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Jasmonates: An Emerging Approach in Biotic and Abiotic Stress Tolerance

Shivani Lalotra, Akhouri Hemantaranjan, Bhudeo Rana Yashu, Rupanshee Srivastava and Sandeep Kumar

Abstract

Plant hormones acts as key signaling compounds in plant stress responses and development under biotic and abiotic stresses. The potential roles of phytohormones had been considered so far and copious investigation is going on in finding the impending role of phytohormones in abiotic and biotic stresses. In the list of known classical plant hormones, Jasmonates, [jasmonic acid and its methyl ester (methyl Jasmonates)] have been recently added and shown as potential tool in enhancing tolerance of plants against various physiological processes. These are oxidized lipids (oxylipins) mainly derived from α -linolenic acids (α -LAs), play an active role in senescence through signaling, flower nectar secretion, Gprotein signaling, physiological activities and development in plants. Exogenous application of jasmonates on different plant parts have proved effective in improving plant abiotic stress tolerance particularly salinity, drought, and temperature (low/high) conditions and also in biotic stress tolerance like pathogen attack or wounding by production of defensive secondary metabolites, through the stimulation of phenyl-propanoid metabolism resulted from accumulation of JA in plant cells or tissues. Based on this prolific role of Jasmonates and its derivatives in different fields of biological sciences these phytohormones have opened new vistas and increasing interest in future Agricultural, Biotechnological and Physiological researches.

Keywords: biotic and abiotic stress, phytohormones, jasmonates and its derivatives, biosynthesis, emerging roles, signal transduction etc.

1. Introduction

The total geographical area of India is 328.7 million hectares [1], and its economy is chiefly dependent on agriculture sector. About 54.6% of the Indian population is affianced in agriculture and allied activities [2], and about 141.4 million hectares is the reported net sown area, and 200.9 million hectares is the gross cropped area with a cropping intensity of 142%. Moreover, the human population is rapidly increasing and needs a substantial increase in agricultural productivity worldwide. There has been a continuous decline in the share of agriculture and allied sector due to the changing climatic scenario, exploding population, and stressful environment which made it unfeasible for proper operation of gross cropped area. Therefore, exploiting recent and innovative strategies, tools, approaches, chemicals, and

technologies is the only solution to increase productivity for the ever-increasing population. Given the importance of agriculture sector, steps have been taken to improve productivity on a sustainable basis by agronomic, biotechnological, genetical, and physiological approaches. Stressful environments are now being recognized as a potential agricultural threat for the sustainable agriculture. The commencement of environmental stresses results in plant defense responses, e.g., expression of stress-responsive genes and production of many defensive proteins and nonprotein compounds through various signaling pathways [3]. Plants produce various volatile or nonvolatile endogenous compounds and also certain mechanisms developed and deployed by plants to counteract environmental stress. Such endogenous compounds are called phytohormones.

2. Phytohormones

Phytohormones are the chemical compounds produced endogenously in very low concentrations that play significant role in the regulation and expression of gene encoding proteins. They are the diverse group of signaling molecules that result in a variety of cellular and developmental processes, signaling networks in plants under biotic and abiotic stress. They work as chemical messengers to communicate cellular activities and act either at their site of synthesis or elsewhere in plants following their transport in higher plants [4, 5]. Different phytohormones interact with each other and show synergetic or antagonist interactions that might be helpful in tolerance mechanisms. A large number of phytohormones are studied to date; among them jasmonates are the emerging players in environmental stress tolerance.

3. Jasmonate: a potent phytohormone

Jasmonates [jasmonic acid (**Figure 2**) and its methyl ester methyl jasmonate (**Figure 1**)] the cyclopentanone phytohormones are a class of oxidized lipids (oxylipins) derived from α -linolenic acids (α -LAs) through lipoxygenase-dependent manner. [6] first isolated JA from culture filtrate of the fungus *Lasiodiplodia* (*Botryodiplodia*) *theobromae*, a plant pathogen, was identified as a plant growth inhibitor, whereas its derivative methyl jasmonate was first isolated from *Jasminum grandiflorum* (jasmine) petal extract [7]. (+)-7-iso-Jasmonoyl-L-isoleucine (JA-Ile) is the best-described bioactive JA [7] till date, but other JAs like *cis*-jasmone, jasmonoyl ACC (JA-ACC), and jasmonoyl isoleucine (JA-Ile) are also studied by scientists with multiple biological functions [9–12]. Various developmental and environmental factors are responsible for the production of JA in membranes and resulted in expression of stress tolerant genes (**Figure 3**). JA is ubiquitously found in the plant kingdom and results in the expression of genes at the transcriptional and post transcriptional levels [13, 14]. An imperative role of jasmonate (when applied exogenously in low concentrations) is reported in enhanced pathogen resistance.

