Jasmonic Acid Dynamics, Signaling and Functions in Plants

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Abstract

Jasmonic acid (JA) is an endogenous growth-regulating substance, initially identified as a stress-related hormone in higher plants, they act as signal molecules, produced within plants, that occur in extremely low concentrations, control all aspects of plant growth and development, from embryogenesis, the regulation of organ size, pathogen defence, stress tolerance etc. Similarly, the exogenous application of jasmonic acid also has a regulatory effect on plants. Abiotic stress often causes large-scale plant damage. In this review, we focus on the jasmonic acid signalling pathways in response to abiotic stresses, including cold, drought, salinity, heavy metals, and light. On the other hand, jasmonic acid does not play an independent regulatory role, but works in a complex signal network with other phytohormone signaling pathways. in response to abiotic stress. In jasmonic acid signaling pathway, the JAZ-MYC module plays a central role in the JA signaling pathway through integration of regulatory transcription factors and related genes. Simultaneously, jasmonic acid has synergistic and antagonistic effects with abscisic acid (ABA), ethylene (ET), salicylic acid (SA), and other plant hormones in the process of resisting environmental stress.

Keywords: Antagonistic, Signaling, Jasmonic acid, Synergistic.

1. Introduction

Jasmonic acid is a plant hormone that plays a key role in regulating plant growth, development and response to environmental stresses. Jasmonic acid and its derivatives play a crucial role in a plant's defence against both biotic and abiotic stresses. The functions performed by jasmonic acids in protection growth and mobilizing plant defense responses constitute a direct path for stress reduction. It is a lipid derived plant hormone that belongs to the oxylipin family of compounds. The chemical structure of jasmonic acid consists of a pentanoic acid side chain with a cyclopentanone ring and a carboxylic acid group. It is involved in signalling pathways that control processes such as seed germination, root growth, flower development and defence against herbivores and pathogens. When plants are under stress, such as from insect attack or physical damage, they produce jasmonic acid as part of their defence response. This hormone triggers the production of defensive compounds, such as toxins and volatile organic compounds, that can deter herbivores and attract predators of the herbivores (Ruan et al. 2019).

2. Structure of jasmonic acid

Jasmonic acid is a lipid derived plant hormone that belongs to the oxylipin family of compounds. It is derived from the fatty acid linolenic acid and contains a cyclopentanone ring. The chemical structure of jasmonic acid consists of a pentanoic acid side chain with a cyclopentanone ring and a carboxylic acid group. Its chemical structure is 3-oxo-2-2′-cis-pentenyl-cyclopentane-1-acetic acid, which is the core of the jasmonic acid structure. Jasmonic acid is an oxo monocarboxylic acid with a (3-oxocyclopentyl) acetic acid substituted by a (2Z)-pent-2-en-1-yl group at position 2 of the cyclopentane ring (Fig. 1).

