et al. 2009b). However, ABA regulates plant's immune response via SA. ABA and SA are found to participate in the defense mechanisms against bamboo mosaic virus (BaMV), it is a positive-sense single stranded [(+) ssRNA] RNA genome (Alazem et al. 2019) (Fig. 1). SA and ABA regulate anti-viral RNA silencing pathway in turn provide resistance against different stress. Under salinity stress, SA induced ABA accumulation have helped plants in osmotic stress adaptation by improving photosynthetic pigments in *S. lycopersicum* (Khan et al. 2015). Similarly, exogenous salicylic acid application has shown to increase the levels of other hormones such as indole-3-acetic acid (IAA) and gibberellic acid under salt (NaCl) stressed plants to enhance their tolerance level (Shaki et al. 2019).

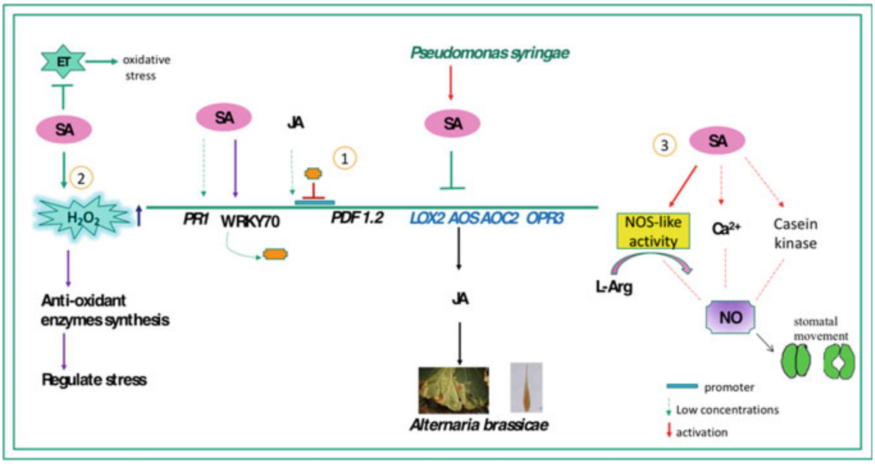

Fig. 2 Illustrates (1) the inhibition of JA pathway by SA via gene regulation to execute pathogenic response against *A. brassicae* and its interaction with other signaling molecules such as (2) H_2O_2, (3) NO and ET to regulate defense responses against stress

5.2 *Ethylene/ Jasmonic Acid*

Salicylic acid and ethylene/ jasmonic acid is the basic pathway for the execution of immune response against both biotic as well as abiotic stress responses in plants (Li et al. 2019). The SA and ET/JA signaling pathway is synergistic as well as antagonistic (Li et al. 2019). However in *myc2 tga256* mutants SA has been found unable to repress ET/JA induced *PDF 1.2* expression (Fig. 2). SA inhibits ethylene production by preventing the conversion of 1-aminocyclopropane carboxylic acid (ACC) to ethylene as ethylene causes oxidative stress (Khan et al. 2015) in stressful conditions (Fig. 2).

SA exerts negative crosstalk with JA (Proietti et al. 2013). A crosstalk of jasmonic acid with auxin regulates root growth under heavy metal (As^{2+}, Cd^{2+}) stress in rice plants (Ronzan et al. 2019) (Fig. 3). JA acid is involved in expression of various genes that regulate oxidative stress. Other hormones such as abscisic acid (ABA), auxin (AUX), cytokinin (CK), gibberellins (GB), strigolactones (SL) and brassinosteroids (BR) participate in the regulation of these pathways (Li et al. 2019).

5.3 *Nitric Oxide and Hydrogen Peroxide*

Nitric oxide is a highly active gaseous molecule which regulates various physiological processes and defense responses in plants (Verma et al. 2020). SA induces NO production through a different pathway other than nitrate reductase in *Arabidopsis thaliana* (Zottini et al. 2007). Their studies have suggested that NOS-like enzyme