Cross talks of jasmonates with signaling pathways generated by various phytohormones like ABA, salicylic acid, ethylene, etc. result in diverse developmental processes like seed germination, seedling growth, pollen fertility, fruit ripening, senescence and tolerance. However, its extent of effectiveness entirely depends on the type of plant species tested or its concentration. MeJA is more volatile than JA, so exposure to it either in solution or in the gaseous phase can elicit plant responses. Apart from its significant role in plants, derivatives of jasmonates, e.g., methyl jasmonate are used as a fragrant constituent in many aromatic mixtures [15].

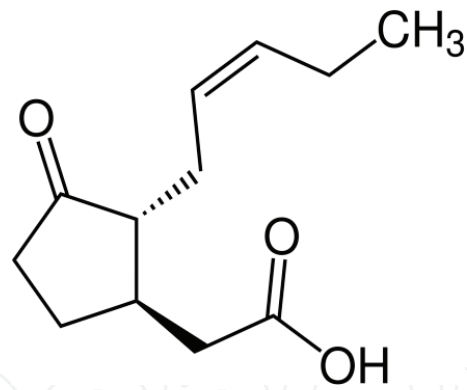


Figure 1.
Chemical structure of methyl jasmonate [3-oxo-2-(2-pentenyl)-, methyl ester].

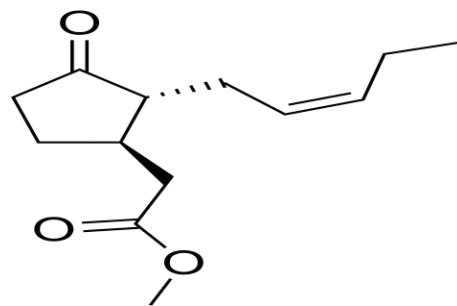


Figure 2.
Chemical structure of Jasmonic acid [3-oxo-2-(2-pentenyl) cyclopentaneacetic acid].

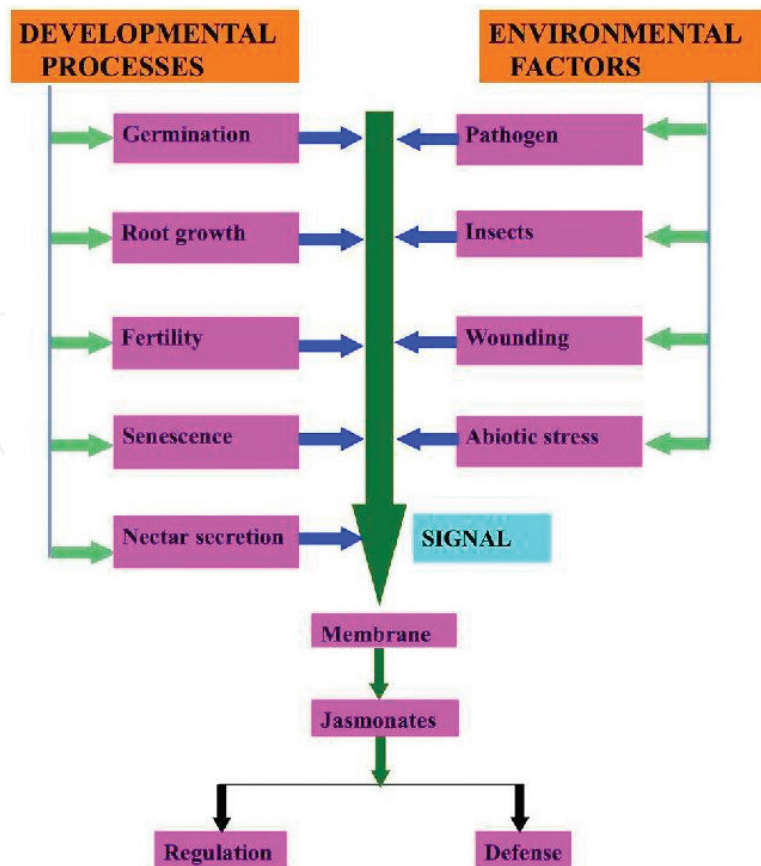


Figure 3.
Various developmental and environmental factors are shown that signals membrane for the production of endogenous jasmonates which further results in the regulation of certain genes and defense mechanisms against stressful environment. Source: Ahmad et al., [16].