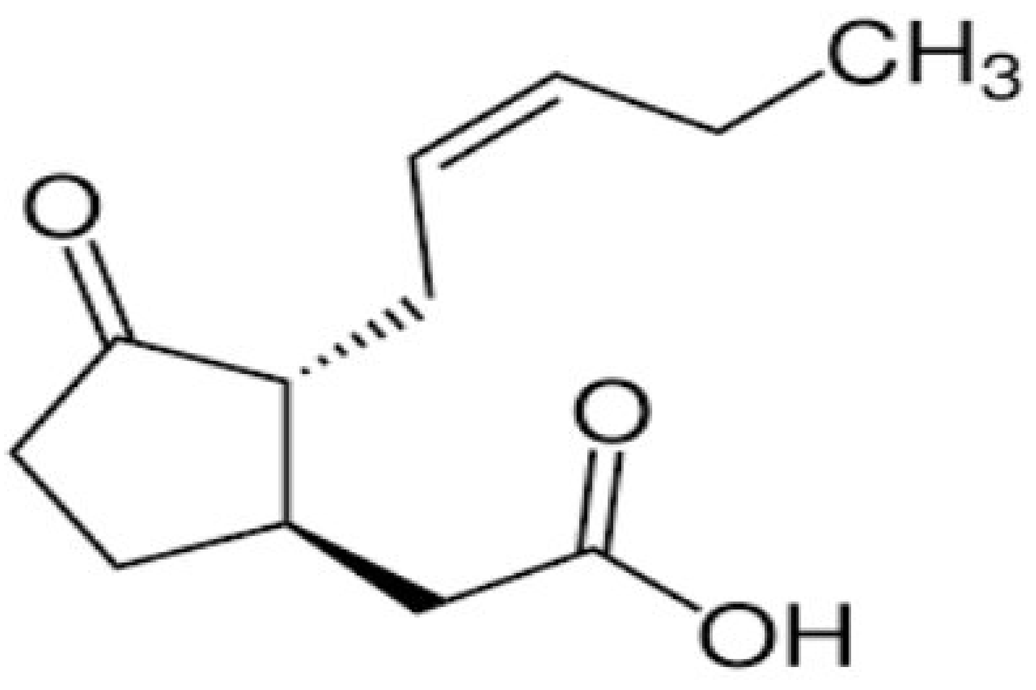

Figure 1. Structure of jasmonic acid

3. Biosynthesis

There are three pathways for the synthesis of jasmonic acids, including the octadecane pathway starting from linolenic acid and the hexadecane pathway starting from hexadecatrienoic acid (Fig. 2). All three pathways require three reaction sites: the chloroplast, peroxisome, and cytoplasm (Taiz et al. 2015).

Biosynthesis of jasmonic acids has been studied in a variety of monocotyledonous and dicotyledonous plants during the last decades. Most of the work is done in the model plants *Arabidopsis thaliana* and *Lycopersicon esculentum* (tomato) (Wasternack and Song 2017). So far, various enzymes in the jasmonic acids synthetic pathway have been identified, and our knowledge of the relationship between the jasmonic acid synthesis pathway and other metabolic pathways is gradually improving. In *Arabidopsis*, there are three pathways for the synthesis of jasmonic acids, including the octadecane pathway starting from α-linolenic acid and the hexadecane pathway starting from hexadecatrienoic acid. All three pathways require three reaction sites: the chloroplast, peroxisome, and cytoplasm. The synthesis of 12-oxo-phytodienoic acid (12-OPDA) or deoxy methylated vegetable dienic acid (dn-OPDA) from unsaturated fatty acid takes place in the chloroplast, which is then converted to jasmonic acid in the peroxisome. In the cytoplasm, jasmonic acid is metabolized into different structures by various chemical reactions, such as MeJA (methyl jasmonate), JA-Ile (jasmonyl isoleucine), *cis*-jasmone (CJ), and 12-hydroxyjasmonic acid (Ghorbel et al. 2021).

