21 Jasmonic Acid

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Jasmonic acid (JA) and its various derivatives are lipid-derived signaling molecules which participate in the regulation of a number of plant processes, including growth, reproductive development, photosynthesis, and responses to biotic and abiotic stress factors. As compared to auxins, ABA, cytokinins, GAs, and ethylene, discovery of JA and elucidation of its roles in plants have been made in the relatively recent past. JA was first isolated from the fungus *Lasiodiplodia theobromae* as a plant growth inhibitor. Among green plants, the free acid (−JA) was first detected and identified as a growth inhibitor from the pericarp of *Vicia faba* (broad bean). The immature fruits of *Vicia faba* contain a mixture of (−) JA and its stereoisomer (+)-7-iso-jasmonic acid (+7-iso-JA) in 65–35% ratio (Fig. 21.1). Hydroxy-jasmon ester of chrysanthemic acid in pyrethrins (a class of insecticides), isolated from *Chrysanthemum cinerariifolium* (*Pyrethrum*), was the first JA metabolite discovered from plants. Active jasmonates, most importantly the methyl esters of jasmonates (JAMe), were initially detected as odorants from the flowers of *Jasminum grandiflorum.*

21.1 Biosynthesis

The biochemical steps leading to JA biosynthesis in plants are partitioned into two organelles—the plastids and peroxisomes. The substrate for JA biosynthesis—α-linolenic acid (a C_{18} polyunsaturated acid)—is released from the plastid membrane lipids by lipase action. Subsequent sequential action of three enzymes, namely, 1,3-lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase (AOC) on α-linolenic acid within the plastids, leads to the formation of oxo-phytodienoic acid (OPDA). OPDA transport across the plastids into the peroxisomes is facilitated by an ABC transporter. Within the peroxisomes, OPDA is converted to (+)-7-iso-jasmonic acid [(+)-7-iso-JA)] through reduction and β-oxidation steps. In the cytosol, (+)-7-iso-JA gets conjugated with isoleucine to form jasmonyl isoleucine (JA-Ile) which is considered the physiologically active form of JA (Fig. 21.1).

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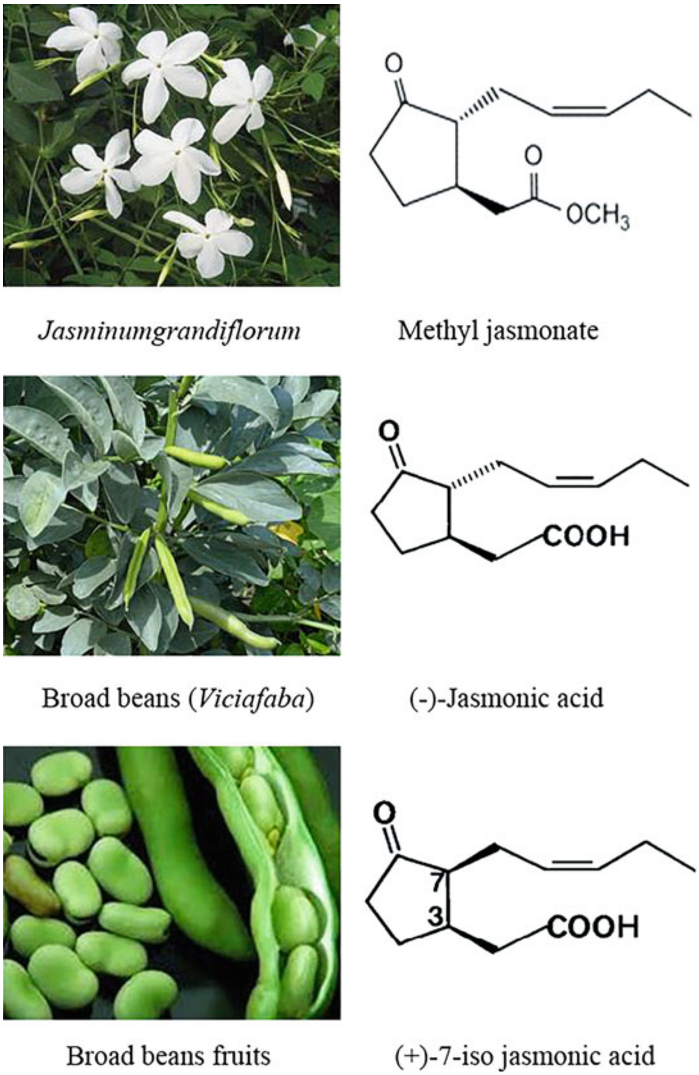