4. Biosynthesis of jasmonates: the octadecanoid pathway

The biosynthetic pathway of jasmonates (**Figure 4**) was identified in Year 1984. The scientists Vick and Zimmerman [17] were the first to illustrate the biosynthetic pathway in a simplified manner which indicated that linolenic acid could be converted into the cyclopentanone 12-oxo-phytyldienoic acid (12-oxo-PDA) through lipoxygenase enzyme. Methodically the pathway was studied in model plants like *Arabidopsis* and tomato. The octadecanoid pathway of Jasmonates completes in two cellular organelles such as chloroplasts and peroxisomes and are considered to be the primary sites [7, 18]. α -Linolenic acid (α -LeA) released from galactolipids (due to wounding or pathogens attack) of chloroplast membranes is found to be the main player of MeJA and JA production [12]. Phospholipases1 (PL1), lipoxygenase, allene oxide synthase, and allene oxide cyclase (AOC) are significant enzymes involved in biosynthesis of jasmonates.

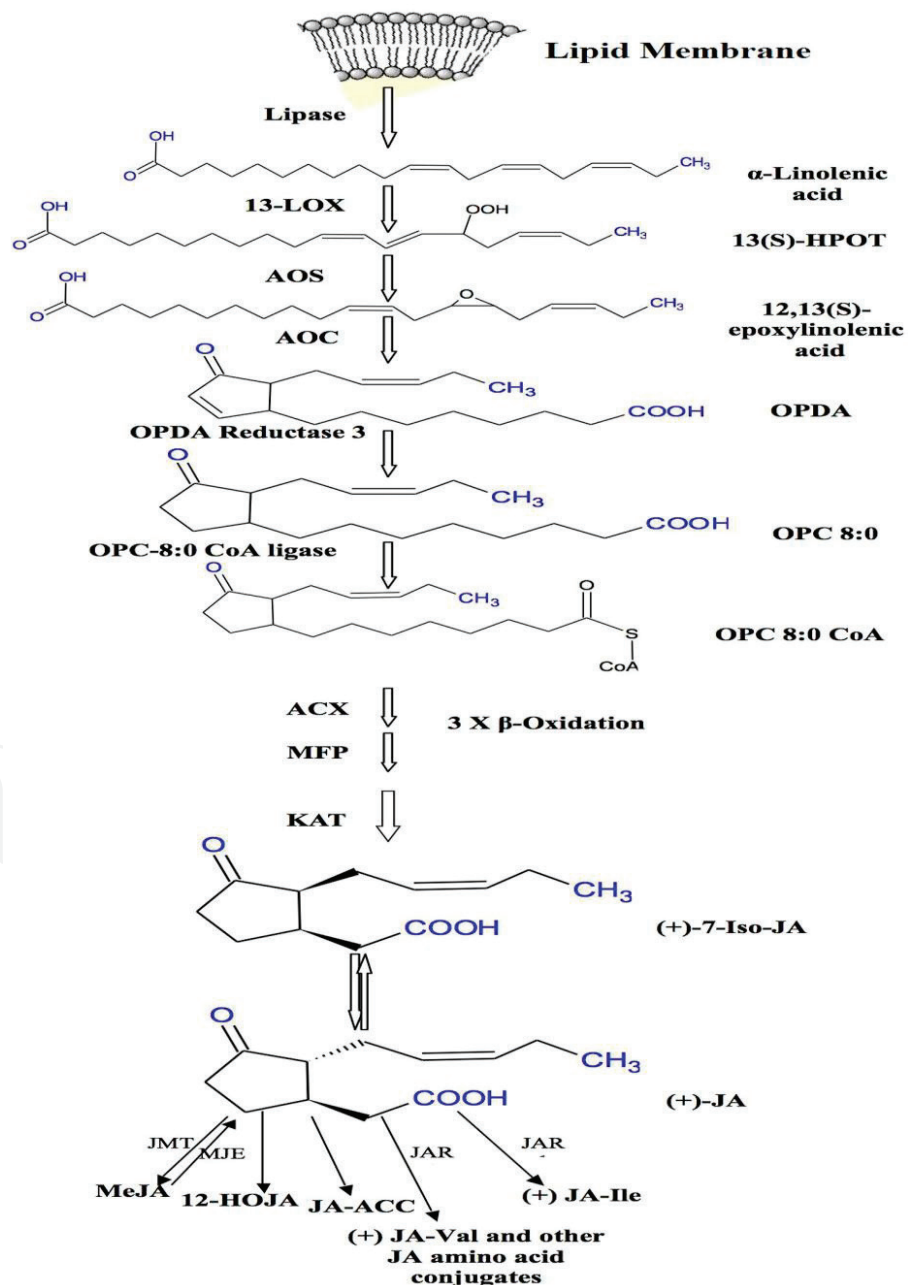


Figure 4. Step wise pathway of jasmonates biosynthesis. Source: Ahmad et al., [16].