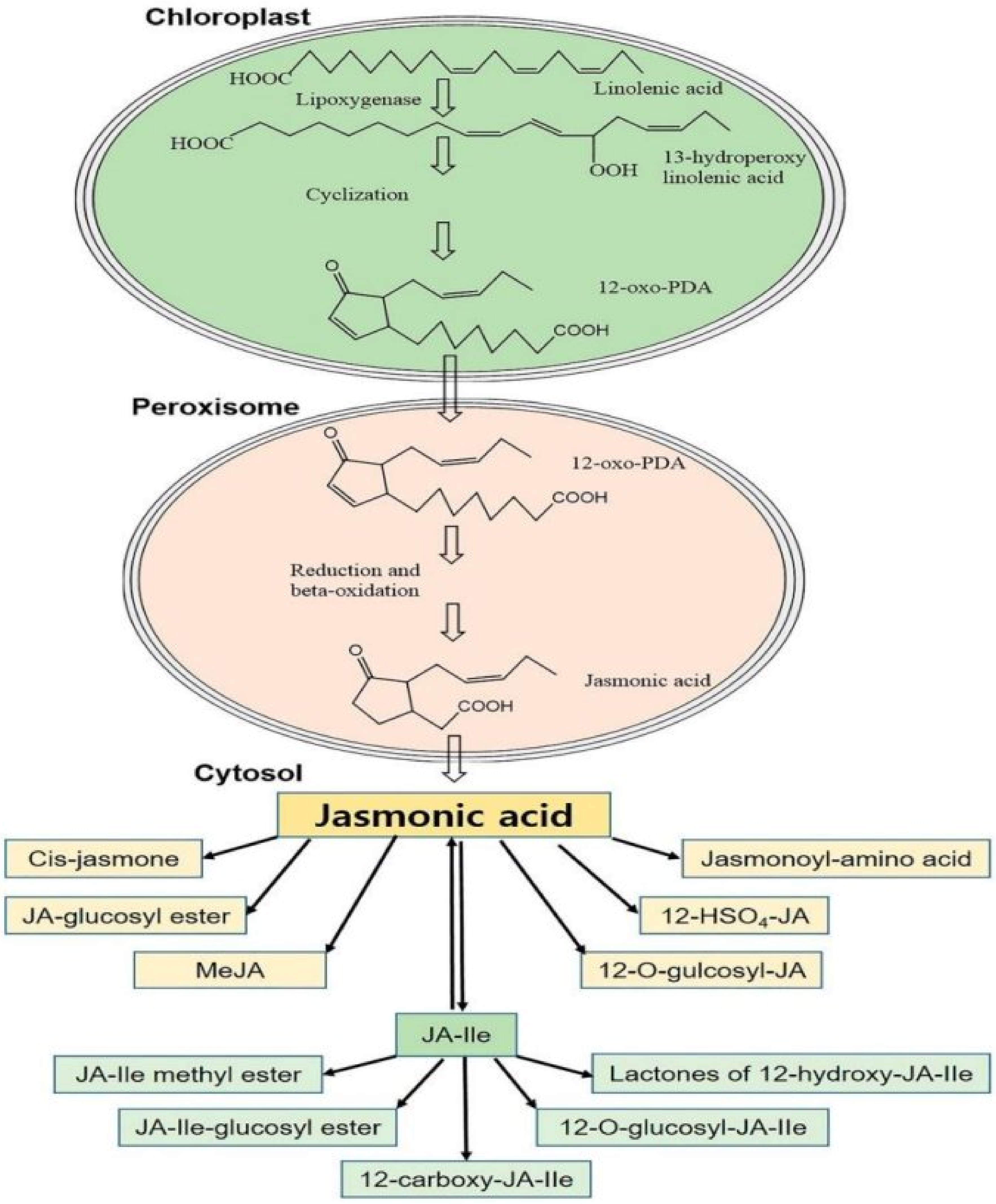

Figure 2. In chloroplast, the precursor of jasmonic acid called linolenic acid is converted into 13- hydroperoxyl linolenic acid by lipoxygenase when plant undergo any abiotic stress conditions. 13- hydroperoxyl linolenic acid undergo cyclisation and reduction it forms 12- oxo phytodienoic acid (12-OPDA). 12 OPDA enters into peroxisome where it undergoes reduction and beta oxidation form jasmonic acid. In cytosol JA undergo various metabolic processes and forms cis- jasmone, jasmonic acid glucosyl esters (JA-

glucosyl ester), Methyl jasmonate (MeJA), jasmonic acid isoleucine methyl ester (JA-Ile methyl ester), jasmonic acid isoleucine glucosyl ester (JA-Ile-glucosyl ester), 12- carboxy- jasmonic acid isoleucine (12- carboxy JA Ile), 12-o- glucosyl jasmonic acid isoleucine (12-o-JA-Ile), lactones of 12-hydroxy –JA- Ile, 12-o- glucosyl jasmonic acid, 12- H2SO4-jasmonic acid and jasmonyl amino acids (Wang et al. 2020).