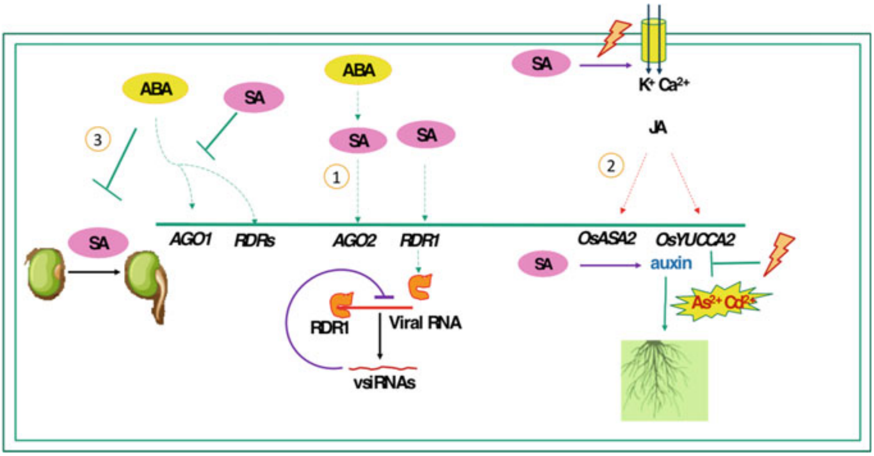

Fig. 3 Illustrates (1) ABA and SA induced RNA silencing pathway via SA induced expression of RDR1. (2) JA induced expression of *OsASA2* and *OsYUCCA2* which leads to auxin biosynthesis that regulates heavy metal stress. (3) Antagonistic effect of ABA on SA to prevent seed germination in stress

activity is involved in the NO production which utilises L-arginine substrate (Verma et al. 2020). This takes place through involvement of calcium and casein kinase 2 (Zottini et al. 2007) (Fig. 2). SA supplementation is found to enhance NO biosynthesis by increasing the activity of NO synthesiszing enzymes, together supplemtation of NO + SNP (sodium nitroprusside, a NO donor) is effective against Ni stress tolerance in *B. napus* (Khan et al. 2015). A combined effect of SA with NO is found to be effective to alleviate the cadmium and osmotic stress in rice and soyabean plants respectively and in other useful cash crops thus proving their interactive effect (Naser Alavi et al. 2014; Mostofa et al. 2019). SA and NO siganling participates heat tolerance response (Rai et al. 2019). SA also controls stomatal movement via NO in higher plants (Fig. 2).

H_2O_2 performs important signaling role in plants it mainly executes synthesis of compounds and enzymes which regulate biotic and abiotic stresses in plants. However, H_2O_2 is produced rapidly inside the cells under stressed conditions it also participates to execute systemic acquired resistance (Verma et al. 2020). SA also induces production of H_2O_2 (War et al. 2011). Also it is found that increased H_2O_2 levels induce SA biosynthesis. H_2O_2 behaves as a signaling molecule in the SA mediated rosamiric acid (RA) production in the cell cultures of *Salv ia miltiorrhiza.* Hao et al. (2014) found on application of DMTU (H_2O_2 scavenger) and inhibition of H_2O_2 production (through application NADPH oxidase inhibitor, IMD) there was no synthesis of RA thus proving siganling role of H_2O_2 in SA mediated responses.

6 Transport of SA and Its Regulation in Gene Expression

In plants salicylic acid acts as a signal to induce systemic acquired resistance. Molders et al. (1996) found that SA is translocated from the cotyledons of cucumber infected by tobacco necrosis virus (TNV) to leaves where it generates systemic acquired resistance (SAR) against C. *lagenarium* (Fig. 1). This shows that SA acts as a long distance signal to execute SAR. Data have also revealed that injection of [14C] BA into cotyledons showed systemic movement of [14C] SA to leaves after infection (Fig. 1). Under stress signaling molecules govern gene expressions which in turn regulate varied plants responses under stress (Singh et al. 2020). *PBS3* and *EPS1* are the two recently identified *Arabidopsis* genes which are important for pathogen-induced SA accumulation. *PBS3* and *EPS1*encode a member of the acyl-adenylate/thioester-forming enzyme family and a member of the BAHD acyltransferase superfamily, respectively which participate in the synthesis of a precursor or regulatory molecule in the SA biosynthesis.