4.1 Role of enzymes involved in jasmonates biosynthetic pathway

- **Phospholipases:** formation of α -LeA from chloroplastic membrane lipids
- **13-Lipoxygenase (LOX):** addition of oxygen molecule to α -LeA and results in formation of an intermediate compound 13-hydroperoxy-9,11,15-octadecatrienoic acid (13-HPOT).
- **Allene oxide synthase (AOS):** oxidation of 13-HPOT to allene oxide
- **Allene oxide cyclase (AOC):** formation of 12-oxo-phytodienoic acid (12-OPDA) an unstable compound from allene oxide.

The AOS and AOC are present in plastids and they act in concert [19]. 12-OPDA is the final product of biosynthetic pathway formed in chloroplast and undergoes three cycles of β -oxidation in the peroxisomes [8]. A methylation reaction by JA methyl transferase results in the formation of jasmonate methyl ester derivative, i.e., methyl jasmonate. Among the six 13-LOXs of Arabidopsis, four of them are (LOX2, LOX3, LOX4, and LOX6) but LOX2 is a vital lipoxygenase in JA biosynthesis.

4.2 Key roles of LOX2

- Responsible for the bulk of JA formation upon wounding [7, 20]
- Oxylin generation during natural and dark-induced senescence

5. Jasmonates signal perception and transduction pathway

Several transcription factors (TFs), repressors, up-regulation and down-regulation of certain genes, and members of ubiquitin-proteasome complexes are involved in JA signal perception and transduction pathway (**Figure 5**). Different independent studies [21, 22] with GC-MS and HPLC analyses in *A. thaliana* revealed that (+)-7-iso-JA-L-Ile is the only natural and direct JA-signaling ligand in plants.

The Skp1/Cullin/F-box (SCF) complex is of proteinous type and is the ubiquitin-proteasome complex. In jasmonate signal transduction pathway *coronatine insensitive1* (*COI1*), the locus encodes an F-box protein that associates with its other counterparts, SKP1, Cullin, and Rbx proteins, to form an E3 ubiquitin ligase [23]. So *COI1* is found to be the jasmonate receptor in signaling pathway. In 2007, [22, 24, 25] scientists in independent research found new family of proteins called jasmonate zim-domain (JAZ) proteins in Arabidopsis, which were found to be the key negative regulator of JA signaling and act as substrate for SCF^{COI1} E3 ubiquitin ligase complex. About 12 JAZ proteins were present in *A. thaliana* and contain N-terminal domain, a highly conserved C-terminal Jas domain that mediates the interaction with the *COI1* and several transcription factors, and the conserved protein-protein interaction domain, the ZIM (TIFY) domain that helps in JAZ dimerization and interaction with novel interactor of JAZ (NINJA).

Moreover, the interaction of *COI1* with the Jas domain of JAZ proteins in the presence of JA-Ile forms the co-receptor complex [26]. SCF^{COI1}, E3 ubiquitin ligase complex, JAZ degrons (*JAZ1* to *JAZ12*) and IP5 form the co-receptor complex and found to be true jasmonates receptors [27].