4. Transmission of signal

The defence response triggered by a signal can result in a local defence response near the wound, a systemic acquired resistance (SAR) at the uninjured site, and even induced defence responses from adjacent plants. Wounding induces expression of genes encoding defense related proteins involved in wound healing in these defence responses, short-distance transmission and long-distance transmission of jasmonic acid signals are involved. With the studies in the area of mechanisms of hormone signalling networks, it has been found that salicylic acid, ethylene, auxin, and other plant hormones interact with jasmonic acid to regulate plant adaptation to the environment. At present, the understanding of complex regulatory networks and metabolic processes after plants perceive environmental signals is still very limited (Hu et al. 2009).

Jasmonic acid not only activates defence-related genes, it also shuts down growth. Jasmonic acid induces growth suppression allows relocation of resources to metabolic pathways involved defence. Jasmonic acid acts through a conserved ubiquitin ligase-based signalling mechanism that bears close resemblance to those described for auxin and gibberellin. Although unconjugated jasmonic acid is hormonally active, many jasmonic acid response require activation of the hormone for optimal activity by conversion into amino acid conjugate, such as jasmonic acid – isoleucine (JA-Ile). This conjugation is performed by enzyme referred to as jasmonic acid resistance (JAR) proteins, which belongs to a family of carboxylic acid conjugating enzymes. JAR1 for example, exhibits a high substrate specificity for jasmonic acid and isoleucine and appears to be of particular importance of jasmonic acid defence signaling.

When levels of bioactive jasmonic acid are low, the expression of jasmonate-responsive genes is repressed by members of the JAZ (Jasmonate ZIM domain) protein family which are key regulators of the jasmonic acid response. JAZ repressors act by binding to the MYC2 transcription factor, a major switch in the activation of jasmonic acid dependent genes. JAZ repressors also maintain the chromatin in a closed state that prevents jasmonic acid responsive transcription factors from binding to their targets to maintain chromatin in the inactive state, JAZ proteins bind to the F box protein COI1, which is an essential component of the SCF protein complex SCFCOI1, a multiprotein E3 ubiquitin ligase, two additional proteins and two histone deacetylase enzymes (HDAC6 and HDA19) act as co repressors along with the JAZ-COI1 complex and are instrumental in maintaining the chromatin in an inactive state. The binding of JA-Ile to the JAZ-COi1 co receptors leads to the ubiquitination of JAZ by the SCF COI1-JA-Ile complex, followed by JAZ degradation of JAZ liberates the MYC transcription factor, which then recruits various other chromatin remodelling proteins and transcription factors that bring about the expression of the early jasmonic acid responsive genes (Li et al. 2021).

4.1 Short distance signal transmission

In plants, mechanical damage or insect feeding can cause rapid and transient accumulation of jasmonic acid and JA-Ile at the site of injury, thereby activating the expression of defence genes surrounding the wound and producing a local defence response. Three well known phytohormones, salicylic acid, jasmonic acid and ethylene are central in regulation of different signaling pathways in plant defense to distinct pathogens. In the local defence response, there are two ways of short-distance transmission of the jasmonic acid signal. First, the systemin produced by the wounding acts as a signalling molecule, which is transmitted to the adjacent site through the apoplast and phloem to activate the jasmonic acid cascade reaction pathway. Second, jasmonic acid and JA-Ile induced by systemin act as signals and are transported to adjacent sites for defensive responses (Turner et al. 2002; Kazan and Manners 2008).

4.2 Long distance signal transmission

Long-distance transmission of jasmonic acid signals is mainly via airborne transmission. Some works has also shown that jasmonic acids are not simply transported along the vascular bundle, but are accompanied by resynthesis of jasmonic acids during transport even jasmonic acid signaling and defence gene expression are systemically activated within hours. The localization of various jasmonic acid synthetases (such as LOX, AOS, etc.) was also found in the companion cell–sieve element complex (CC-SE) of tomato vascular bundles, and the sieve molecules in the phloem have the ability to form the jasmonic acid precursor OPDA (phytodienoic acid). Communication between salicylic acid and JA dependent defence signaling pathways has been identified. Other advances in induced resistance signaling, such as the implication that ethylene is involved in the generation of systemic signal molecules, the suggestion of the involvement of lipid derived molecules in long distance signaling and the identification of new components of various systemic defense signaling pathways, shed new lights on how plants actively defend themselves against harmful organisms (Turner et al. 2002).