Fig. 21.1 Naturally occurring jasmonic acid, its derivatives, and the plants from which they were first isolated

21.2 Metabolism and Homeostasis

JA modulates various aspects of plant development through a variety of its conjugated forms, namely, cis-jasmone, methyl jasmonate, jasmonyl-1-β-glucose, cucurbic acid, and some more. Conjugation of jasmonic acid with isoleucine and other amino acids is catalyzed by an enzyme encoded by JAR1 (JASMONATE

RESISTANT 1) locus in *Arabidopsis*. *jar1* mutants are resistant to exogenous JA in a root growth inhibition assay. In addition to the biosynthesis of JA isoleucine (JA-Ile) from (+)-7-iso-JA, JA is also the precursor for a volatile derivative, namely, methyl jasmonate, the product of a SAM-dependent carboxymethyl transferase, (−)-JA, and methyl (−) JA are the major naturally occurring jasmonates in plant tissues (Fig. 21.1). Their respective stereoisomers, (+)-7-iso-JA and methyl (+)-7-iso-JA, also exhibit significant biological activity, though not in all systems. Cis-jasmone is another volatile compound synthesized by the decarboxylation of JA. Jasmonyl-1-β-glucose has been reported from the cell cultures of tobacco and tomato where it is formed by the conjugation of the carboxyl group of JA with glucose. 12-hydroxy-(+)-7-iso-jasmonic acid, also called as tuberonic acid, has been reported from potato, where it exhibits tuber-inducing activity (Figs. 21.2 and 21.3).

JA levels in plant tissues are determined by: (1) substrate availability, (2) a feedback loop which affects the expression of JA biosynthesis genes, (3) cell- and tissue-specific distribution of enzymes associated with JA biosynthesis, and (4) post-translational regulation of JA.

Evidence includes the following: (1) Observation of low JA levels in transgenic lines overexpressing JA biosynthesis enzymes and their induction upon wounding suggests a requirement of release of α-linolenic acid as the substrate for JA biosynthesis. (2) Induction of genes involved in JA biosynthesis following JA application suggests a positive feedback loop. (3) Differential distribution of various JA biosynthesis enzymes in different tissues has also been observed. (4) A rapid accumulation (burst) of JA within few seconds of wounding suggests post-translational regulation of JA biosynthesis.

21.3 Physiological and Developmental Roles

21.3.1 Trichome Formation

Biosynthesis of alkaloids, flavones, terpenoids, and defense proteins in trichomes correlates with their active role in plant defense mechanisms. Genetic analysis has shown a strong involvement of JA in trichome formation as well as monoterpene synthesis within them. On similar lines, another phenomenon of agricultural importance is JA-mediated formation of cotton fibers, which represent single-cell trichomes from seed surface.

21.3.2 Reproductive Functions

JA has been detected as an odorant in the flowers of some plants, and thus it plays a role in attracting pollinating insects. Characterization of some *Arabidopsis* mutants has demonstrated a role of JA in flower development with reference to the male sterility trait. Sex determination in maize also requires JA through modulation of 13-LOX activity.