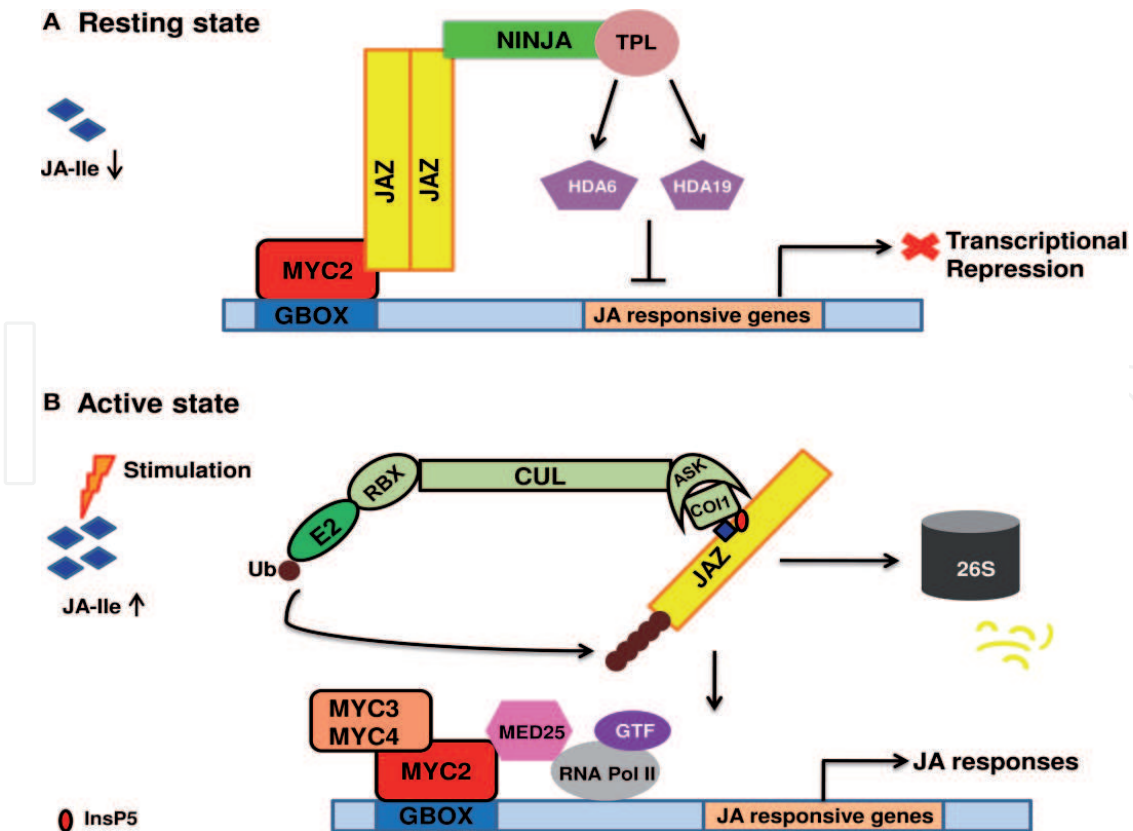


Figure 5.
Signal transduction pathway of jasmonic acid.

A number of co-repressors also play their role simultaneously in signal transduction pathway. Corepressors in transcriptional regulators inhibit transcription initiation. TOPLESS (TPL) and TPL-related proteins (TPRs) are members of Groucho/ Tup1 co-repressor family that causes histone deacetylation and demethylation which resulted in chromatin modification, eventually mediated repression of genes. [10]. Interaction of TPL with JAZ proteins takes place via ethylene response factor (ERF)-associated amphiphilic repression (EAR) motif. Those JAZ proteins having absence of repression motif recruit TPL through an adapter protein called novel interactor of JAZ (NINJA) [28].

MYC2 the master regulator of many biological processes is a bHLH transcription factor mediating the transcriptional regulation of JA. Other transcription factors that controls JA mediated signaling are MYC3, MYC4, MYB, GL3, EGL3 AP, GL1, etc.

5.1 Role of MYC2 in JA mediating signal transduction

- An activator of JA-induced root growth inhibition
- Anthocyanin biosynthesis, oxidative stress tolerance
- Mediating resistance to necrotrophic pathogens, insects
- Biosynthesis of tryptophan and indole glucosinolates

Various homologs of MYC2 like MYC3 and MYC4 binds with G-box (5'-CACGTG-3') and G-box-related hexamers and regulate the transcription of downstream targets [29].

6. Emerging roles of Jasmonates

6.1 Inhibitory action on seedling growth

Exogenous application of JA possibly shows inhibition of primary root growth, leaf expansion, and hypocotyl elongation which ultimately leads to inhibitory action in seedling growth [30]. InsP5 enhances the interaction of COI1 with JAZ9 and the inhibitory effect of JAs on root growth [31]. JA represses leaf expansion by inhibiting the activity of the mitotic cyclin CycB1;2 and cell division, rather than by affecting cell size. Transcription factor like MYC2 and its close homologs shows both positive and negative effects on hypocotyls in red/far-red light and blue light conditions; it works positively in inhibition of hypocotyl elongation in red/far-red light and negatively regulates the inhibition of hypocotyl elongation by blue light. ERF109 binds to and activates *anthranilate synthase A1 (ASA1)* and *YUCCA2* (promoters of the auxin biosynthetic genes) and results in the promotion of lateral root formation in Arabidopsis [32].