A large number of studies showed that in addition to vascular bundle transmission, there are other long-distance transmission routes for jasmonic acid signals. Compared with jasmonic acid, which has difficulty in penetrating the cell membrane without carrier assistance, jasmonic acid easily penetrates the cell membrane and has strong volatility, and thus can be spread by airborne diffusion to distant leaves and adjacent plants. It has been confirmed in a range of plants, such as *Arabidopsis thaliana*, *Nicotiana tabacum*, *Phaseolus lunatus*, and *Artemisia kawakamii*, that JA can be transmitted by air between damaged and undamaged leaves or between adjacent plants (Thaler et al. 2002).

4.3 Jasmonic acid receptor

In a screen for delayed floral organ abscission in *Arabidopsis*, a novel mutant of CORONATINE INSENSITIVE1 (COI1), the F box protein that has been shown to be jasmonic acid co receptor. The ABC transporter AtJAT1/AtABCG16 with jasmonic acids transport ability was screened by a yeast system. Radioactive isotope uptake experiments and autoradiography experiments showed that AtJAT1/AtABCG16 acts as a high-affinity transporter to regulate the subcellular distribution of JAs. AtJAT1/AtABCG16 is localized on the nuclear and plasma membranes of plant cells and mediates the transport of jasmonic acids across the plasma membrane and the bioactive JA-Ile across the inner membrane of the nuclear membrane to activate JA responses at low concentration. When the concentration of jasmonic acids is high, the function of the jasmonic acid transporter on the cytoplasmic membrane is dominant, which reduces the intracellular jasmonic acid and JA-Ile concentrations to desensitize the jasmonic acid signal. The jasmonic acids signalling pathway is activated in other cells by transporting jasmonic acid to the apoplast. AtJAT1/AtABCG16 can regulate the dynamics of JA/JA-Ile in cells, which leads to the quick transport of JA-Ile into the nucleus when the plant is under stress, as well as the quick desensitization of the JA signal to avoid the inhibition of plant growth and development by the defence response (Kim et al. 2013).

The understanding of jasmonic acid receptors has undergone a complex process. In 1994, Feys first found that the *Arabidopsis coronatine insensitive1* (*coi1*) mutant lost all responses to jasmonic acid, and further studies indicated that the *COI1* gene encodes an F-box protein that is a component of E3 ubiquitin ligase. In this case, COI1 associates with the SKP1 protein and Cullin protein to form the SCF-type E3 ubiquitin ligase that is referred to as SCF^{COI1}, which targets the repressor proteins for degradation by ubiquitination. The outburst of COI1 protein is of great significance for the study of the jasmonic acid signaling pathway (Singh and Jwa 2013).

It was once thought that COI1 is the receptor for jasmonic acid signalling in cells, until the discovery of a jasmonate Zinc finger Inflorescence Meristem (ZIM)-domain (JAZ) protein family, which gave a new understanding of the jasmonic acid signal transduction pathway. In 2007, three research groups simultaneously found that JAZ proteins act as repressors in the jasmonic acid signalling pathway. To date, 13 JAZ proteins have been found in *Arabidopsis*, most of which have two conserved domains, Jas and ZIM. The JAZ protein interacts with COI1 via the Jas domain and interacts with MYC2 via the ZIM domain. Therefore, many researchers believe that JAZ proteins are the target protein of COI1 and the degradation of JAZ proteins is a key step to relieve the inhibition of the jasmonic acids pathway. However, in 2011, Sheard et al. proposed different views on jasmonic acids receptors through the analysis of crystal structure and confirmed that the COI1–JAZ complex is a high-affinity receptor for the bioactive JA-Ile; that is, COI1 and JAZ are coreceptors of jasmonic acid signaling. It is currently believed that plants perceive stimuli from the external environment to generate JA-Ile, which promotes the interaction between COI1 and JAZ proteins. Subsequently, JAZ proteins are degraded after being transferred to the 26S proteasome, and simultaneously, transcription factors (TFs) are released to activate the expression of downstream genes (Sheard et al. 2011).