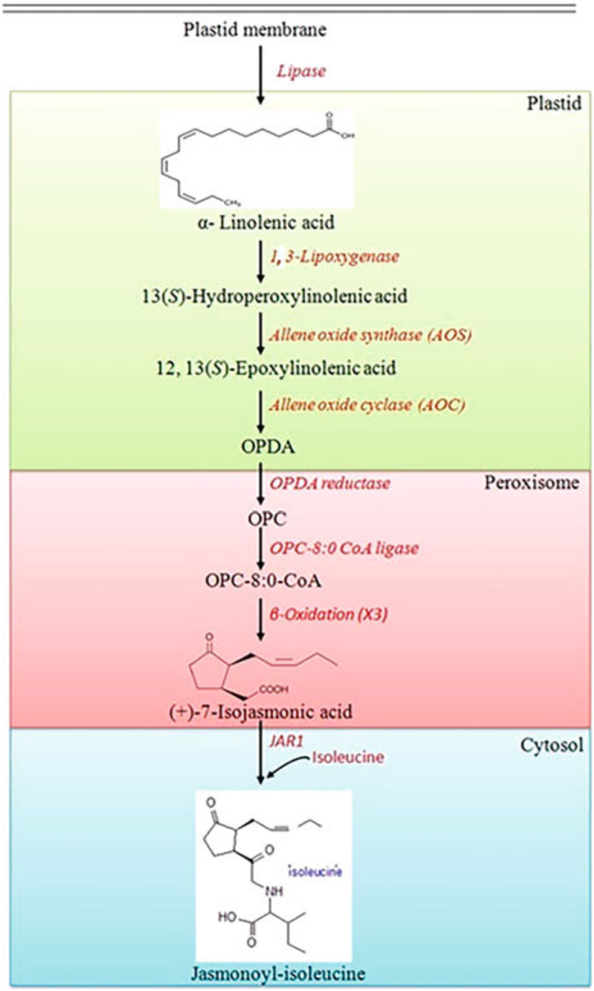

Fig. 21.2 Pathway for jasmonic acid biosynthesis in plants

21.3.3 Induction of Secondary Metabolites Production

Subjecting plant cell cultures to fungal elicitors enhances JA content which triggers the formation of a number of alkaloids in several plant species. It includes SA-induced biosynthesis of nicotine, vinblastine, artemisinin, glucosinolates, anthocyanins, and benzylisoquinoline alkaloids. JA is also responsible for the rapid induction of some transcription factors responsible for the expression of several genes for the production of secondary compounds such as benzylisoquinoline, nicotine, and morphine.

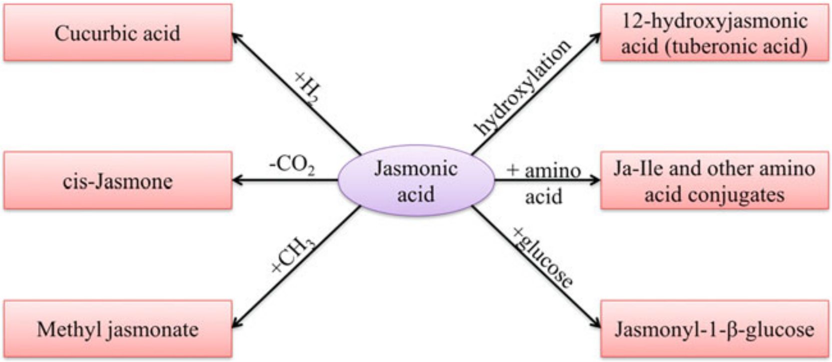

Fig. 21.3 Jasmonic acid metabolism in plants through modification of various groups associated with this molecule

21.3.4 Role as a Senescing Promoting Factor

JA-specific proteins, called JIPs (JA-inducible proteins) of varying molecular masses, accumulate in senescing barley leaf segments subjected to JA treatment. This accumulation is accompanied by enhanced degradation of several housekeeping proteins, such as Rubisco (small and large subunits). A thionin was one of the first JIPs identified in senescing barley leaf segments which is induced in response to JA treatment. Its overexpression in tobacco leads to repression of leaf proteins. The function of JIPs is, however, still not fully resolved. 13-LOX, a 90–95 kDa JIP localized in chloroplasts, provided first evidence for a link between JA-induced gene product (JIP) and activation of JA biosynthesis. Other JA-inducible proteins associated with senescence include chlorophyllase (which catalyzes chlorophyll breakdown) and proteins involved in chlorophyll stability. Senescence-promoting activity of JA also leads to repression of mRNA and protein levels of Rubisco activase in a COI1-dependent manner.