6.2 Role in plant reproductive development

Various transcription factors of R2R3-MYB family like MYB21, MYB24, and MYB57 are direct targets of JAZ proteins (**Figure 6**). These TFs have significant role in mediating JA-regulated stamen development [33]. Formation of MYB-MYC complexes due to the association of MYB21 and MYB24 with the IIIe bHLH factors MYC2, MYC3, MYC4, and MYC5 controls stamen development in Arabidopsis [34]. Besides the role of JA on stamen development, JA plays a major role in seed and embryo development in tomato. The *jasmonic acid-insensitive1 (jai1)* mutant, which exhibits a loss of function of the tomato homolog of COI1, cannot set viable seeds. Moreover, production of OPDA and a residual amount of JA, in tomato mutant *acx1a*, set viable seeds. Gene silencing (*OPR3* silenced gene) in *SiOPR3* a transgenic line of tomato produces comparable amount of OPDA to wild type and sets only a few viable seeds; methyl-JA treatment can restore the seed setting of *SiOPR3*. This further suggests the role of methyl jasmonate in maternal control of seed development [35].

6.3 Role in abiotic stress tolerance

Numerous morphological, physiological, biochemical and molecular changes take place due to abiotic stresses like drought stress, salinity stress, high- and low-temperature stress, heavy metal toxicity, etc.; these stresses adversely affect plant growth and productivity. JA is believed to play a role in plant responses to abiotic stresses including drought, salt, and heat stress. Salinity is one of the perilous stresses that causes physiological drought and is responsible for delayed seed germination, seedling establishment and reduced growth and yield of any crop. Under salt stress, jasmonates proved to be an imperative phytohormone in mitigation. Jasmonates recovered salt inhibition on dry mass production in rice [36] and diminished the inhibitory effect of NaCl on the rate of $^{14}\text{CO}_2$ fixation, protein content in *Pisum sativum* [37]. The pleiotropic effects of MeJA in protecting plants have been reported for several plants [38], reported in his studies JA is responsible for the amelioration of chilling injury, water stress, and salinity stress in *Oryza sativa* L., *Lycopersicon esculentum* L. [39], *Fragaria vesca* [40], and *Hordeum vulgare*. High-temperature stress destructively influences plant processes and disturbs the cell homeostasis [41]. Heat shock proteins (HSPs) are synthesized in plants in response to high temperature that prevent denaturation and assist refolding of

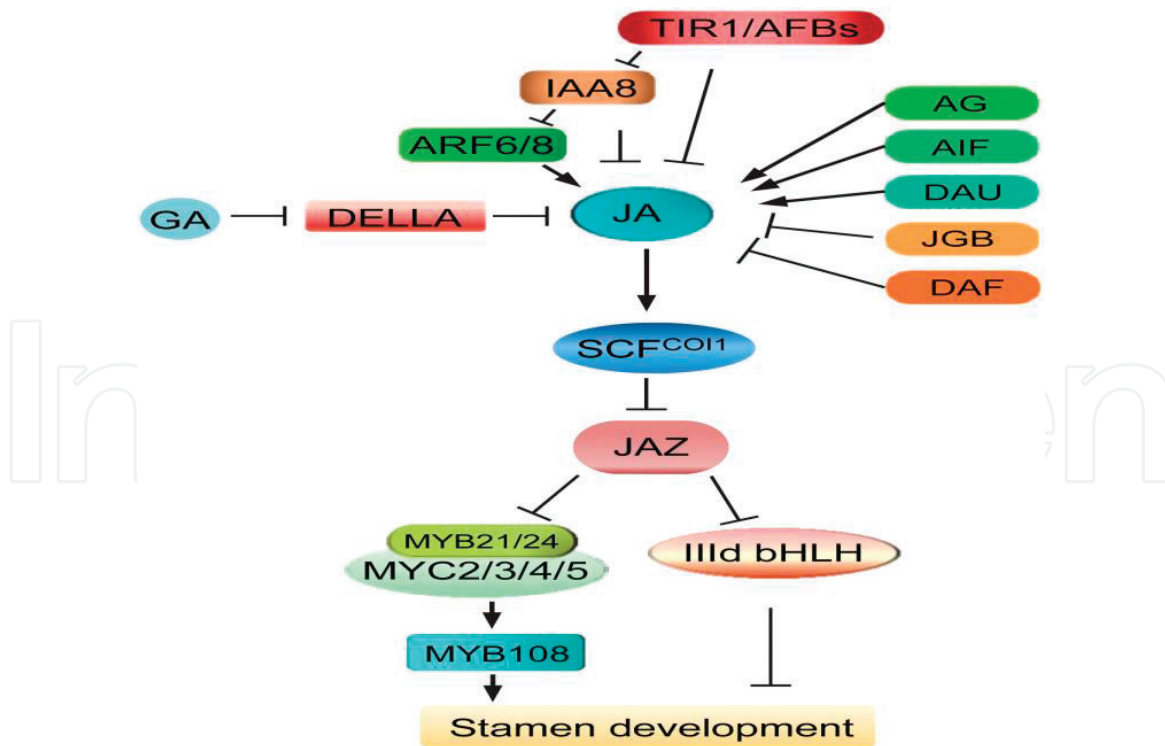


Figure 6. JA signaling and crosstalk in stamen development (Source: Huang et al, [42]).