4.3.1 Jasmonic acid transcription factor

JA-Ile activates the MYC transcription factors by directly binding to JAZ and COI1, which results in the degradation of JAZ through the 26S proteasome pathway. Recent studies have shown that the MYB transcription factors also bind with JAZ repressors and can be activated by the degradation of JAZ in the presence of JA-Ile. In addition, several other transcription factors (TFs) such as NAC, ERF, and WRKY are also involved in the jasmonic acids signaling. These JA-responsive TFs regulate the expression of many genes involved in the growth and development of plants, and especially the responses and adaptation of plants to the environment. Studies have also shown that jasmonic acid signaling can also induce the MAP kinase cascade pathway, calcium channel, and many processes that interact with signalling molecules such as ethylene, salicylic acid, and abscisic acid to regulate plant growth and development (Heitz et al. 2016; Ali and Baek 2020).

4.3.2 MYC transcription factor

The basic helix–loop–helix (bHLH) transcription factor MYC2 is a well-known regulatory protein encoded by the *JIN1* gene. Most members of the JAZ protein family interact with MYC2. For a long time, it was believed that only the MYC2 protein can directly interact with the JAZ protein. Two other bHLH proteins, MYC3 and MYC4, share high sequence similarity with MYC2, suggesting they probably have similar functions. Indeed, MYC3 and MYC4 interact with JAZ proteins in vivo and in vitro, have similar DNA-binding specificity to MYC2, and act synergistically and distinctly with MYC2. A closely related TF, MYC5 (bHLH28), is induced by jasmonic acids and required for male fertility. Besides transcriptional activators, JA-associated MYC2-like (JAM) proteins, JAM1, JAM2, and JAM3, were discovered as transcriptional repressors via forming protein–protein interactions with JAZs to regulate jasmonic acids responses (Sasaki-Sekimoto et al. 2014).

4.3.3 MYB Transcription factor

Most of the jasmonic acids -responsive MYB TFs belong to the R2R3-MYB family, which are widely distributed in plants and required for many processes. MYB51 and MYB34 regulate the synthesis of tryptophan and glucosinolates and act downstream of MYC2. However, many studies have found that MYB TFs can directly bind to JAZ proteins, indicating the release from JAZs to activate their target genes. For instance, in *Arabidopsis*, MYB21 and MYB24 are key factors in stamen and pollen maturation and MYB75 can positively regulate the anthocyanin accumulation and trichome initiation. Recently, a set of MYB TFs, MYB11, MYB13, MYB14, MYB15, and MYB16, were identified as repressors in the regulation of rutin biosynthesis in buckwheat (Ruan et al. 2019).

4.3.4 NAC transcription factor

ATAF1 and ATAF2 TFs in the *Arabidopsis* NAC family are both induced by jasmonic acid signaling and involved in plant resistance to drought, salt stress, *Botrytis cinerea*, and other pathogens. At the same time, ATAF1 and ATAF2 have an important regulatory effect on oxidative stress, flowering, and pod development of plants. Two other NAC TFs in *Arabidopsis*, ANAC019 and ANAC055, are also present downstream of the MYC2 protein and regulate seed germination, cell division, and the synthesis of secondary walls of cells. In addition, ATAF1, ATAF2, ANAC019, and ANAC055 are also involved in the crosstalk between jasmonic acid and salicylic acid signaling pathways (Fraga et al. 2021).