21.3.5 JA and Photomodulation of Plant Development

Seed development, photomorphogenesis, shade avoidance, and skotomorphogenesis are some of the light-mediated developmental responses in plants and are governed by the actions of GA, ABA, auxin, and CK. It is now known that light regulates JA biosynthesis. JA-related genes mediate hypocotyl growth in far red light. Furthermore, light dependence of JA biosynthesis and JA-dependent processes is now evident during some plant developmental processes. This includes extrafloral nectar formation and responses to necrotrophic pathogens and herbivores.

21.3.6 Response to Herbivores

In addition to production of secondary metabolites, JA also triggers the biosynthesis of defense proteins which interfere with herbivore digestive system. This includes the synthesis of **α-amylase inhibitors** in legumes and production of **lectins** (carbohydrate binding proteins) which bind to epithelial cells lining the digestive tract of the herbivore, thereby interfering with nutrient absorption. Some plants produce **cysteine proteases** which disrupt the membrane of the gut epithelium of insects. A number of **proteinase inhibitors** produced in some legumes and tomato block the activity of herbivore proteolytic enzymes such as trypsin and chymotrypsin. An 18-amino acid peptide—**systemin—**is biosynthesized accompanying JA accumulation in some plants. It is believed to induce the synthesis of proteinase inhibitors.

21.3.7 Mycorrhizal Interactions and Modulation

An increase in JA level in wounded tissue correlates with increased mycorrhizal association in roots. JA also appears to play a role in plant resistance to nonpathogenic plant growth-promoting rhizobacteria and fungi. This is referred as **induced systemic resistance**.

21.4 JA-Induced Gene Expression

In the late 1980s to the early 1990s, various researchers provided evidence for JA-induced changes in gene expression. The JA-induced proteins (JIPs) of varying molecular masses have been reported to accumulate in plants following long-term JA treatment. Evidence has also been provided for induction of vegetative storage proteins (VSPs) in response to wounding and JA treatment. This was followed by the observation of alkaloid formation upon elicitation of cell cultures with yeast elicitor which follows a preceding rise in JA levels in the tissue. These observations paved way for numerous reports on JA-responsive pathways and genes and also gave directions for research in JA-mediated plant-herbivore interactions and plant-to-plant communication via volatiles, such as sesquiterpenes, leaf aldehydes, and leaf alcohols.

21.5 JA-Mediated Signaling

Similar to auxin, JA acts through a conserved ubiquitin ligase-based signaling mechanism (Fig. 21.4). JA receptors are F-box proteins, COI1, a component of SCF-COL E3 ubiquitin ligase which targets **JAZ (JASMONATE ZIM DOMAIN)** family of transcriptional repressors for degradation, thereby activating the expression of JA-sensitive genes. Although unconjugated JA is active as a hormone, most JA responses require its conjugation with isoleucine (JA-Ile) by the action of the

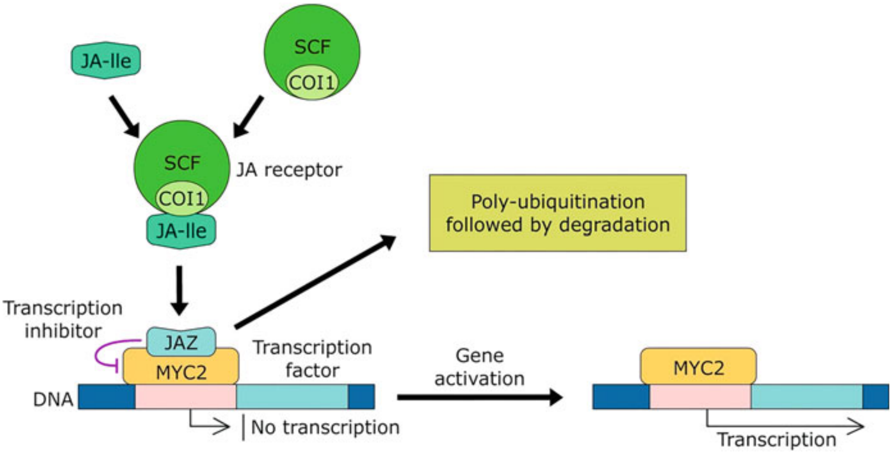

Fig. 21.4 Jasmonic acid signaling. Jasmonic acid needs to be first conjugated to an amino acid to bind to COI1 (JA receptor) as part of a SCF^{COI1} protein complex. This complex targets JAZ (transcription repressor) leading to the degradation of this protein via polyubiquitination followed by degradation in a proteasome. MYC2 (transcription factor) initiates transcription of JA-dependent genes, including those for defense