damaged proteins. Electrolyte leakage assays in heat-stressed plants after application of low-concentration MeJA demonstrates the cell viability responses. Heating WT Arabidopsis led to the accumulation of several jasmonates including OPDA, MeJA, JA, and JA-Ile, and the expression of jasmonate inducible gene PDF1.2 was found to be high upon heat stress exposure. Suppressor of G2 allele of SKP1 (SGT1) protein operates as a cofactor of heat shock protein 90 (HSP90) in both plants and mammals forming functional complexes and providing thermotolerance. JA also showed essential role in heavy metal and nutrient toxicity. In a study by [43], they reported that the excess amounts of boron present in soil decrease the net photosynthetic rate, closing of stomata, internal CO₂ concentration, and total chlorophyll content in leaves. Foliar application of boron-stressed plants of *Artemisia* with MeJA started to stimulate the synthesis of antioxidant enzymes, reduce the amount of lipid peroxidation, and enhance artemisinin content. [44] found that the first report on jasmonate-induced anticancer activities exhibited their capacity to cause both cell death and suppression of cell proliferation. MJ was studied in topical application for precancerous and cancerous skin lesions [45].

6.4 Role in biotic stress tolerance

Two types of responses are shown by plants due to tissue injury, and jasmonates plays a significant role in these responses by signaling in plants. Two types of responses are local response and systemic response (**Figure 7**).

In local response during tissue damage, various attacker-derived signals or damaged-associated plant-derived signals are produced; these signals are either chemical or physical in nature and are recognized by PRRs pattern recognition receptors present on cell surface. This recognition event activates *de novo* synthesis of JA and JA-Ile by an unknown pathway. SCF^{COI1}/26 proteasome activation by JA-Ile results in degradation of JAZ proteins. These proteins are responsible for the repression of transcription factors (TFs) involved in the expression of defense-related traits.