4.3.5 Ethylene responsive transcription factor

Microarray experiments at the genetic level have confirmed that jasmonic acid signaling can induce the transcription of many *ERF* genes. The first evidence for a link between AP2/ERF TFs and jasmonic acid signaling was found in *Catharanthus roseus*. The jasmonic acids-induced ORCA proteins, ORCA2 and ORCA3, belong to the AP2/ERF-domain family and can activate the expression of monoterpenoid indole alkaloid biosynthesis genes. Based on the observation of ORCAs, the *Arabidopsis* ERF proteins, ERF1 and ORA59, function dependently on jasmonic acids and/or ET for the defenses against *Botrytis cinerea*. Moreover, ORA59, rather than ERF1, acts as the integrator of JAs and ET signals and regulates the biosynthesis of hydroxycinnamic acid amides. The JAs-induced ORA47 can activate the expression of the jasmonic acids biosynthesis gene *AOC2*, indicating that ORA47 might act as an important regulator in the positive jasmonic acids-responsive feedback loop. Moreover, jasmonic acids-responsive AtERF3 and AtERF4 act as repressors by not only down regulating their target genes' expression, but also interfering with the activity of other activators. Interestingly, the activity of above TFs is not directly repressed by JAZ proteins, suggesting the presence of adaptors or corepressors in the jasmonic acid signaling pathway (Gan et al. 2007).

4.3.6 WRKY transcription factor

WRKY transcription factors play an important regulatory role in plant development, senescence, and coping with environmental stress. In *Arabidopsis*, there are 89 members in the WRKY transcription factor family. It has been shown that some WRKY TFs are regulated by the jasmonic acid signaling pathway, such as WRKY70, WRKY22, WRKY50, WRKY57, and WRKY89. These WRKY transcription factors are mostly associated with plant defense functions. In *Nicotiana attenuata*, two WRKY transcription factors, NaWRKY3 and NaWRKY6, regulate the expression of jasmonic acids biosynthesis-related genes (*LOX*, *AOS*, *AOC*, and *OPR*) to increase the levels of jasmonic acid and JA-Ile. In addition, *Arabidopsis* WRKY57 interacts with the inhibitor JAZ4/JAZ8 in the jasmonic acid signaling pathway and the inhibitor IAA29 in the auxin signaling pathway, thereby regulating the interaction between jasmonic acid and auxin-mediated signaling pathways and effects on plant leaf senescence (Jiang et al. 2014).

5. Functions of jasmonic acid

5.1 Regulating plant responses to abiotic and biotic stresses as well as plant growth and development

Jasmonic acid is a plant-signalling molecule closely associated with plant resistance to abiotic stress. In abiotic stress, JA is usually involved in physiological and molecular responses. Physiological responses often include accumulation of amino acids (isoleucine and methionine) and soluble sugars, activation of the antioxidant system (superoxide anion radical, peroxidase, NADPH-oxidase) and regulation of stomatal opening and closing. Molecular responses often involve the expression of jasmonic acid-associated genes (*JAZ, AOS1, AOC, LOX2,* and *COI1*), interactions with other plant hormones (ABA, ET, SA, GA, IAA, and BR), and interactions with transcription factors (MYC2 and bHLH148) (Taiz et al. 2015).

5.2 Growth inhibition

Jasmonic acid has been shown to inhibit primary growth by reducing cell division in the meristem zone and inhibiting cell elongation in the elongation zone.

5.3 Senescence

Exogenous application of jasmonic acid caused premature senescence in attached and detached leaves such as *Arabidopsis*, the jasmonic acid-signaling pathway is required for jasmonic acid to promote leaf senescence. Jasmonic acid levels in senescing leaves are 4-fold higher than in non-senescing ones. Concurrent with the increase in jasmonic acid level in senescing leaves, genes encoding the enzymes that catalyse most of the reactions of the jasmonic acid biosynthetic pathway are differentially activated during leaf senescence. Both jasmonic acid and H_2O_2 are two crucial signalling molecules positively regulating leaf senescence, whereas whether and how they are coordinated in leaf senescence remains elusive. Here, we report that H_2O_2 accumulates in jasmonic acid-treated leaves, while scavenging the increased H_2O_2 can significantly suppresses jasmonic acid-induced leaf senescence and the expression of *senescence-associated genes* (*SAGs*). The mutant *myc2* with a mutation of *MYC2*, a master transcription factor in JA signalling pathway, exhibits delayed leaf senescence with increased catalase activity and decreased H_2O_2 accumulation compared with the wild type upon jasmonic acid treatment. Further study showed that MYC2 downregulates *CATALASE 2* (*CAT2*) expression by binding to its promoter, thus promoting jasmonic acid-induced H_2O_2 accumulation and leaf senescence. Moreover, the delayed leaf senescence with reduced H_2O_2 accumulation and *SAGs* expression of the *myc2* mutant is significantly reverted by the *cat2-1* mutation in *myc2 cat2-1* double mutant. Thus, promoting leaf senescence in a MYC2 dependent manner in Arabidopsis (Zhang et al. 2020).

