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

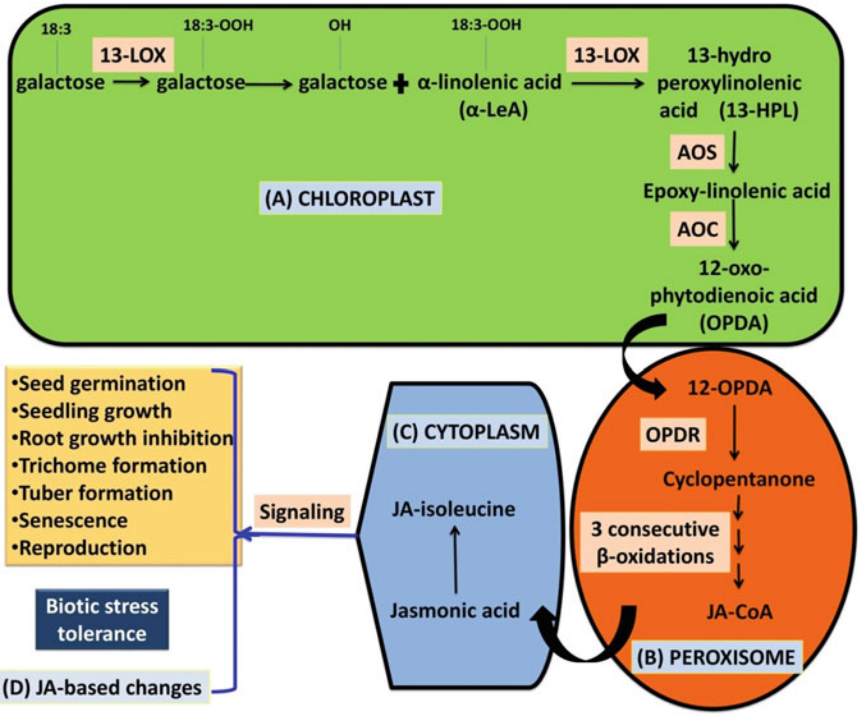

Fig. 1 **a** Release of galactolipids (from chloroplast membrane) and their metabolization gave α-linolenic acid (α-LeA; JA precursor). 13-LOX mediated action over α-LeA produce the 13-hydro peroxylinolenic acid (13-HPL). A transient epoxy intermediate is developed by allene oxide synthase (AOS) activity 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).

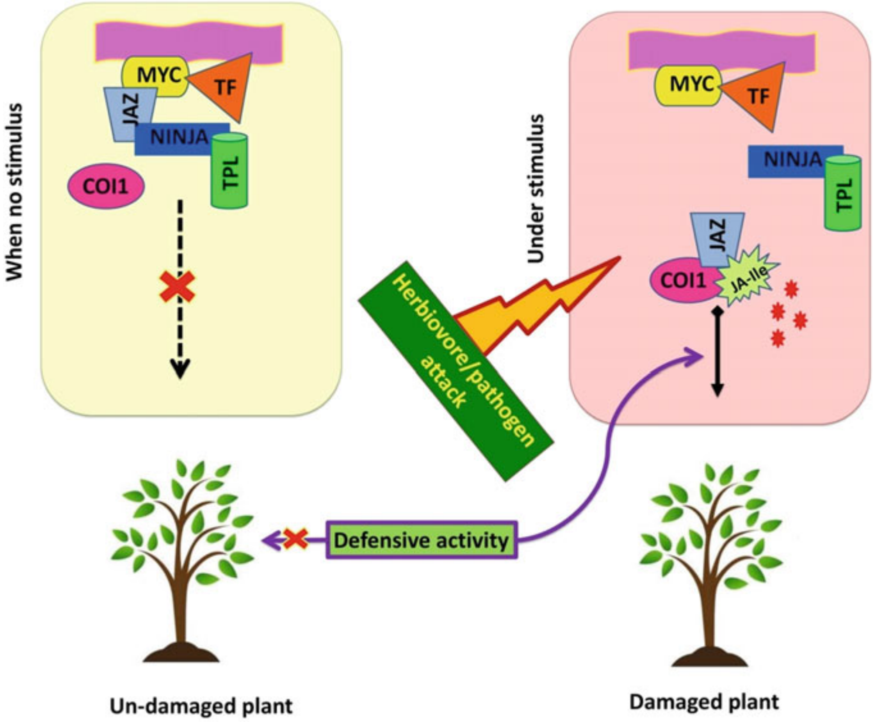

Fig. 2 Jasmonic acid (JA)-based security aligned with biotic stresses in plants. In un-damaged plants, repressor proteins JAZ (JASMONATE ZIM) unite with positive TFs like basic helix-loop-helix MYCs. Under normal conditions, JA pathway is suppressed by NINJA (NOVEL INTERACTOR OF JAZ) and their recruited 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 micrganisms 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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