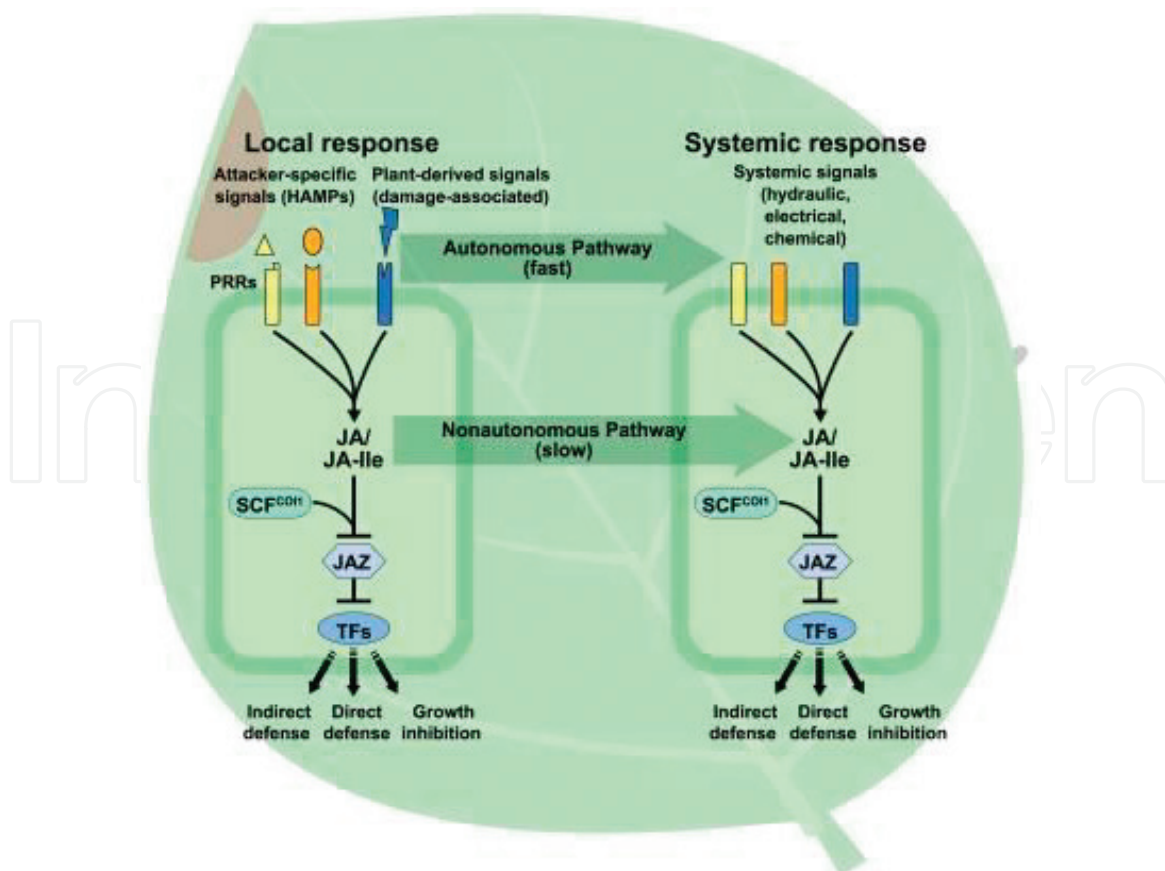


Figure 7.
 Role of JA in tissue damage (source: Abraham et al. [46]).

Systemic responses are mediated by two distinct pathways involving JA. Cell-nonautonomous pathway is a slow pathway and cell autonomous pathway is a fast pathway in defense responses. In cell-nonautonomous pathway upon leaf damage, JA is produced and translocated to undamaged leaf where it triggers JA responses in target cells whereas, in cell autonomous pathway, wound-induced production of a mobile signal (other than JA) activates JA/JA-Ile synthesis and subsequent responses in distal tissues. To optimize the spatial and temporal expression of responses the two pathways may work synergistically.

6.5 Role in the promotion of leaf senescence and seed germination

Exogenous application of low concentration of methyl jasmonate below 1 micro molar do not promote premature leaf senescence, but if the concentration increases beyond 30 micro molar, symptoms of premature leaf senescence were seen in the early stages of plant growth by upregulating the expression of senescence-associated genes and by downregulating photosynthesis-related genes. JA promotes leaf senescence in a COI1-dependent manner; TFs MYC2, MYC3, and MYC4 mediate JA/dark-induced leaf senescence by upregulating the expression of senescence-associated genes (e.g. *senescence-associated gene 29* [SAG29]) and chlorophyll catabolic enzyme genes (CCGs) (e.g. *pheophorbide A oxygenase*), as well as by down-regulating photosynthesis-related genes (e.g., *chlorophyll A/B binding protein 1*), whereas in germination process, JA delays the ABA-mediated inhibition of seed germination in Arabidopsis. During the cold-stimulated germination of wheat (*Triticum aestivum*) seeds, JA biosynthesis-related gene expression and JA biosynthesis increase rapidly in the dormant embryos after transfer to room temperature, and JA suppresses ABA biosynthesis to promote cold-stimulated germination [47].

Other key roles of jasmonates are:

As most of the work of jasmonates did in model plant *Arabidopsis*, so numerous roles of JA could be found in *Arabidopsis*, but some positive roles are also found in other plants.

- Delay of flowering in *Arabidopsis*
- Regulation of stomatal closure and reopening in *Arabidopsis*
- Promotion of trichome formation
- Inhibition of apical hook formation in *Arabidopsis*
- Inhibition of petal expansion in *Arabidopsis*
- Gravitropism in plants
- Sex determination in maize

7. Conclusion

The twin challenges like declining food and nutritional security and changing climatic scenario require the use of such biotechnological, physiological, genetical, and agronomical strategies to accomplish the demands of food to exploding population. Increasing abiotic stress made land barren or unutilizable for crop production. Tolerance to biotic and abiotic stresses is a challenge of agro-economic impact. Moreover, in a field condition additive effect of a number of stresses may further result in decreased soil fertility and crop yields. Researches on tolerance mechanisms and cross talks by phytohormones proved to be constructive for researchers in developing tolerant plants against particular stress. From the above information on jasmonates, the role of jasmonates in plant development is very well established but there is limited information available in the literature on how plant processes vary from species to species with JA application; a large number of components/genes of JA/MeJA including its receptors have been identified, but their appropriate functions still need to be explored, also various genes involved in growth regulation at different stages of development are yet to be identified.

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