5.4 Tendril coiling

A coiling-inducing factor was isolated from some tendrils and identified by nuclear magnetic resonance and mass spectrometry. When applied to detached tendrils, exogenous α-linolenic acid, but not linoleic acid or oleic acid, induced tendril coiling. Further investigations showed that metabolites of α-linolenic acid, jasmonic acid and, even more so, methyl jasmonate, are highly effective inducers of tendril coiling. Methyl jasmonate was most active when administered by air and, in atmospheric concentrations as low as 40–80 nM, induced a full free-coiling response with similar to mechanical stimulation. Methyl jasmonate could be one of the endogenous chemical signals produced in mechanically stimulated parts of a tendril and, being highly volatile, act as a diffusible gaseous mediator spreading through the intracellular spaces to trigger free coiling of tendrils (Kim et al. 2013).

5.5 Flower development and leaf abscission

Development of inflorescences and flowers in plants is controlled by the combined action of environmental and genetic signals. Investigations reveal that the phytohormone jasmonate plays a critical function in plant reproduction such as male fertility, sex determination and seed maturation. Jasmonic acid promoted the abscission of bean petiole explants via the degradation of cell wall polysaccharides in the abscission zone (Taiz et al. 2015).

5.6 Initiates the production of defence proteins that inhibit herbivore digestion

Jasmonic acid initiates the production of defence proteins, most of the proteins interfere with the herbivore digestive system, some legumes synthesise alpha amylase inhibitors, which block the action of the starch digesting enzyme a-amylase. Some others produce lectins which bind to the epithelial cell line of the digestive tract and interfere with the nutrient absorption by the herbivore. A more direct attack on the insect herbivore's digestive system is performed by some plants through the production of a specific cysteine protease, which disrupt the peritrophic membrane that protects the gut epithelium of many insects. While none of these genes are essential for the vegetative growth of the plant, they have likely evolved from normal "housekeeping" genes during the coevolution of plants and their insect herbivores. The best-known antidigestive proteins in plants are the proteinase inhibitors. Found in legumes, tomato, and other plants, these substances block the action of herbivore proteolytic enzymes. After entering the herbivore's digestive tract, they hinder protein digestion by binding tightly and specifically to the active site of protein hydrolysing enzymes such as trypsin and chymotrypsin. Insects that feed on plants containing proteinase inhibitors suffer reduced rates of growth and development that can be offset by supplemental amino acids in their diet. The defensive role of proteinase inhibitors has been confirmed by experiments with transgenic tobacco. Plants that had been transformed to accumulate increased levels of proteinase inhibitors suffered less damage from insect herbivores than did untransformed control plants (Heitz et al. 2016).

6. Conclusion

Jasmonic acid is a lipid derived plant hormone that orchestrates a wide range of physiological processes through its intricate signaling pathways. Its signaling pathways is complex and involves interaction with other hormones and signaling molecules. It is a crucial regulator of plant growth, development and responses to environmental cues, including biotic and abiotic stresses. Jasmonic acid functions in plant defence mechanism against herbivores, pathogens and adverse environmental conditions, highlighting its significance in plant survival and adaptation. The complex interplay of jasmonic acid with other hormone and signaing molecules underscore its versatile role in shaping plant responses to diverse stimuli. Further research on jasmonic acid signaling and its functions in plants could provide valuable insights into improving crop productivity and resilience in the face of changing environmental conditions, it also holds promise for enhancing our understanding of plant biology. The studies on jasmonic acid made great progress, and the jasmonic acid signal transduction pathway has also been established, but there are still many questions regarding the regulatory process which need to be answered.

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