enzyme called as **jasmonic acid resistance (JAR) protein**. When endogenous levels of JA are low, the **JAZ** protein family repress the expression of JA-responsive genes. JAZ repressors function by binding to the **transcription factor MYC2** which is a major switch in the activation of JA-inducible genes. The sequential action during JA perception is as follows: (1) JA-Ile complexes with COI1 (as SCF^{COI1}); (2) COI1-JA-Ile complex binds with JAZ (repressor protein) and releases it from the MYC2 (transcription factor). JAZ then undergoes polyubiquitination and subsequent degradation; (3) MYC2 (transcription factor), which does not any more have binding with the transcription factor (JAZ), is activated, and it transcribes JA-inducible genes.

Summary

- Jasmonic acid (JA) and its various derivatives are lipid-derived signaling molecules which participate in the regulation of a number of plant processes, including growth, reproductive development, photosynthesis, and responses to biotic and abiotic stress factors.
- The biochemical steps leading to JA biosynthesis in plants are partitioned in two organelles—the plastids and peroxisomes. The substrate for JA biosynthesis—α-linolenic acid (a C_{18} polyunsaturated acid)—is released from the plastid membrane lipids by lipase action. In the cytosol, (+)-7-iso-JA gets conjugated with isoleucine to form jasmonyl isoleucine (JA-Ile) which is considered the physiologically active form of JA.

- JA modulates various aspects of plant development through a variety of its conjugated forms, namely, cis-jasmone, methyl jasmonate, jasmonyl-1–βglucose, cucurbic acid, and some more.
- JA levels in plant tissues are determined by (1) substrate availability, (2) a feedback loop which affects the expression of JA biosynthesis genes, (3) cell- and tissue-specific distribution of enzymes associated with JA biosynthesis, and (4) post-translational regulation of JA.
- JA is involved in trichome development, formation of cotton fibers, flower development with reference to male sterility trait, alkaloid biosynthesis, senescence promotion, and biosynthesis of defense proteins.
- The JA-induced proteins (JIPs) of varying molecular masses have been reported to accumulate in plants following long-term JA treatment.
- Similar to auxin, JA acts through a conserved ubiquitin ligase-based signaling mechanism. JA receptors are F-box proteins, COI1, a component of SCF-COL E3 ubiquitin ligase which targets **JAZ (JASMONATE ZIM DOMAIN)** family of transcriptional repressors for degradation, thereby activating the expression of JA-sensitive genes.

Multiple-Choice Questions

1. Among green plants, the first jasmonic acid was isolated from:
   (a) *Chrysanthemum cinerariifolium*
   (b) *Jasminum grandiflorum*
   (c) *Vicia faba*
   (d) *Arabidopsis thaliana*
2. Organelle where JA biosynthesis occurs is plants are:
   (a) Plastids and mitochondria
   (b) Plastids and peroxisomes
   (c) Mitochondria and chloroplasts
   (d) Peroxisomes and mitochondria
3. JA performs which of the following roles in plants:
   (a) Senescing promoting factor
   (b) Photomodulation of plant development
   (c) Response to herbivores
   (d) All of the above
4. Which of the following is the receptor for JA-mediated signaling?
   (a) COI1 (coronatine insensitive 1)
   (b) JAZ (jasmonate zim domain)
   (c) JAR (jasmonate acid resistance)
   (d) MYC2

Answers

1. a 2. c 3. d 4. a

Suggested Further Readings

Miersch O, Meyer A, Vorkefeld S, Sembdner G (1986) Occurrence of (+)-7-iso-jasmonic acid in *Vicia faba* L. and its biological activity. J Plant Growth Regul 5:91–100

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