6.1 SA Induced Gene Expression Under Abiotic Stress

PR proteins are responsible for resistance responses to pathogens and systemic acquired resistance (SAR). Over expression of *PR* gene causes enhanced tolerance to heavy metal stress in plants (Kang and Guo 2014). SA facilitates expression of *PR1* gene by changing the chromatin structure increasing acetylation (H3Ac, H4Ac) and methylation (H3K4me2, H3K4me3) (Chen et al. 2020). Under chilling stress, low concentration of methyl salicylate (MeSA) caused increased transcription of *PR-2b* and *PR-3a* thereby showing their regulatory role of these genes (Kang and Guo 2014). Exogenous SA application caused expression of the *MYB* and *P5CS* genes in order to provide resistance against salt stress, genes such as *DREB, MYB, P5CS*, and *BADH* show response against drought and salt stress (Zeng et al. 2018). Similarly, tolerance against salt stress was improved by the expression of *bZIP62, DREB2, ERF3,* and *OLPb* as well as anti-oxidant genes such as APX (ascorbate peroxidase) and superoxide dismutase (SOD) genes in SA treated rosemary plants and also were highly expressed (El-Esawi et al. 2017). SA pretreatment is also found to increase the levels of glutathione (GSH) and ascorbate (AsA) by regulating the gene expression of genes involved in their synthesis and thus enhances tolerance againt drought, cold and chilling stress (Kang and Guo 2014). Studies of Li et al. (2013) have reported that SA regulates transcription of ASA–GSH cycle enzymes thereby enhancing their contents and salt tolerance of wheat seedlings exposed to salt stress. SA is found to regulate drought tolerance by increasing the expression of *PR4c* and *PR4d* genes (Wang et al. 2011). SA together with ABA regulates expression of *AGO*, *DCL* and *RDR* genes and transcription factors (Alazem et al. 2019) (Fig. 3). However, combinely both oppose the expression of *AGO1* and *RDRs* but ABA induces expression of *AGO2* via

SA (Fig. 3). Exogenous jasmonic acid methyl ester application increased transcription of auxin biosynthetic genes *OsASA2* and *OsYUCCA2* under heavy metal stress (Ronzan et al. 2019). Molecular studies revealed that salicylic acid induced expression of genes *SOS1 and NHX1* in safflower plants cope up them with salinity-stress (Shaki et al. 2019).

6.2 SA Induced Gene Expression Against Pathogenesis

SA provides resistance to disease; it activates plant pathogenesis-related (*PR*) genes (Chen et al. 2009). SA induces expression of *RDR1*, RDR1 further stimulates expression of virus-derived short-interfering RNAs (vsiRNAs) which act of viral RNA and provide resistance to plum-pox virus (Alazem et al. 2019) (Fig. 3). SA plays beneficial roles in infected tobacco plants, it develops hypersensitive response as well as systemic acquired resistance in non-infected regions in TMV (Tobacco mosaic virus). Yang et al. (2015) have studied that enhanced transcription of salicylic acid biosynthesis gene in hybrid varieties of *Arabidopsis* plants enabled them with resistance towards bacterial pathogen *Pseudomonas syringae* pv. tomato (Pst) DC3000 (Fig. 2). SA blocks jasmonic acid (JA) pathway by blocking gene expression of *LOX2, AOS, AOC2* and *OPR3* which are JA biosynthesis genes and provides resistance against *Alternaria brassicae* (Fig. 2). SA negatively regulates JA pathway by blocking expression of gene *WRKY70,* a transcription factor which further prevents expression of JA mediated *PDF 1.2* gene expression (Fig. 2). Also mutant plants which lacked SA synthesis gene were unable to have resistance towards pathogen. However, expression of bacterial salicylate hydroxylase gene in transgenic tobacco *nahG* plants hampered the disease resistance response which proved that SA is essentially required for such response.

7 Conclusions and Future Perspective

SA is synthesized under biotic stress such as pathogenesis as a defense mechanism in plants. It is translocated from the site of synthesis to site of pathogenesis where it executes systemic acquired resistance against pathogen. SA executes immune responses against pathogen by regulating jasmonic acid pathway. SA regulates various physiological processes in plants through its crosstalk with abscisic acid, jasmonic acid, ethylene and other signaling molecules such as H_20_2 and NO, it boost ups anti-oxidant system via them to regulate stress. SA regulates gene expression of various genes in different kind of stresses such as chilling, drought, heat, heavy metal and salinity stress and improves tolerance towards them. SA is also found to enhance the gene expression of anti-oxidant system genes to regulate oxidative stress in plants. With the increasing demand of food for ever-increasing world population, SA plays a dominant role to regulate various kind of abiotic as well as biotic stress in plants thus to improve productivity. Futher application of gene-editing and insertion of SA coding genes in plants exposed to stress will help them cope stress through SA induced pathways.

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